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Studies on Rhodymeniales from Hokkaido*

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CONTENTS

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Introduction

The red algal order Rhodymeniales currently includes two families, Rhodymeniaceae and Champiaceae.

SCHMITZ (1889) introduced a new order Rhodymeninae with six families, Sphaerococcaceae, Rhodymeniaceae, Delesseriaceae, Bonnemaisoniaceae, Rhodomelaceae, and Ceramiaceae. He altered the name to Rhodymeniales in 1892 (cf. SCHMITZ-HAUPTFLEISCH 1896). Among the six families, however, the Delesseriaceae, Rhodomelaceae, and Ceramiaceae were removed to Ceramiales by OLTMANNS (1904), the Bonnemaisoniaceae to Nemaliales by KYLIN (1928), and the Sphaerococcaceae to Sphaerococcales by SJÖSTEDT (1926).

With the efforts of SJÖSTEDT (*l. c.*), KYLIN (*l. c.*), and BLIDING (1928), taxonomic characters of the Rhodymeniales were clarified. The order consists of rather naturally distinctive groups, compared with a few other orders of Rhodophyceae (KYLIN 1956, SPARLING 1957). It is characterized currently by the procarp bearing one or two auxiliary-cell branches composed of two cells (except for *Epymenia obtusa* which bears three-celled ones), that are initiated directly from the supporting cell before fertilization. However, these

cell branches become distinctive generally only after fertilization. The thallus is flattened, slightly flattened, cylindrical or hollow, and shows multiaxial growth with meristems located at the apex or margin. Tetrasporangia occur either terminally or intercalarily in the cortical layer, and are divided cruciately or tetrahedrally (except for *Coeloseira* which bears polysporangia). Spermatangia originate from superficial cortical cells. Cystocarps are surrounded by a pericarp with ostiole. The life history is known to be generally of triphasic haplodiplont, so called *Polysiphonia*-type.

According to BLIDING (*l. c.*) the Rhodymeniales are divided into two families, Rhodymeniaceae HARVEY (1849) and Champiaceae KÜTZING (1843) *orth. mut.* The Rhodymeniaceae are characterized by a lack of inner filamentous cells in the medulla, cruciately or tetrahedrally divided tetrasporangia, and three-celled carpogonial branch not forming a large fusion cell in cystocarp formation, while the Champiaceae have filamentous cells in the medulla, tetrahedrally divided tetrasporangia, and three- to four-celled carpogonial branch forming a large fusion cell in cystocarp formation.

The family Rhodymeniaceae was divided by SCHMITZ (1889) into two subfamilies, Gloiocladioideae and Rhodymenioideae, and by KYLIN (1931) into three, Fauchioideae, Rhodymenioideae and Hymenocladioideae. The Fauchioideae was separated from the others by the presence of *tela arachnoidea* (a net-work of cells in pericarp), and the Hymenocladioideae by the occurrence of intercalary and tetrahedrally divided tetrasporangia. The Gloiocladioideae SCHMITZ was equivalent to the Fauchioideae KYLIN. SPARLING (1957), however, preferred to divide the family Rhodymeniaceae into two, Rhodymenioideae and Hymenocladioideae, because she believed that the character adopted by KYLIN for the Fauchioideae was not significant, and this subfamily was to be included in the Rhodymenioideae.

On the other hand, the family Champiaceae was divided by KYLIN (1931) into two subfamilies, Lomentarioideae and Champioideae. The former was distinguished by a three-celled carpogonial branch, conversion of almost all the cells of gonimoblast into carposporangia, and the terminal formation of tetrasporangia, while the latter was characterized by the four-celled carpogonial branch, conversion of superficial cells of gonimoblast into carposporangia, and the intercalary formation of tetrasporangia.

Recently, GUIRY (1974) proposed a new family, Palmariaceae, based on *Palmaria palmata* (L.) O. KUNTZE (syn. *Rhodymenia palmata* (L.) GREV.), including the genera *Halosaccion* and *Leptosarca*. The family was characterized by the occurrence of stalk cell in the formation of tetrasporangia and the absence of female gametophyte.

Some important studies dealing with vegetative structure and reproductive organs of members belonging to the Rhodymeniaceae were reported by KUCKUCK (1912), BØRGESEN (1920), OKAMURA (1907～1935), SJÖSTEDT (1926), KYLIN (1930), and SPARLING (1957), while those of members belonging to the Champiaceae were by NÄGELI (1847), BERTHOLD (1882), DEBRAY (1886, 1890), BIGELOW (1887), HAUPTFLEISCH (1892), DAVIS (1892, 1896), HASSENKAMP (1902), OKAMURA (1902～1935), BØRGESEN (1920), KYLIN (1923, 1931), BLIDING (1928), ROSENVINGE (1931), SVEDELIUS (1937), HOLLENBERG (1940), and LEE & KUROGI (1973).

However, detailed studies, especially dealing with the developmental anatomy of reproductive organs had been investigated only on the following members among some thirty six genera; *Fauchea* (SJÖSTEDT 1926, KYLIN 1930, SPARLING 1957), *Faucheocolax* (SPARLING 1957), *Gloioderma* (SPARLING 1957), *Gloiocolax* (SPARLING 1957), *Chrysymenia* (BLIDING 1928), *Erythrymenia* (SPARLING 1957), *Botryocladia* (BLIDING 1928), *Rhodymenia* (SJÖSTEDT 1926, KYLIN 1930, SPARLING 1957, TOKIDA & MASAKI 1959), *Rhodymeniocolax* (SPARLING 1957), *Epimenia* (SPARLING 1957), and *Hymenocladia* (SPARLING 1957) of Rhodymeniaceae, *Lomentaria* (HAUPTFLEISCH 1892, KYLIN 1923, BLIDING 1928, SVEDELIUS 1937), *Binghamia* (LEE & KUROGI 1973), *Champia* (HAUPTFLEISCH 1892, DAVIS 1896, BLIDING 1928), *Chylocladia* (HAUPTFLEISCH 1892, HASSENKAMP 1902, KYLIN 1923, BLIDING 1928), *Gastroclonium* (HAUPTFLEISCH 1892, BLIDING 1928), and *Coeloseira* (HOLLENBERG 1940) of Champiaceae.

In this work, the following ten members of Rhodymeniales collected from Hokkaido, Japan were considered; *Halosaccion yendoi* (sp. nov.), *H. firmum*, *Palmaria palmata*, *P. marginicrassa* (sp. nov), *Rhodymenia intricata*, *R. pertusa*, and *Chrysymenia wrightii* of Rhodymeniaceae, and *Lomentaria hakodatensis*, *L. catenata*, and *Champia parvula* of Champiaceae. The investigations were carried out mainly on the phenology, variation of outer appearance, anatomy of vegetative structure, and the development of reproductive organs.

Materials and Methods

The materials used for the study were collected from May, 1966 to October, 1968 in various places of Hokkaido as shown in Figure 1. The periodic observations of the plants concerned were carried out at Oshoro, Muroran, Erimo, and Akkeshi; *Halosaccion yendoi* at Akkeshi, *H. firmum* at Erimo, *Palmaria palmata* at Oshoro, Muroran and Akkeshi, *P. marginicrassa* at Akkeshi, *Rhodymenia intricata* at Oshoro, *R. pertusa* at Mu-

roran, *Chrysymenia wrightii* at Oshoro, *Lomentaria hakodatensis* at Oshoro and Muroran, *L. catenata* at Oshoro, and *Champia parvula* at Muroran.

The Oshoro Bay, located on the Japan Sea Coast, is affected by the Tsushima Warm Current through the year, whereas Muroran and Erimo areas, located on the Pacific Coast, are affected by the Tsushima Warm Current during the summer season and by the Kurilian Cold Current during

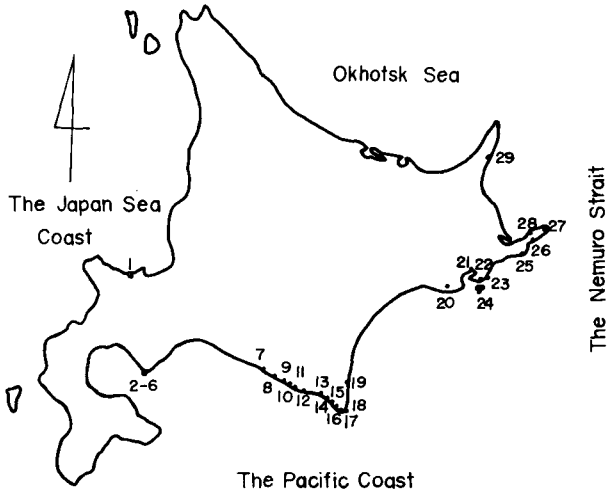

Fig. 1. The map of Hokkaido showing the collecting stations.

1. Oshoro (*Shiribeshi District*); 2. Charatsunai, Muroran, 3. Denshinhama, Muroran, 4. Etomo, Muroran, 5. Tokkarisho, Muroran, 6. Masuichi, Muroran (*Iburi District*); 7. Higashisizunai, 8. Harutachi, 9. Mitsuishi, 10. Ikantai, 11. Hamatoei, 12. Urakawa, 13. Samani, 14. Nishihirau, 15. Higashitoyo, 16. Horoizumi, 17. Minamitoyo, 18. Erimo (*Hidaka District*), 19. Shirahama (*Tokachi District*); 20. Kombumori, 21. Kakijima, Akkeshi, 22. Aikappu, Akkeshi, 23. Tokotan, Akkeshi, 24. Daikokujima Isl., Akkeshi (*Kushiro District*); 25. Ochiishi, 26. Habomai, 27. Nosappu, 28. Nemuro, 29. Rausu (*Nemuro District*).

TABLE 1. Sea water temperature of monthly average in February and August

Place	Feb. (°C)	Aug. (°C)	Reference
Oshoro	3.8	20.5	Data from the Mar. Biol. Station (1966)
Muroran (Charatsunai)	3.4	18.1	Data from the Inst. Alg. Research (1966)
Hidaka (Urakawa)	0.5	19.1	Data from the Hokkaido Fish. Exp. Station (1965)
Akkeshi (Aikappu)	−1.2	17.7	Data from the Mar. Biol. Station (1965)

the winter season. On the other hand, Akkeshi area, located on the Pacific Coast, is affected only by the Kurilian Cold Current through the year. The maximum and minimum surface water temperatures on monthly average in these four areas are shown in Table 1.

The plants were sectioned with freezing microtome. The slices were stained with 0.5% aniline blue in water solution or erythrosin in 95% alcohol solution. The former was specially effective for the analysis of developments of tetrasporangia, spermatangia and cystocarps. The specimens were mounted in glycerin-water solution.

In this paper, the nuclear activity was generally not considered except when they were possible without special treatment. The herbarium specimens including the type specimens of *Halosaccion yendoi* and *Palmaria marginicrassa* are preserved in the Herbarium of Department of Botany, Faculty of Science, Hokkaido University (SAP).

Halosaccion KÜTZING (1843)

The genus *Halosaccion* was established by KÜTZING on the basis of three species, *H. hydrophora*, *H. firmum* and *H. fucicola*, transferred from *Dumontia* described by POSTELS and RUPRECHT (1840). However, in 1849, KÜTZING returned the species to *Dumontia*. Later, RUPERECHT (1851) revived this genus *Halosaccion*, and KÜTZING (1866) adopted it again, adding three further species.

The genus is characterized by the simple or branched hollow thalli containing a distinct cellular structure, cruciately divided tetrasporangia occurring terminally in the superficial cortical layer, and lack of cystocarps.

The systematic position of this genus has been disputed from early times by many workers (RUPRECHT 1851, J. AGARDH 1852, HARVEY 1853, SETCHELL & GARDNER 1903, OKAMURA 1936), because of absence of cystocarps. KÜTZING, when establishing the genus, placed it beside *Chrysymenia*, and RUPRECHT arranged it next to *Rhodymenia*. J. AGARDH (*l. c.*, 1876) arranged it beside *Dumontia*. SETCHELL & GARDNER and OKAMURA put it under Rhodymeniaceae, without mentioning clearly its systematic position. Recently KYLIN (1956) placed it in *Rhodymenia* group, whereas GUIRY (1974) put it under Palmariaceae.

Tetrasporangia of the genus were observed from early times, and spermatangia were reported in *H. ramentaceum* by KUCKUCK (1897), JÓNSSON (1901) and LUND (1959), in *H. yendoi* (as *H. saccatum* KÜTZ.) and *H. firmum* by LEE & KUROGI (1968 a). However, the true cystocarp of the genus has not been found yet, though so many investigators have searched for it.

***Halosaccion yendoi* sp. nov.**

(Text-figs. 2～7 : Plate I, A-B)

Halosaccion saccatum KÜTZING sensu YENDO (1909) p. 129 (*pro parte*); TOKIDA (1932) p. 17 (*pro parte*); (1954) p. 191 (*pro parte*); OKAMURA (1936) p. 680 (*pro parte*); KAWABATA (1936) p. 209 (*pro parte*); NAGAI (1941) p. 201 (*pro parte*); YAMADA & TANAKA (1944) p. 73; LEE & KUROGI (1968 a) p. 452, figs. 1-3.

Japanese Name : *Benifukuronori* (OKAMURA)

Type Locality : Aikappu, Akkeshi

Type Specimen : Holotype, SAP No. 032337 (Tetrasporic plant)
Paratype, SAP No. 032338 (Male plant)

Materials

Kushiro District. Aikappu, Akkeshi : June 18, 21, July 28～9, Aug. 26, 28, Dec. 29, 1966 ; Feb. 8, Apr. 15, June 26, 1967 ; Oct. 9～10, 1968. Daikokujima isl., Akkeshi : June 20, 1966 ; June 23, July 7, 1967. Tokotan, Akkeshi : June 19, 1966 ; June 24, 1967. Kakijima, Akkeshi : June 25, 1967. Kombumori : May 7, 1967 (by S. KAWASHIMA). *Hidaka District.* Erimo : Mar. 30, 1967. *Nemuro District.* Nemuro : May 15, 1967 ; May 12, 1968. Habomai : May 11, 1968. Nosappu : May 11, 1968. Rausu : May 13～4, 1968.

In Herb., Department of Botany, Fac. Sci., Hokkaido Univ. (SAP) No. 15468 Sikotan Shima, Kuriles, July 1933 (by S. KAWABATA). No. 13678 Robben Isl., Saghalien, July 1930, July 1932 (By J. TOKIDA). No. 022795 Sikotan Shima, Aug. 1936 (by S. INOH).

In Herb., Faculty of Agriculture, Hokkaido Univ. (SAPA) No. 2151, 2152 (♂), 2147 Etorohu, Aug. 7, 1937 (by M. NAGAI). *without number* (several sheets) on *Ptilota pectinata*, Kunashiri, Kuriles, July 18, 1929 (by. M. NAGAI & M. SHIMAMURA).

Description

Thallus solitarius vel gregarius, saccatus, oblongus aut ovatus, interdum oblanceolatus, membranaceus, tenuis, simplex, breviter stipitatus, haptero discoideo adhaerens substrato, 10～15 cm altus, 4～5 cm latus ad partem lattissimam ; hapteron 2～3 mm diam., singulariter vel aliquot frondiferum ; stipes teres, 1～2 mm diam. ; frons e stipe abrupte dilatata inflata ad partem mediam, obtusa ad apicem, plus minusve distincto puncto pigmentorum dispersorum super paginam ; frons in sectione ex stratis corticalibus et medullosis composita, 100～160 μm crassa, strato corticali unius vel duarum cellu-

larum seriato, cellulis superficialibus vallis simile ordinatis, quadrangulatis vel depresso globosis, abundantibus pigmentis, 6.9～8.4 μm altis, 8.4～9.2 μm latis, strato medulloso duarum vel trium cellularum seriato, una vel duabus cellulis interioribus grandibus, multiangulatis, hyalinis, 55～70 μm altis, 80～100 μm latis, cellulis exterioribus parvis planis, 25～35 μm latis, cavitate centrali marginata cellulis medullosis crassoparietibus, pilis unicellulosis evolutus cellulis superficialibus, dispersis aggregate ; tetrasporangia praesentia terminale in cellula superficiali corticali, cum cellula stipitata, elliptica, cruciate divisa, 22～30 μm. lata, 32～40 μm longa, ramis sterilibus in soris constantibus ex duabus vel tribus cellulis mutatis oblongis ; spermatangia elliptica aut oblonga, evoluta subterminale super cellula matricale spermatangii, 5.5 μm lata, 8.5 μm longa ; cystocarpia ignota ; color in aestate dilute purpureus, hieme atropurpureus ; specimina adhaerentia papyro firme. Annua.

Thallus solitary or gregarious, saccate, oblong to ovate, sometimes oblanceolate, membranaceous, thin, simple, shortly stipitate, attaching to substratum by means of discoid holdfast, 10～15 cm high, 4～5 cm wide at the broadest part ; holdfast 2～3 mm in diam., carrying single or a few fronds ; stipe terete, 1～2 mm in diam. ; frond abruptly broadened from stipe, inflated at middle portion, obtuse at apex with more or less distinct spots of pigments scattered over surfaces ; frond in section composed of cortical and medullary layers, 100～160 μm thick, cortical layer one or two cell-rowed, superficial cells arranged like palisade, quadrate to depressed-globose, with abundant plastids, 6.9～8.4 μm high, 8.4～9.2 μm wide, medullary layer two to three cell-rowed, inner one or two cells large, polygonal, hyaline, 55～70 μm high, 800～100 μm wide, outer cells small, flat, 25～35 μm wide, central cavity bordered with thick walled medullary cells, unicellular hairs developed from superficial cells, scattered in groups ; tetrasporangia developed terminally on superficial cortical cell, with stalk cell, elliptical, divided cruciately, 22～30 μm wide, 32～40 μm long, sterile branches in sori consisting of two to three oblong modified cells ; spermatangia elliptical to oblong, developed subterminally on spermatangial mother cell, 5.5 μm wide, 8.5 μm long ; cystocarps not known ; color light purple in summer, dark purple in winter ; specimens adhering to paper firmly. Annual.

Habitat : Lower tidal zone, on rocks and other algae.

Distribution : Pacific Coast (Muroran to Nosappu), Nemuro Strait and Okhotsk Sea Coasts of Hokkaido, Japan ; Southern Kuriles ; and Saghalien.

Phenological Observation

The present species was investigated at Akkeshi. There the plants

grew solitarily or gregariously on rocks, and commonly on other algae such as *Palmaria palmata*, *P. marginicrassa*, *Rhodomela larix*, *Ptilota pectinata*, and *Corallina pilurifera*, etc. They inhabited the lower tidal zone, where the wave action was not so violent.

The investigations were carried out periodically from June, 1966 to July, 1967 and October, 1968. In July and August, 1966, there were lots of germlings less than 1～2 cm high, and also some old thalli bearing spermatangial or tetrasporangial sori at the same time. These old thalli were frequently eroded or partly shed away in the upper portion. In December, the germlings became about 4 cm high on an average. Some of them bore tetrasporangial or spermatangial sori in early stages of development. There were no more old plants at the time. In February, 1967, the plants became about 6 cm high and 2.5 cm wide on an average. Most of them were fertile. Tetrasporic plants were abundant, and male plants were encountered rather frequently. From December to February the habitat was generally covered with ice at lower tide. Since February, they seemed to grow rather rapidly, so that in April they became mostly over 10 cm high and 5 cm wide on an average. The largest one was 15 cm high and 6.5 cm wide at the broadest part. At the time, the plants occurred gregariously along the coast, though they never formed a compact mat at this location (cf. YENDO 1909, YAMADA 1935, NAGAI 1941, TOKIDA 1954). There were scarce sterile thalli among them. Since then, the plants decreased in number rapidly. In June, almost all the plants encountered were old and small, showing the upper portion eroded or shed away. Sometimes, they were ruptured longitudinally and rolled up inwardly from the ruptured margin. On the other hand, the early germlings were encountered rarely at the same time. These were aggregated so many on the frond of *P. marginicrassa*, as if these were proliferated from the alga.

In addition, when I visited in October, 1968, there were few plants. They were mostly less than 1～2 cm high. No fertile thalli, nor old ones were encountered at the time.

Considering the above investigation, *Halosaccion yendoi* at Akkeshi area seems to appear in late June to July and becomes most luxuriant in height and number of thalli from March to May of next year. Since then, they begin to decrease in number rapidly. Some of them remain until the next germlings appear. The reproductive organs, both tetrasporangia and spermatangia, are developed since December. They remain until old thalli disappear. Tetrasporic plants are abundant, while male plants frequent.

At Cape Erimo, the plants were encountered in March, 1967, on *Ptilota*

pectinata. They were about 10～15 cm high and 3～4 cm wide at the broadest part. In May, 1968 from Nemuro District such as Nemuro, Habomai, Nosappu and Rausu, the plants were frequently eroded or shed away in the upper portion. Sometimes, numerous perforations appeared on the thallus before erosion. These plants were 20～25 cm high and 8～12 cm wide on an average.

No female thalli were found from these areas, although so many individuals had been investigated for this purpose at every collection.

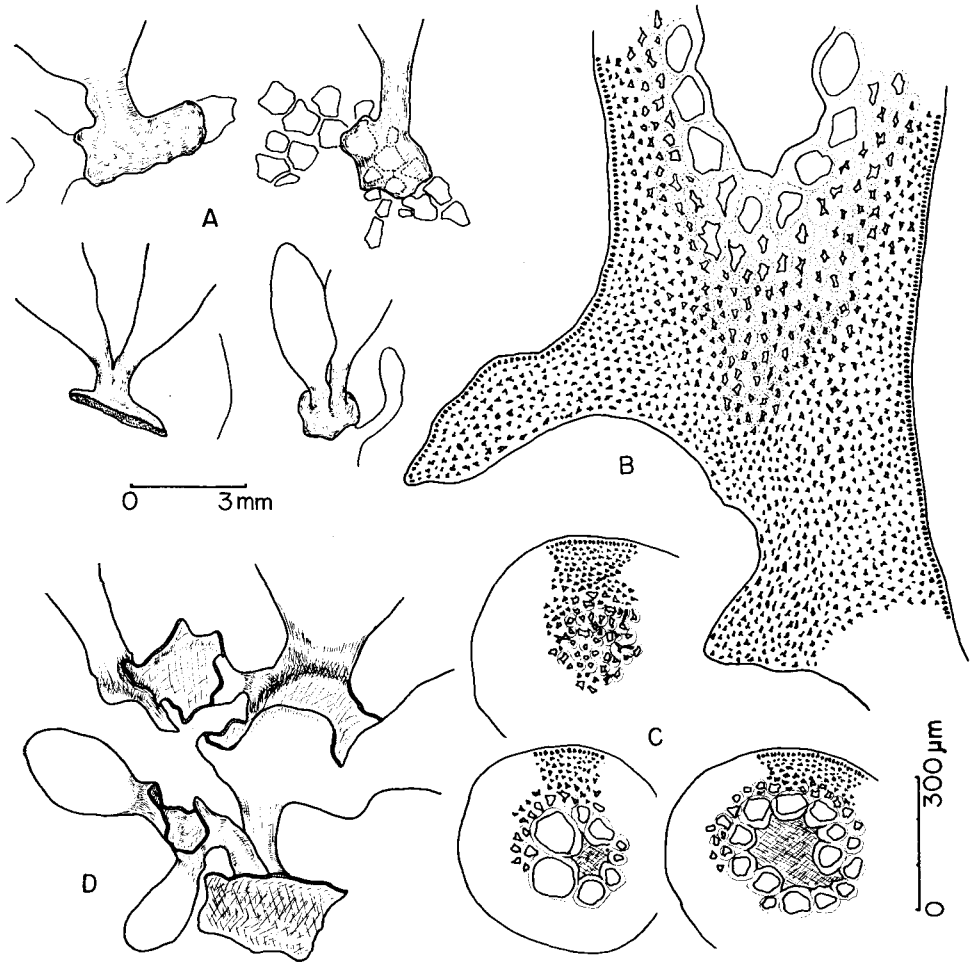

Fig. 2. *Halosaccion yendoi* I. K. LEE
A, basal part showing holdfast; B, longitudinal section of holdfast; C, successive transverse sections of stipe; D, regeneration of new fronds from ruptured margin of old thalli.

Morphological Observation

External Appearance

The alga is saccate and simple. It is oblong to lanceolate in young stage, and oblong to ovate after maturation. However, the plants collected in Nemuro District are characterized by oblanceolate to spatulate or elliptical to obovate forms and specially large size.

The thallus is tender in substance and membranaceous in texture with smooth surface, which does not become hard or firm even after maturation. There appear frequently distinct freckles or spots resembling tetrasporangia over the surface, which are the plastids densely contained in the superficial cortical cells, and are distinctive in summer, but not so clear in winter.

The plant has a small discoid holdfast. A single or a few fronds are produced from it. The stipe is simple, distinct, short and terete. The branched ones are rare (Fig. 2 A, below left). The frond is dilated cuneately in divergence of 45°~80°, or sometimes more than 120°. The plants from Nemuro District are commonly less than 30°.

The apex is round, subacute or more commonly obtuse. As seen in *H. glandiforme* (TURNER 1819, RUPRECHT 1851), there are several microscopic pores on the apical portion of the frond. A dirty liquid of yellow-brown color, seems to be sea-water, fills the thallus a half to two third in volume of the cavity, and air occupies the rest, so that the plant is erect when it is submerged. Mud or small grains of sand are found within. It is interesting that particles larger in diameter than the pores are frequent, as mentioned by RUPRECHT. In a mature thallus, more than 10~15 pores of which diameters are not equal can be counted in a single thallus.

A few plants collected in June at Aikappu have the apical portion divided once dichotomously, and several plants encountered regenerate new fronds from the ruptured margin of old thalli. Sometimes, the regenerated fronds are ruptured again and more fronds are regenerated, too (Fig. 2 D).

Structure of *Thallus*

The thallus is composed of outer cortical and inner medullary layers and central cavity (Fig. 3 B). Superficial cortical cells are slightly compressed-globose and broader than high. They are arranged in a compact palisade and contain plastids abundantly. The superficial cell divides periclinally inwards, forming a flat and small cell.

The medullary layer is composed of two to three rows of cells. Outer one or two rows are composed of small cells in various sizes. The cells are flat and compressed, poorly containing the plastids located near the outer

surface. Inner one or two rows are composed of large and hyaline cells, which are originally globose, but become frequently irregular in form. Sometimes, there are a few small cells instead of a large one. The cell wall, especially the innermost wall facing the central cavity, is thickened as the thallus becomes old. The young thallus has oblong superficial cells which are divided obliquely as the thallus grows (Fig. 3 A).

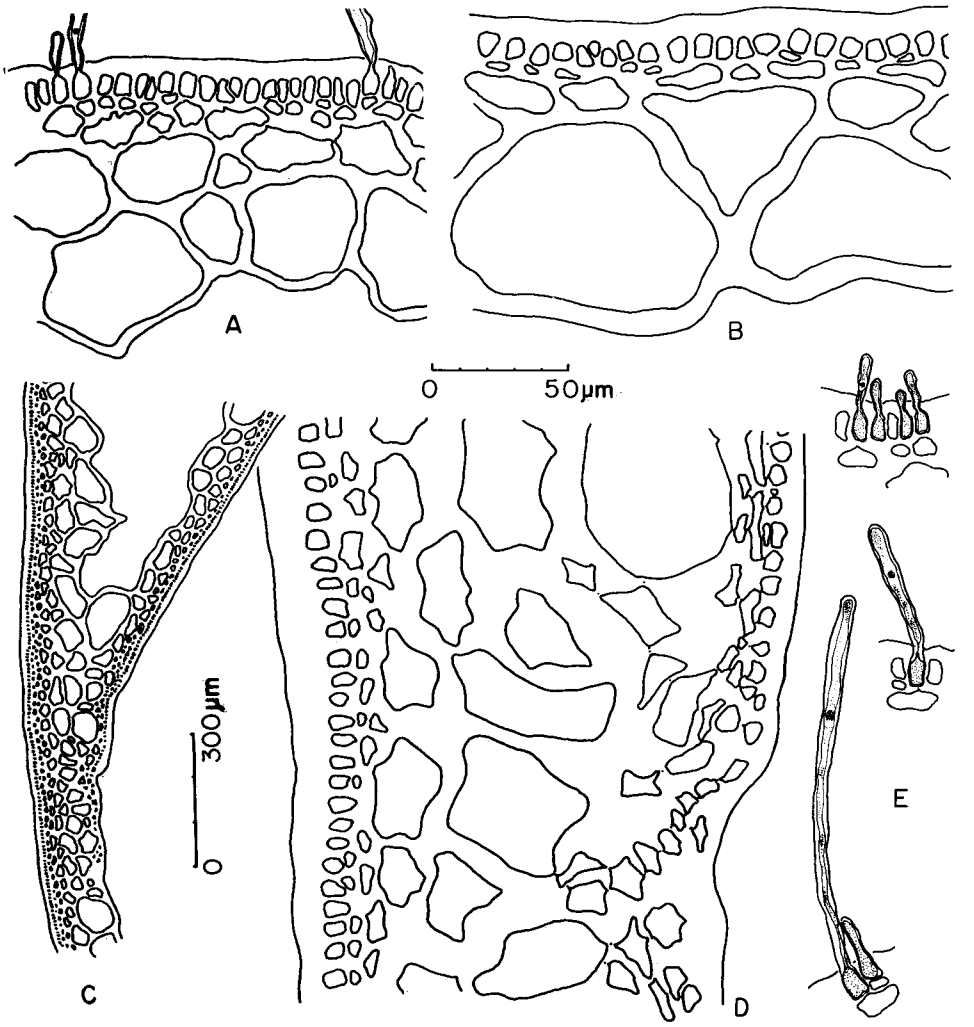

Fig. 3. *Halosaccion yendoi* I. K. LEE

A-B, transverse section of thalli, A being young, bearing hairs; C, a regenerated portion in longitudinal secsion; D, the same magnified, showing a regeneration of cortex from medulla; E, development of hairs.

The holdfast, in longitudinal section, is composed of thick walled round to elliptical cells inward and quadrate cells outwards. The protoplasm of inner cells becomes stellate, connecting radially with adjacent cells (Fig. 2 B). In the central portion, the inner cells are elongate toward the stipe. When a few holdfasts are piled up one on the other, the contacting borders remain distinct.

The stipe is solid in the lower part, and hollow in the upper part (Fig.

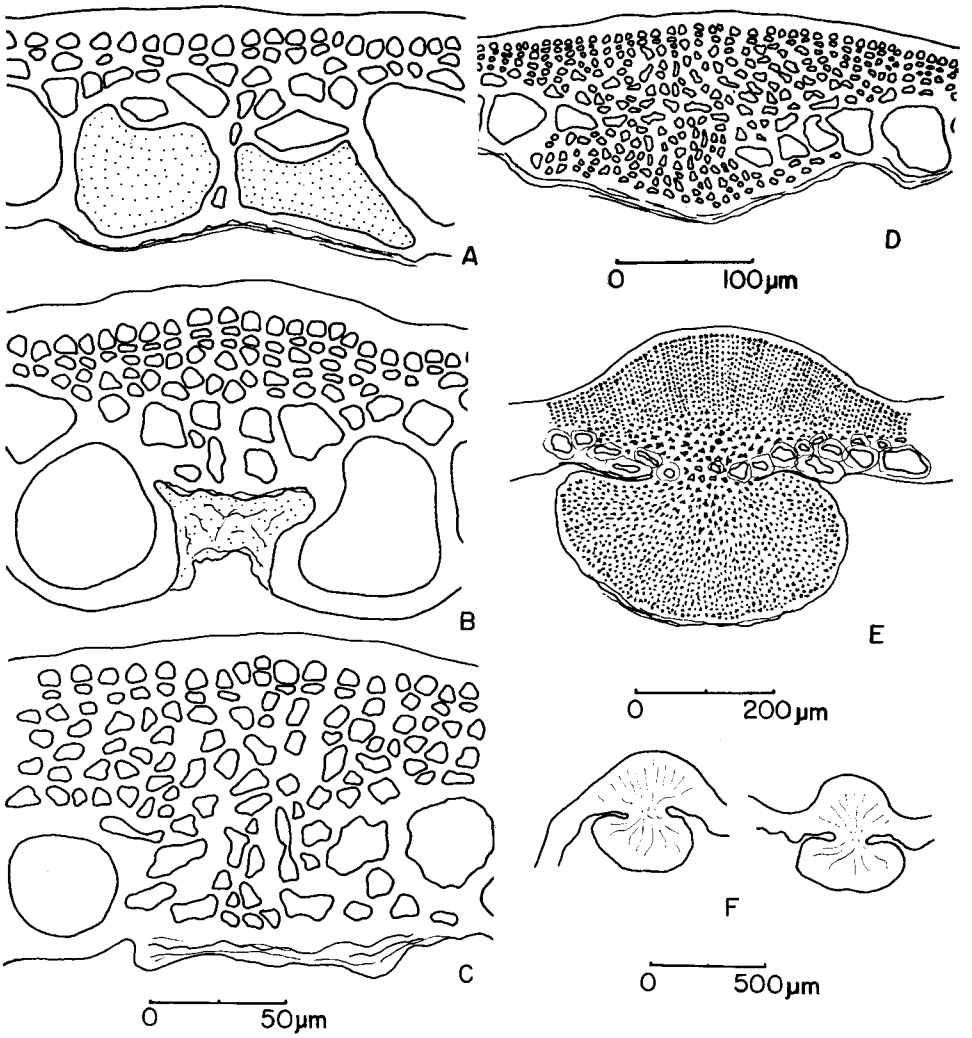

Fig. 4. *Halosaccion yendoi* I. K. LEE
A–F, development of a gall in transverse section of thalli.

2 C). The central cavity is developed by a rupture of innermost cells, and widens its diameter upwards, showing a reverse parabolic form in longitudinal section.

Unicellular hairs are abundant in young thallus. They are found also in middle to upper portion of the mature thallus within tetrasporangial and sometimes in young spermatangial sori. The hair is protruded from the top of superficial cortical cell, having a slight constriction at the base (Fig. 3 E).

The regeneration of new saccate fronds is initiated with the development of many small cells from the medullary cells at the ruptured margin (Fig. 3 D). These small cells form a new cortical layer, and connect to the original cortical cells of the wounded margin. Superficial cells are developed from this new layer. They increase in number by anticlinal or oblique divisions. A new frond begins to grow from these cells, developing a central cavity inwards (Fig. 3 C).

One specimen bearing peculiar galls in the thallus surface was found (Fig. 4). They were mistaken for cystocarps in the field. This gall-bearing plant was 3.5 cm high and epiphytic on the fibrous hapteron of *Alaria praelonga* collected on June, 1966 at Aikappu. No other thallus bearing such galls was encountered again.

The factor to induce such a gall is not clear. However, it is formed by the modification of an innermost medullary cell. Then, irregularly shaped small cells are cut off from the outer medullary cells connected with the modified cell (Fig. 4 A). As the cell division proceeds, the superficial cells of the portion initiate periclinal divisions, and are arranged in perpendicular rows, showing a mountainous elevation from the surface (Fig. 4 B). These newly formed cells produce many secondary pit-connections. On the other hand, the modified medullary cell is destroyed by a rupture of the wall facing the central cavity. The other gall is also formed toward the central cavity from the initial portion (Fig. 4 C–D). The outer gall becomes hemispherical in shape, while the inner one hemispherical to kidney-shaped (Fig. 4 E–F).

Reproductive Organs

Tetrasporangia: The tetrasporic plants are very variable in height. The small thalli bearing the sori are about 1.5 cm (Aikappu, Feb. 1967), while the large one is more than 25 cm high (Nemuro, May 1967, Rausu, May 1968).

Tetrasporangial sori appear at random in middle to upper portion of the thallus at first, showing indefinite aggregations. Sori are fused as they touch, and are dispersed over the whole surfaces except for the stipe and uppermost portion of the thallus. The sori in the upper portion are generally

in early stages of the development. The plant bearing the mature sori becomes reddish purple and submembranaceous.

The tetrasporangium originates from a superficial cortical cell (Fig. 5E–G). The tetrasporangium-initial has dense contents and a large nucleus. As it

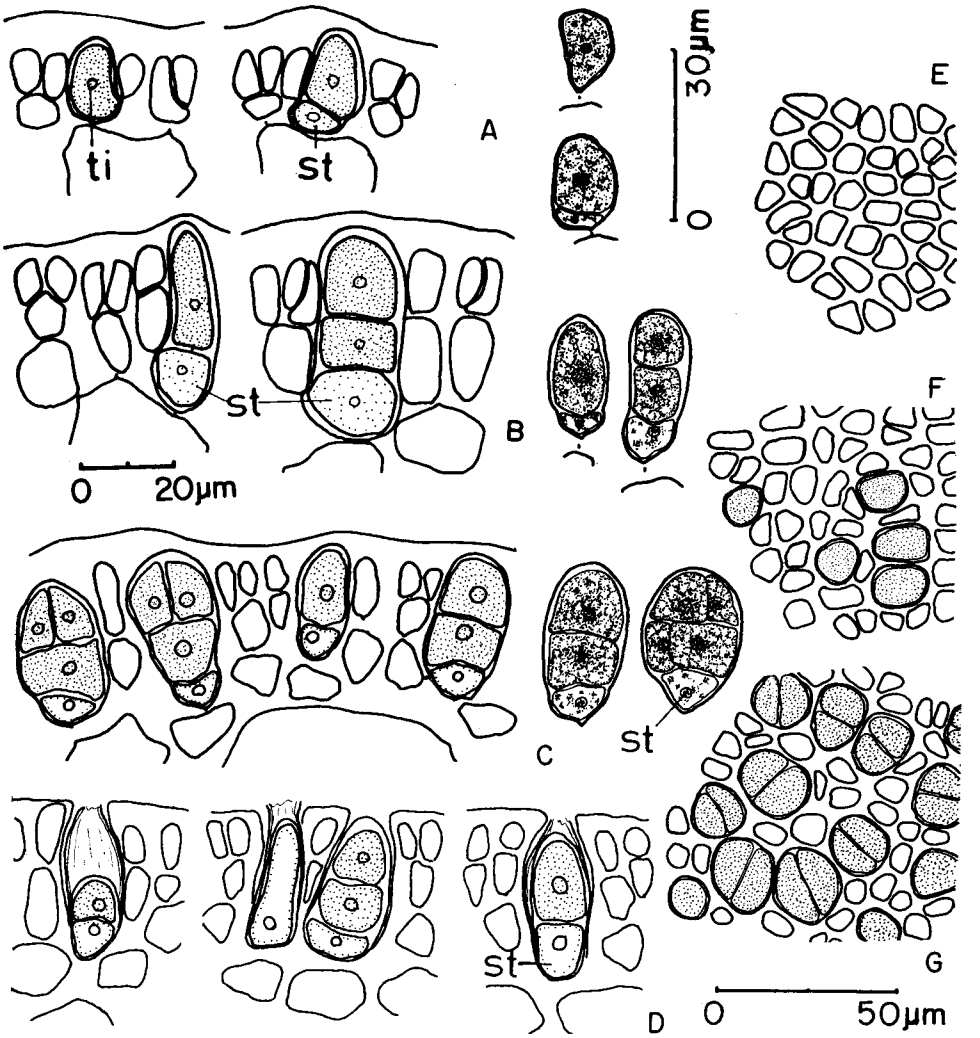

Fig. 5. *Halosaccion yendoi* I. K. LEE

A–C, development of tetrasporangia in transverse view; D, regeneration of secondary tetrasporangia from stalk cells; E, sterile cortex in surface view; F–G, development of tetrasoprangia in surface view.

st: stalk cell, ti: tetrasporangium-initial.

becomes about 12.8 μm high, a periclinal division occurs at about one fifth from its base, both cells being surrounded by a common wall (Fig. 5 A). The upper cell becomes a tetrasporangium and the lower one a stalk cell of the sporangium. Some of the initials, however, cut off the sterile cell obliquely before the division, and are divided into the sporangium and stalk cell. The sterile cell is then connected with the latter. The young sporangium is elongate, much longer than the stalk cell. When it becomes about 28 μm high, tetraspores are formed cruciately by periclinal and then anticlinal divisions of the sporangium (Fig. 5 C). The stalk cell is obovate in shape at first, then concave as the sporangium grows. A mature tetrasporangium is elliptical and 32$\sim$40 μm in length and 22$\sim$30 μm in width, while the stalk cell is about 9.4 μm high and 14.5 μm wide.

Accompanied by young sporangia, the sterile cells are also elongate and divided periclinally into two cells or obliquely into two outer and one inner cells. The outermost cells are frequently divided again in the same manner as the previous divisions. The sterile cell connected with the stalk cell is also divided in the same way. As a result, the sterile cell branches become two to three cell-rowed. They are almost similar in height to the tetrasporangium bearing a stalk cell. In fully mature sori these sterile cells become quadrate to polygonal and about two times as long as broad.

After the liberation of spores, the stalk cell is elongated within the empty cavity of the sporangium, and cuts off a secondary sporangium transversely (Fig. 5 D). Sometimes, this elongate stalk cell remains undivided. The secondary tetrasporangium is distinguished by remains of the previous wall.

The germination of tetraspores *in situ* is similar to the ones reported previously in the other species of Florideae (TOKIDA *et al.* 1965; cf. FRITSCH 1945, p. 727). In germination, each of the four spores in a sporangium seems to have a similar potential, so that they divide independently. Sometimes, one of the lower spores remains without division for a long time, while the others are divided successively. They develop a common single base by the fusion of these newly formed cells, even though four spores make divisions respectively.

The primary division of the spore *in situ* is quite indefinite in direction. The divisions are continued without enlargement of the cells for a while (Fig. 6 A–D). Later, this cell mass is protruded spherically from the thallus surface (Fig. 6 E–F). However, there is no rupture of the outer gelatinous wall of the mother thallus. The cells are connected with the mother thallus by the stalk cell, which remains without division. They extend over the surface,

forming a mushroom shape in outline (cf. TOKIDA *et al.* 1965). The cells are arranged anticlinally (Fig. 6 H). From the central portion they re-divide so that an erect thallus is developed (Fig. 6 I–J). When the germling becomes about 90 μm high, larger medullary cells are developed at the central portion, where the central cavity is formed later by the rupture of the cells. No stipe is distinguishable in the germlings less than 1 cm high.

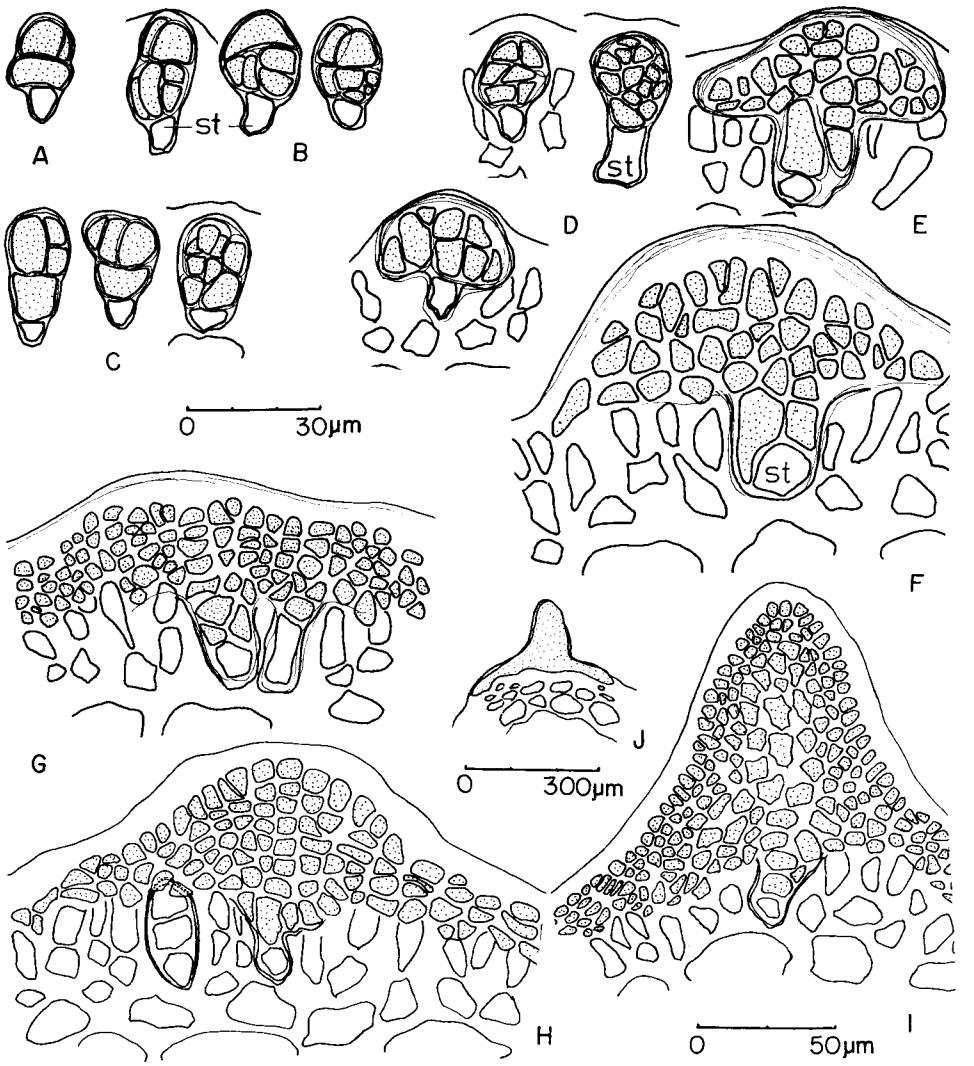

Fig. 6. *Halosaccion yendoi* I. K. LEE
A–J, germination of tetraspores *in situ*.
st: stalk cell.

Sometimes, the germination of spores *in situ* occurs at the same time in two adjacent sporangia. The two cell masses are fused with each other, and develop a single discoid base (Fig. 6 G), where a single frond is erected generally.

Spermatangia: LEE & KUROGI (1968 a) reported the spermatangium formation of this species as *H. saccatum* KÜTZING. At Akkeshi area, the male plants were collected at the same time as tetrasporic ones, though they were not so abundant. The plants bearing spermatangial sori were also variable in height. When the sori are fully mature, the thallus becomes light purple with almost eroded surface. They disperse in a similar manner to the tetrasporangial sori.

In cross section, two spermatangia are developed subterminally on a single spermatangial mother cell. The spermatangial mother cell originates from a superficial cortical cell. When the cortical cell becomes about 10 μm long, it cuts off obliquely three to four cells from the upper corners (Fig. 7 A–B). Each of these cells is divided into two spermatangial mother cells and a flat basal cell (Fig. 7 C–D).

When the mother cell becomes 8～10 μm high, the first spermatangium is protruded subterminally. It grows within the common wall surrounding the mother cell. The second spermatangium is protruded opposite the first.

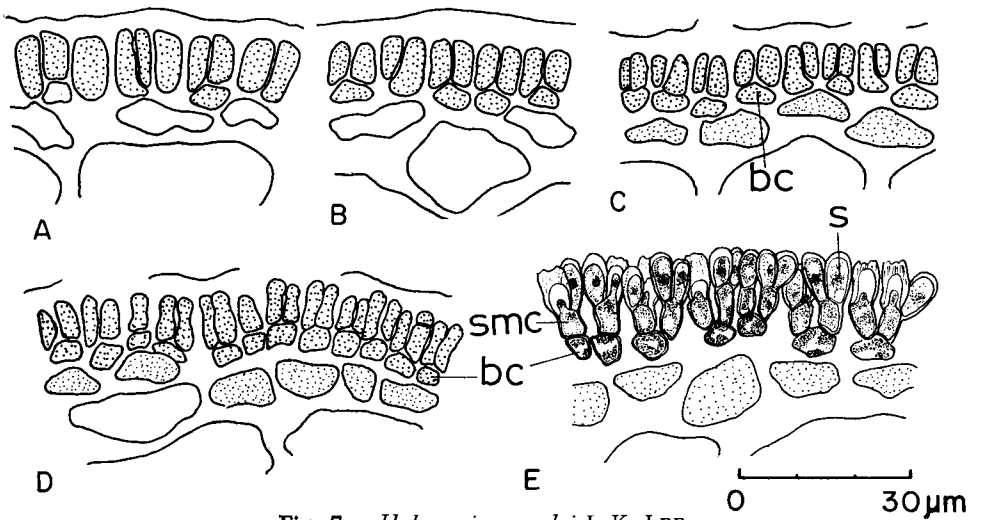

Fig. 7. *Halosaccion yendoi* I. K. LEE

A–B, oblique divisions of elongate superficial cortical cells in transverse view; C, formation of spermatangial mother cells from the divided cells; D–E, development of spermatangia subterminally from mother cells.
s: spermatangium, smc: spermatangial mother cell, bc: basal cell.

Frequently both spermatangia are mature at the same time (Fig. 7 E). A fully mature spermatangium is elliptical to oblong and about 8.5 μm in length and 5.5 μm in width, while the mother cell is oblong and 6.0～7.8 μm in height and 3.0～3.8 μm in breadth.

During the development of spermatangia, plastids in the epidermal cell are observed until the primary division occurs on the elongate cell. Sooner or later they disappear when the mother cells are cut off. There are no plastids in the mother cells, nor in spermatangia and spermatia. However, the basal cell of the spermatangial mother cells always contains plastids. The gelatinous outer layer of the thallus is shed when the spermatangium is protruded upon the mother cell.

The spermatium is liberated through the ruptured apex of the spermatangial wall. It conveys all the contents of the spermatangium, leaving only the empty cavity. A spermatium is surrounded by a fine protoplasmic membrane, and bears a distinct nucleus and large vacuoles.

After the liberation of spermatium, a secondary spermatangium is developed within the previous cavity. At the beginning of this development, a fine cell wall with hyaline contents is protruded from the mother cell. A nucleus migrates into it, then the spermatangium is mature. After the liberation of secondary spermatium, a tertiary spermatangium is rarely formed within the two previous walls. It is distinguished only when the previous walls are discerned. With increase of spermatangia, there is a decrease in the contents of the mother cell.

Even after the spermatangium formation is discontinued, the mother cell does not recover the contents. It remains without modification of the cell until the thallus is eroded.

Discussion

Since YENDO (1909), this simple, saccate, thin and membranaceous alga occurring in Hokkaido and adjacent region has been treated as *Halosaccion saccatum* (LEPECHIN) KÜTZING (1866) in Japan. Originally *H. saccatum* KÜTZ. sensu YENDO was based on *Fucus saccatus* sensu TURNER (1819, excluding plate 241, fig. d right) and is conspecific with *Halosaccion glandiforme* (GMELIN) RUPRECHT (1851). However, YENDO, believing that *Ulva glandiformis* GMELIN (1768), basionym of *H. glandiforme*, was not conspecific with TURNER's taxon, adopted *H. saccatum* KÜTZING for this plant.*

* According to KÜTZING (1849, p. 719; 1866, p. 27), *Halosaccion saccatum* is based on *Fucus saccatus* LEPECHIN (1775) and is different from the later homonym, *Fucus saccatus* sensu TURNER (1819) as mentioned by POSTELS & RUPRECHT (1840). Therefore, POSTELS & (Continued)

However, the plant at hand is quite different from so called *H. glandiforme* not only in outer appearance, but in structure of vegetative thallus, and in tetrasporangium formation. In the Herbarium of Department of Botany, Faculty of Science, Hokkaido University (SAP), there are several specimens under the name, *H. saccatum* KÜTZING. They are divided into two groups : one is dark purple, slightly rigid, and adhered to paper incompletely, while the other is purple, very thin, and adhered to paper completely. Anatomically the two are quite different in the structure of thallus. The former has perpendicularly arranged cortical cells which are frequently fused side by side in H-shape, and has thick-walled medullary cells in which the cytoplasm is stellately modified (cf. OKAMURA 1936, fig. 325), while the latter has no such characters at all.

The former plant accords well with *H. glandiforme* (GMELIN) RUPRECHT diagnostically, not only in outer appearance, but in anatomical character of vegetative thallus (cf. RUPRECHT 1851, pl. 16, figs. a-p). The latter plant, *H. yendoi*, is, therefore, separated from the former.

Our plant, *H. yendoi* is characterized by thin, membranaceous and soft frond, which adheres to paper firmly in drying the specimen. In anatomy, the cortical layer is one or two cell-rowed, superficial cortical cells do not fuse with the adjacent cells, the medullary layer is two to three cell-rowed, and the cells of medulla never show stellately modified protoplasmic strands as seen in *H. glandiforme* mentioned above. Moreover, in tetrasporangium formation, the sterile cells in the sorus are divided into branched rows, and some of them are connected with stalk cell of the sporangia.

This new species occurs commonly along the coast of Hokkaido, except for Japan Sea Coast and Pacific Coast from Muroran to Hakodate. In the Herbarium of Hokkaido University (SAP), some of the plants collected from Etorohu, Kunashiri and Sikotan of the Southern Kuriles, and from Robben

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RUPRECHT proposed *Dumontia hydrophora* for TURNER's plant (TURNER 1819, plate 241, figs. a, b, c, d left only), which was combined with *Halosaccion*, as *H. hydrophora* (POST. et RUPR.) KÜTZING (1843). RUPRECHT later (1851) placed *D. hydrophara*, including TURNER's *F. saccatus*, with *Ulva glandiformis* GMELIN (1768), making the combination *Halosaccion glandiforme* (GMELIN) RUPRECHT. However, YENDO (1909) did not agree with RUPRECHT's opinion, but adopted *H. saccatum* KÜTZING as the earliest name for these plants (the binomial must be used as *H. saccatum* (LEPECHIN) KÜTZING). Considering YENDO's discussion, however, he did not notice that *H. saccatum* KÜTZ. was based on LEPECHIN's plant and not on POSTELS & RUPRECHT's *D. hydrophora*.

Since no one can conclude at present that *U. glandiformis* (basionym of *H. glandiforme*) and *D. hydrophora* (basionym of *H. hydrophora*) are conspecific or not, it seems to be reasonable for me to adopt *H. glandiforme* for these algae, as currently used in America and Europe.

Island of Saghalien are identified with this species. Therefore, the true *H. glandiforme* is not found yet in the coasts of Hokkaido.

Considering only the shape of thallus, *H. yendoi* is similar to *H. glandiforme*, but in vegetative structure it shows rather an affinity to *H. ramentaceum*. From the latter, however, it is distinguished quite easily by its simple frond.

Halosaccion firmum (POSTELS et RUPRECHT) KÜTZING

(Text-figs. 8～12 : Plate I, C-D)

(1843) Phycol. Gener., p. 439. RUPRECHT (1851) p. 292 ; J. AGARDH (1852) p. 357 ; (1876) p. 259 ; KÜTZING (1866) p. 27, pl. 78, figs. d-f ; KJELLMAN (1889) p. 29 ; De TONI (1900) p. 605 ; SAUNDERS (1901) p. 436 ; YENDO (1909) p. 131 ; OKAMURA (1916) p. 53 ; (1936) p. 680 ; ZINOVA (1933) p. 33 ; YAMADA (1935) p. 23 ; YAMADA & TANAKA (1944) p. 73 ; LEE & KUROGI (1968 a) p. 452, figs. 4～6.

Dumontia firma POSTELS et RUPRECHT (1840) p. 19, pl. 35, fig. B, pl. 40, figs. 82～3 ; KÜTZING (1849) p. 720.

Fucus saccatus LEPECHIN sensu TURNER (1819) p. 104, pl. 241, fig. d *dextra*.

Halosaccion glandiforme (GMELIN) RUPRECHT sensu SETCHELL & GARDNER (1903) p. 318, *ex minor parte*.

Japanese Name : *Katabenifukuronori* (YAMADA)

Type Locality : Kamchatka

Materials

Hidaka District. Erimo : Sep. 28, Nov. 14, 1966 ; Mar. 30, May 10, Sep. 18, Dec. 9, 1967 ; Jan. 28, 1968. Minamitoyo, Erimo : Aug. 30, Sep. 28, 1966. *Tokachi District*. Shirahama : Sep. 28, 1966. *Nemuro District*. Rausu : May 13～4,1968.

Description

Thallus gregarious or sparse, saccate, linear-lanceolate to lanceolate, sometimes elongate oblong, coriaceous, firm, thick, simple, shortly stipitate, attaching to substratum by means of discoid holdfast, 8～15 cm high, 2～3 cm wide at the broadest part, holdfast extending irregularly and widely, erecting numerous fronds ; stipe terete, 1～1.5 mm long, 0.7～1.0 mm wide ; frond slightly inflated near base, gradually narrow upwards, round to obtuse at apex, in section composed of irregularly divided cortical and medullary layers, 220～350 μm thick, cortical layer composed of three to five oblong cell-rows arranged perpendicularly to surface, with more plastids outwards, superficial

cells spatulate, uneven in arrangement, 8.3～15.2 μm high, 3.5～4.0 μm wide, inner cells oblong to elongate tetragonal, almost similar in size to superficial cells, medullary layer composed of six to eight irregularly arranged cell-rows, medullary cells round to elliptical, almost hyaline, gradually large and thick walled inwardly, with stellate protoplasmic connections between sister cells, innermost cells 48～55 μm in diam., central cavity bordered with thick walled medullary layer; hairs absent; tetrasporangia dispersed in sori over whole surface except for apical and basal portions, developed terminally in superficial cortical cell, with stalk cell, elongate elliptical, divided cruciately, 40～48 μm in length, 20～28 μm in width, sterile branches in sori consisting of elongate slender cells; spermatangia elongate oblong, developed subterminally on spermatangial mother cell, 15.8 μm in length, 3.7 μm in width; cystocarps not known; color brownish to dark purple in fresh, blackish purple in drying; specimens not adhering to paper on drying. Perennial.

Habitat : Lower tidal zone, on rocks and other algae.
Distribution : Hokkaido; Kamchatka; Alaska; Bering Sea; and Kuriles.

Phenological Observation

This species was investigated at Erimo. There were many plants epiphytic on *Corallina pilurifera*, or growing on rocks gregariously. The substratum was exposed at lower tide, but kept wet generally by the wave action. The plants grew so compactly that most of them could be held erect thalli by mutual support even in exposed condition. There were numerous thalli cast ashore, too.

Observations were carried out periodically from September, 1966 to January, 1968. In March, 1967, there were many germlings less than 1～2 cm high and ones protruded newly from old bases of previous thalli. There also remained old plants almost eroded or shed away in upper portion among the germlings. The young plants seemed to grow rather slowly at the beginning. In May, they were less than 2～3 cm high on an average and packed so compactly that they covered the substratum like a mat when they were exposed at spring low tide. There were no more the old fronds seen in March. In September the plants were 6～7 cm high and not rarely 8～10 cm among the larger plants. Tetrasporangial sori in early developmental stages were found among these large plants. Some others seemed to bear spermatangial sori in early stages of development, though it was very difficult to discern. In December the plants became about 10 cm high and 1.5 cm wide on an average, and in January, 1968, about 10～13 cm

high and 1.5～2 cm wide at the broadest part. The largest one was 15.5 cm high and 3 cm wide. It was interesting that no sterile thalli were found among fully grown plants in January and March. For instance, in January, the majority of fully grown thalli collected were tetrasporic, except for about 10% of male thalli.

In addition, the plants collected in August, 1966 at the same area were about 3 cm high and had no reproductive organs yet, while the ones in November, 1966 were 10 cm high on an average, and had either spermatangial or tetrasporangial sori.

Considering the investigations, the plants at Erimo begin to appear from March to April and grow slowly until September. They grow rapidly and become most luxuriant in number and height from November to February of next year. Until April they decrease in number rapidly and are eroded or shed away. Both tetrasporangia and spermatangia appear since September, and remain until the old thalli disappear.

On the other hand, the plants collected in May, 1968 at Rausu were very large compared with the ones at Erimo. One of them was 22 cm high and 3 cm wide at the broadest part. There were lots of germlings less than 3～5 cm high, as many as half eroded old thalli. The latter had mature tetrasporangial or spermatangial sori.

No female thallus was found at these areas, even though so many thalli were investigated for this purpose at every collection.

Morphological Observation

External Appearance

The plant is saccate and simple. The young thallus less than 1～2 cm high is generally ovoid to oblong-ovate, and has no distinct stipe. As the plant grows, it becomes linear-lanceolate to lanceolate, or sometimes elongate oblong. The stipe is discernible after the elongation of thalli.

The apex is round to obtuse. As seen in *H. yendoi*, there are several microscopic pores on the apical portion. They were observed not only on young thalli but in adult ones (cf. SETCHELL & GARDNER 1903). The liquid of yellow-brown color and the mud or small sand fill the central cavity. When the thallus becomes old, there appear irregularly shaped pores over the thallus surface by erosion. Then, it is shed away from the upper portion. Sometimes, it is ruptured vertically before the erosion.

The discoid holdfast extends widely, where a single frond is protruded at the beginning. As it becomes large, there appear numerous new fronds additionally. Moreover, most of the bases remain until next year, and protrude also many new fronds again. As a result, many plants grow compactly.

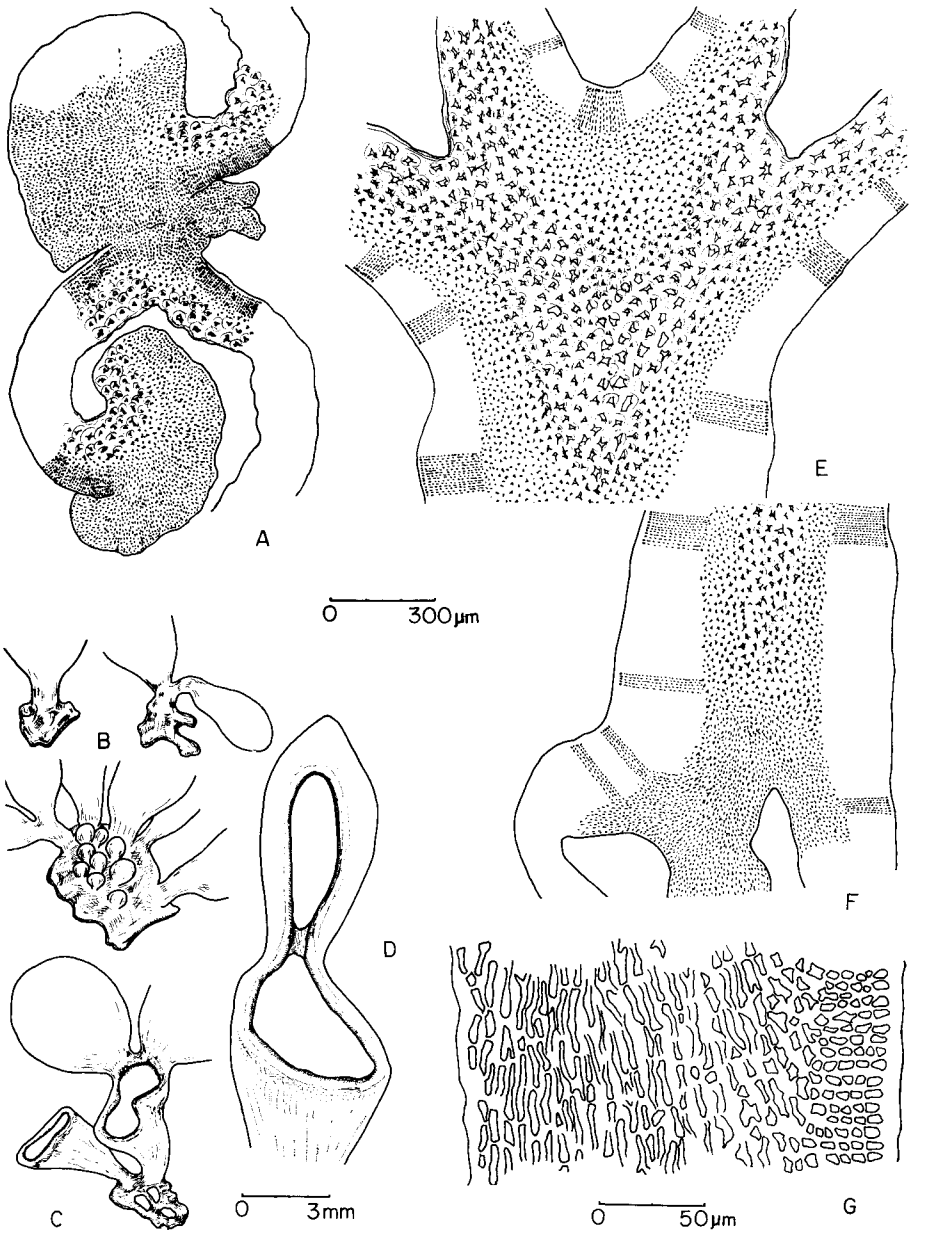

Fig. 8. *Halosaccion firmum* (POST. et RUPR.) KÜTZING

A, fusion of thallus in transverse section; B, basal part showing holdfasts; C, regeneration of new fronds from ruptured margin of old thalli; D, fusion of thallus at ruptured margin; E, longitudinal section of branched stipe; F, longitudinal section of holdfast; G, part of the same magnified.

Often the thallus branches once dichotomously at the middle to upper portion or rarely at the stipe, too (Fig. 8 B, right). The branched fronds are encountered more at Rausu. Some of them ramify a few times at the same portion. However, the ramification seems not to occur ordinarily in this plant.

As mentioned by YENDO (1909), the regeneration of new fronds from the ruptured margin old thallus is rather frequent (Fig. 8 C; Erimo, Mar. 1966). However, since the old thallus does not remain later, these regenerated fronds do not grow to maturation. The germination of tetraspores *in situ* is also not rare, as seen in *H. yendoi* (Fig. 11). The fusion of the frond between the ruptured margins is encountered, too (Fig. 8 A, D).

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers and central cavity (Fig. 9 C). The two layers, however, are not clearly distinguished. The cortical layer is composed of three to five rows of oblong cells arranged perpendicularly to the surface. These cells are branched once to a few times dichotomously. The plastids in the cells become denser outwards. Inner cells are frequently fused with adjacent ones, and form an H-shape in cross section of the thallus. The superficial cells are oblong to spatulate with almost the same width throughout, but not equal in height, nor even in arrangement.

The medullary layer is composed of six to eight irregular rows of round to elliptical cells, which increase gradually inwards in size and wall thickness. The inner cells become hyaline, and have stellately modified protoplasm owing to radial connections with adjacent cells. Sometimes, the connecting area of the protoplasm bulges spherically and is covered with a thick wall.

The young thallus has a single row of vertically elongate cortical cells, later forming more rows by periclinal or dichotomous divisions as the thallus grows (Fig. 9 A-B). The medullary layer is thin walled with round to slightly compressed cells. For instance, in middle part of a 1.5 cm high thallus, the cortex is composed of two to three rows of cells, and the medullary layer four to five rows.

The holdfast in longitudinal section is composed of thick walled round to elliptical cells inwards and anticlinally elongate cells outwards. The inner cells become gradually elongate upwards (Fig. 8 F-G). The stipe is solid in lower part, and hollow in upper part. The central cavity is formed by the rupture of large central cells. A ramified stipe has the central cavity above this ramification (Fig. 8 E).

The regeneration of new fronds shows a similar anatomical character

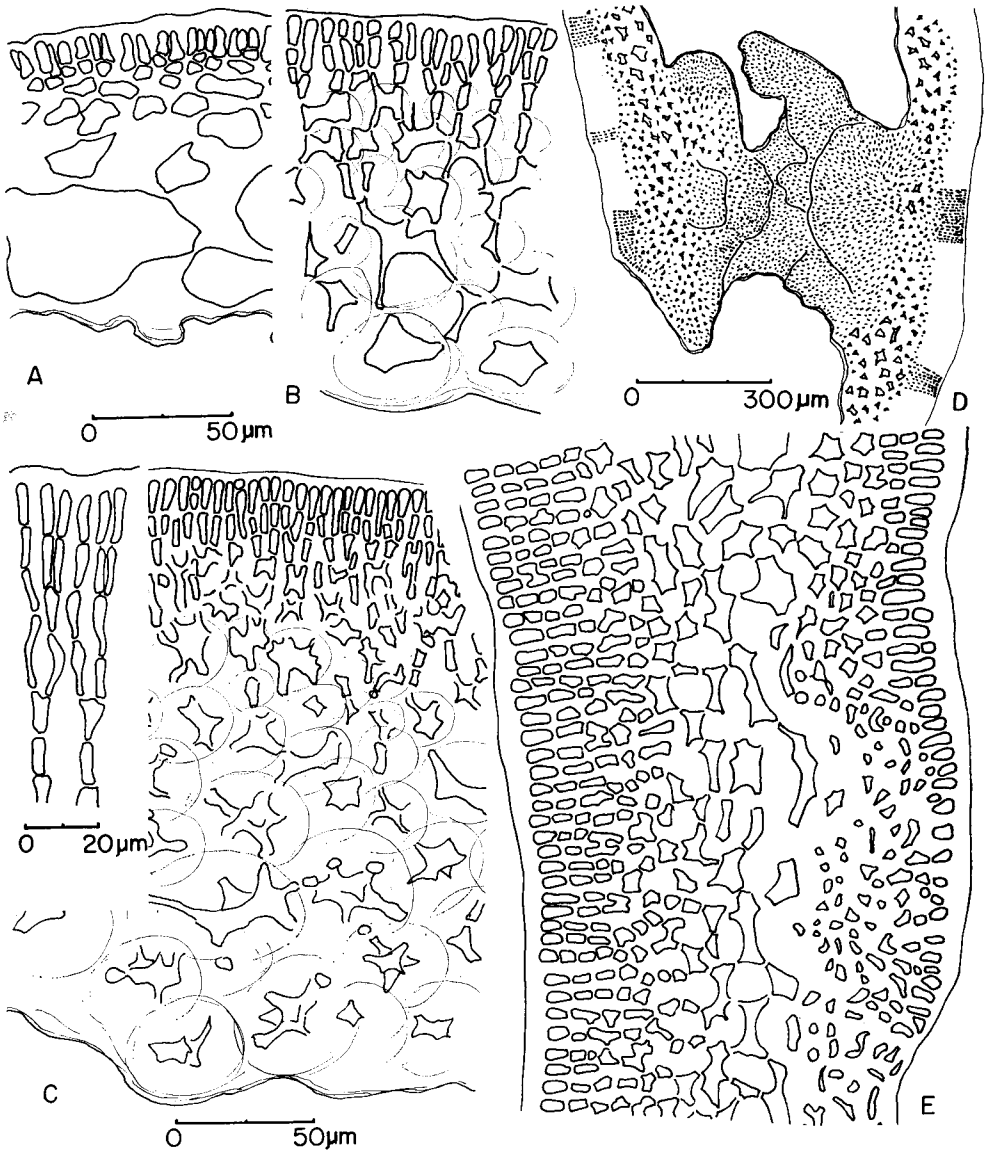

Fig. 9. *Halosaccion firmum* (POST. et RUPR.) KÜTZING

A-C, transverse sections of thalli at middle portion, A being germling of 1.5 cm high, B young and C mature fronds; D, longitudinal section of frond in regeneration; E, part of the same magnified, showing a regeneration of cortex from medulla.

to that of *H. yendoi* (Fig. 9 E). When the regenerated portion contacts with the other part of the thallus, the two become fused (Fig. 9 D). There were found frequently almost spherical galls, easily mistaken in the field for cystocarps, on the thallus surface (cf. RUPRECHT 1851). They are formed probably by some stimulation, such as a mechanical wound, so that the cortical cells are divided repeatedly and elevated from the thallus surface.

No hairs are observed in this species.

Reproductive Organs

Tetrasporangia: Tetrasporic thalli were generally large. Tetrasporangial sori are developed at random from middle to upper portion of the thallus at first, and extend over the whole surface (Fig. 10 A–C). The soral area is scarcely distinguishable at the beginning. As the sori are mature, the thallus becomes somewhat reddish purple.

In cross section, tetrasporangia are developed among sterile cells of cortex rather compactly. They originate from superficial cortical cells. Among the cortical cells tetrasporangium-initials are inflated with dense contents and a comparatively distinct nucleus. The initial is elongate without division and becomes spatulate with a slender base (Fig. 10 D, G). When the initial becomes about 28 μm high, it is divided periclinally or sometimes obliquely into the sporangium above and stalk cell below. The former is three to five times longer than the latter. Both are surrounded by a common wall as seen in *H. yendoi* (Fig. 10 E, H).

When the young sporangium becomes about 35 μm high and 14 μm wide, it is divided cruciately into tetraspores (Fig. 10 F, I). The stalk cell is enlarged and becomes obovate to concave in form. A mature tetrasporangium is 40$\sim$48 μm in length and 20$\sim$28 μm in width, while the stalk cell is about 11 μm high and 12.5 μm wide.

The sterile cortical cells in tetrasporangial sori are not modified in rows compared with those of non fertile zone, but become elongate and slender as the adjacent sporangia grow. However, in mature sori the sterile cell branches are generally shorter than the tetrasporangial ones. So, the outer surface of the soral area is uneven when observed under the microscope (Fig. 10 F).

After the liberation of tetraspores, secondary tetrasporangium is formed commonly from the stalk cell remaining (Fig. 10 K). The primary sporangial wall is thick and distinct. It shrinks slightly but remains for a long while (Fig. 10 J).

The germination of tetraspores *in situ* is quite similar in the manner of development to those of *H. yendoi*. In this germination, cell divisions

occur mostly in the outer two spores at first, and then the inner spores later. However, these four germlings form a single common base (Fig. 11 A–F). Medullary cells of the germling are developed rather early, but the central cavity is formed later, compared with those of *H. yendoi*. The

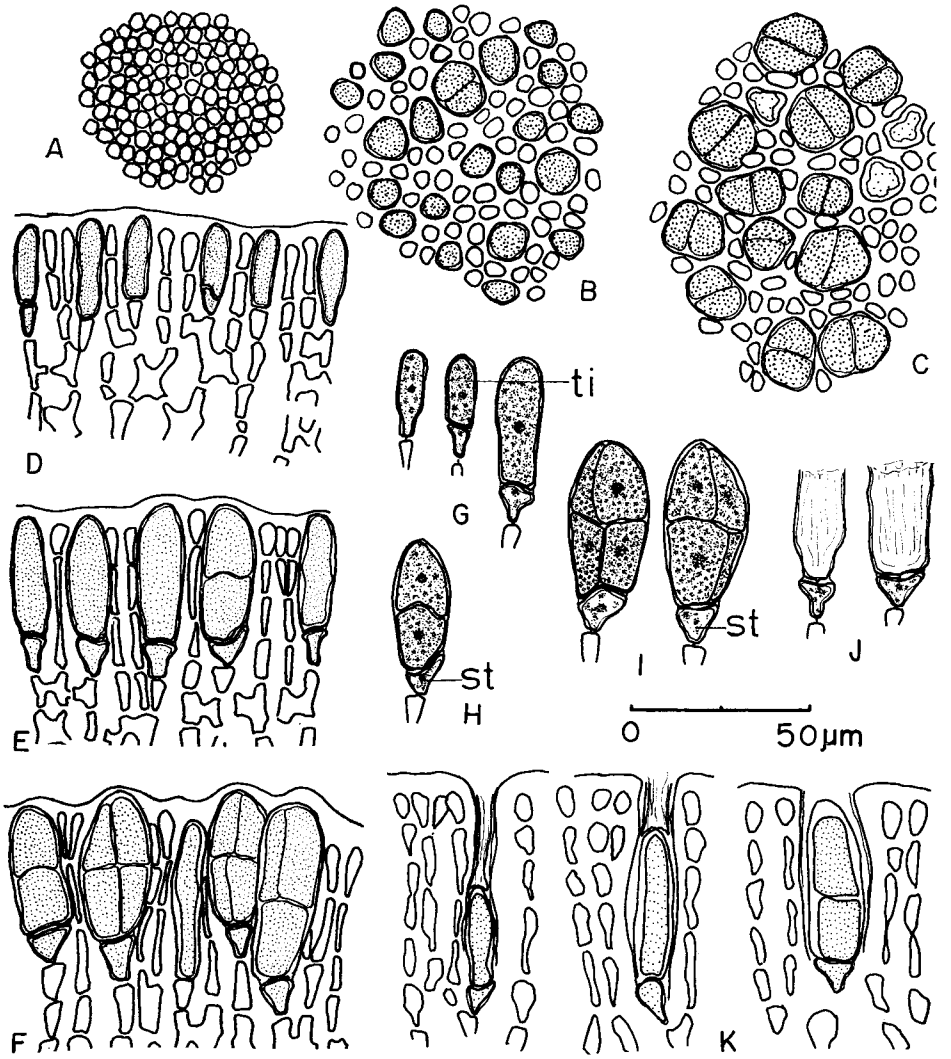

Fig. 10. *Halosaccion firmum* (POST. et RUPR.) KÜTZING

A, sterile superficial cortical cells in surface view; B–C, development of tetrasporangia in surface view; D–I, the same in transverse view; J, empty sporangia with stalk cells; K, regeneration of secondary sporangia from stalk cells.

ti: tetrasporangium-initial, st: stalk cell.

stipe is also scarcely distinguishable until the germling becomes a few centimeters high (Fig. 11 G–I).

Spermatangia: The spermatangium formation of this species was reported by LEE & KUROGI (1968 a).

As seen in *H. yendoi*, spermatangial sori disperse on the thallus surface in a similar manner to tetrasporangial sori. The male thallus is scarcely

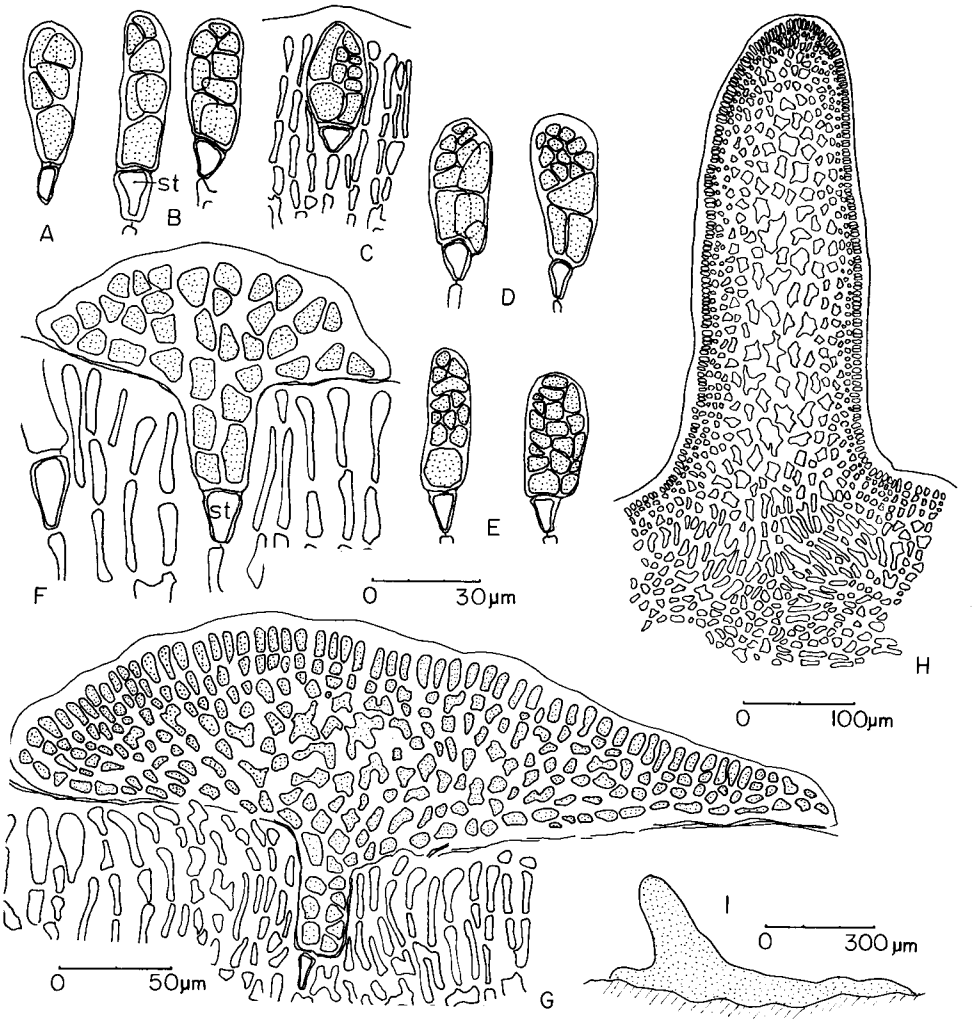

Fig. 11. *Halosaccion firmum* (POST. et RUPR.) KÜTZING
A–I, germination of tetraspores *in situ*.
st: stalk cell.

distinguished from sterile ones in the field, even after the full maturation. Moreover, it is very difficult to discern the initial developmental stages observed from the surface even under the microscope.

In cross section, two spermatangia are developed subterminally on a mother cell (Fig. 12 C). As the superficial cortical cell is elongated to about 11 μm high and 4.8 μm wide, it cuts off obliquely two spermatangial mother cells from its upper corners, and remains as a basal cell (Fig. 12 A–B). When the mother cell is about 15.4 μm high, it protrudes the first spermatangium from one corner of the top. The spermatangium and the mother cell are surrounded by a common wall. The second spermatangium is protruded subterminally on the other corner of the same mother cell after the first is formed (Fig. 12 C). Frequently two spermatangia are mature side by side at the same time. A mature spermatangium is elongate oblong and about 15.8 μm in length and 3.7 μm in width. The mother cell is also oblong and 12.0~12.8 μm high and 3.4~4.3 μm wide.

The plastids are not found in the mother cells, nor in spermatangia and spermatia, while they remain in the basal cell of the mother cell. There occurs a modification of inner cortical cells in soral area. At the beginning,

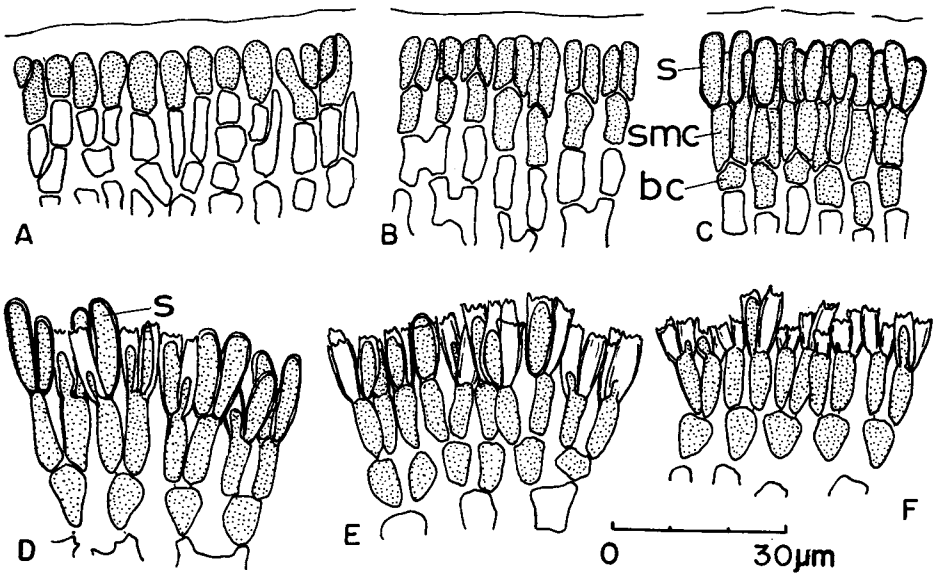

Fig. 12. *Halosaccion firmum* (POST. et RUPR.) KÜTZING

A–B, formation of spermatangial mother cells from superficial cortical cells; C, development of spermatangia subterminally on mother cells; D–E, successive development of spermatangia; F, later stage of development.

s: spermatangium, smc: spermatangial mother cell, bc: basal cell.

these inner cortical cells are oblong. When the mother cell begins to protrude spermatangia, however, they are enlarged to elliptical or tetragonal forms. In mature sori these inner cortical cells are 6.8～9.5 μm high and 5.2～8.6 μm wide at the broadest part. The basal cell of the mother cells becomes obovate to elliptical and about 8.6 μm in height and 6.1 μm in width.

The spermatium is liberated, conveying all the contents of the spermatangium. It has a large nucleus and vacuoles, and is surrounded by a fine protoplasmic membrane.

The secondary spermatangium is developed in a similar manner to that of *H. yendoi*. It is protruded generally out of the shortened wall of the previous spermatangium (Fig. 12 D–E). The tertiary spermatangium is rarely found within the cavity of previous two walls, and frequently as a small protrusion (Fig. 12 F).

Discussion

KÜTZING (1843) combined *Dumontia firma* POST. et RUPR. (1840) with his new genus *Halosaccion*, as *H. firmum*, but returned it to *Dumontia* in 1849. Later, RUPRECHT (1851) did once again the same combination for this species, which was accepted later by KÜTZING (1866) and thereafter.

According to RUPRECHT, among the specimens illustrated by TURNER (1819) as *Fucus saccatus*, a tough textile alga sent by Tilesius (plate 241, fig. d right) was quite the same alga as POSTELS & RUPRECHT's *Dumontia firma*.

Halosaccion firmum is a well defined species, though SETCHELL & GARDNER (1903) put it under *H. glandiforme*. In young stages of the development, both species are somewhat difficult to distinghish. However, as they grow, they become quite different in outer appearance. *H. firmum* is mostly oblanceolate to lanceolate, very firm, and scarcely adheres to paper in drying the specimen, while *H. glandiforme* is mostly elliptical to oblong, slightly rigid, and adheres to paper incompletely. In anatomical characters, *H. firmum* has cortical cells arranged in branched filaments, no hairs at all even in young stages, somewhat longer but slender tetrasporangia, and has branched filaments of sterile cortical cells in tetrasporangial sori. The branched filaments are more modified and slender than those of *H. glandiforme* (unpublished data).

Regarding the life history, it is a noticeable fact that fully grown plants collected at Erimo in January and March are all fertile, bearing either tetrasporangial or spermatangial sori, but no cystocarps at all. As a result, the possibility of the appearance of female thalli is not expected at the locations investigated.

Palmaria STACKHOUSE (1801)

The genus *Palmaria* was proposed by STACKHOUSE (p. xxxii) as a substitute name for *Ceramium* STACKHOUSE (1797 ; non ROTH 1797). Later, he (1809) placed there three species, *P. expansa*, *P. lanceolata* and *P. olivacea*, which are based on *Fucus palmatus* LINNAEUS (1753, p. 1162 ; cf. PAPENFUSS 1950). However, the genus *Rhodymenia* GREVILLE (1830) was conserved against *Palmaria* (cf. SILVA 1952), and *Rhodymenia palmata* (L.) GREV. was given instead.

Recently, comparing *Rhodymenia palmata* with the type species, *R. pseudopalmata* (LAMOUR.) SILVA, GUIRY (1974, 1975) revived the generic name *Palmaria* (lectotypified first by RUPRECHT, 1851, with *P. expansa*) for the former species, as *P. palmata* (L.) O. KUNTZE (1891), and separated it from *Rhodymenia*. According to him, the genus *Palmaria* is characterized by a solid, flat thallus, multiaxial, composed of cortical and medullary layers, the tetrasporangium is cruciately divided bearing a stalk cell, and the carposporophyte generation is lacking in the life history.

Palmaria palmata (L.) O. KUNTZE

(Text-figs. 13～17 : Plate II, A-C)

(1891) Rev. gen. plant. vascul., p. 909. GUIRY (1974) p. 509. *Palmaria expansa* RUPRECHT (1851) p. 268, pl. 16, figs. r, s.

Fucus palmatus LINNAEUS (1753) p. 1162 ; TURNER (1809) p. 114, pl. 115.

Ceramium palmatum STACKHOUSE (1797) p. xxiv.

Ulva palmata De CANDOLLE (1805) p. 12 : LYNGBYE (1819) p. 24.

Delesseria palmata LAMOUROUX (1813) p. 37.

Halymenia palmata C. AGARDH (1817) p. 35 ; (1822) p. 204 ; POSTELS & RUPRECHT (1840) p. 18, pl. 34.

Rhodymenia palmata (L.) GREVILLE (1830) p. 93 ; HARVEY (1849) pls. 217～8 ; (1853) p. 148 ; J. AGARDH (1852) p. 376 ; (1876) p. 329 ; KJELLMAN (1883) p. 147 ; De TONI (1900) p. 512 ; (1924) p. 289 ; JÓNSSON (1901) p. 137 ; SETCHELL & GARDNER (1903) p. 314 ; OKAMURA (1916) p. 48 ; (1933) p. 90, pl. 4, figs. 1～3 ; (1935) p. 76, pl. 343, figs. 4～9, pl. 344, figs. 6～8 ; (1936) p. 674, fig. 322 (1) ; DELF & GRUBB (1924) p. 327 ; KILLIAN (1926) p. 189 ; KYLIN (1925) p. 41 ; (1931) p. 22 ; WESTBROOK (1928) p. 149, pl. 2, figs. 30～48 ; ROSENVINGE (1931) p. 569, figs. 564～571 ; TOKIDA (1932) p. 16 ; (1954) p. 187 ; INAGAKI (1933) p. 46 ; ZINOVA (1933) p. 32 ; YAMADA (1934) p. 349 ; (1935) p. 23 ; KAWABATA (1936) p. 209 ; TAYLOR (1937) p. 306, pl. 41, fig. 7, pl. 42, fig. 3 ; DAWSON (1941) p. 133, pl. 18,

figs. 3～4; NAGAI (1944) p. 195; YAMADA & TANAKA (1944) p. 72; INOH (1947) p. 178, figs. 172～174; KANG (1966) p. 86; FUNAHASHI (1966) p. 140.

Sphaerococcus palmatus KÜTZING (1843) p. 409, pl. 63, I; (1849) p. 781; (1868) p. 31, pls. 89～90.

Fucus dulcis GMELIN (1768) p. 189, pl. 26.

Fucus sarniensis Merten in ROTH (1806) p. 103, pl. 1; TURNER (1808) p. 95, pl. 44.

Sphaerococcus sarniensis KÜTZING (1849) p. 779.

Japanese Name: *Darusu* (OKAMURA)

Type Locality: Not clear (*in Oceano* by LINNAEUS)

Materials

Shiribeshi District. Oshoro: June 3～4, 13, July 11, Sep. 11, Oct. 7, Nov. 10, 1966. Feb. 11, Mar. 11, May 27, July 7, Aug. 3, 17, Dec. 18, 1967. Jan. 24, Apr. 14, 1968. *Iburi District*. Charatsunai, Muroran: May 22, July 20, Oct. 13, 1966. Jan. 25, Mar. 2, 1967. Etomo, Muroran: Feb. 2, Mar, 30, Apr, 27, May 27, 1967. Feb. 21, 1968. Denshinhama, Muroran: Dec. 28, 1966. Jan. 26, Mar. 3, 1967. Mar. 11, 1968. Masuichi, Muroran: Oct. 12, Nov. 13, 29, 1966. Tokkarisho, Muroran: June 23, 1967. *Kushiro District*. Aikappu, Akkeshi: June 18, 21, Aug. 26, 28, Nov. 15, Dec. 29, 1966. Feb. 8, Apr. 15, June 26, 1967. Oct. 9～10, 1968. Daikokujima Isl., Akkeshi: June 20, 1966. Tokotan, Akkeshi: June 19, 1966. Kakijima, Akkeshi: June 25, 1967. Kombumori: May 7, 1967 (by S. KAWASHIMA). *Hidaka District*. Samani: Mar. 29, 1967. Harutachi: Mar. 29, 1967. Ikantai: Mar. 29, 1967. Erimo: Mar. 30, 1967. Minamitoyo: Sep. 28, 1966. *Nemuro District*. Nemuro: Apr. 14, May 17, 1967. May 12～3, 1968. Rausu: May 13～4, 1968. Habomai: May 11, 1968.

Description

Thallus gregarious or solitary, flat, membranaceous to coriaceous, with densely pigmented spots dispersed over surfaces, simple or branched once to five times dichotomously to palmately, with or without stipe, attaching to substratum by means of discoid holdfast, 20～50～(110) cm high, (1.5)～2～8～(18) cm wide at the upper broadest part; holdfast round, more than 1 mm in diam.; stipe terete, simple or branched, 0.3～1 mm in diam.; frond cuneate at base, gradually or abruptly broadened upwards, obtuse or erose at apex, entire or irregularly serrate at margin, sometimes with numerous pinnate branches or irregular clefts around margin, in old plant with numerous proliferations from margin as well as surfaces, in section composed of cortical

and medullary layers, 300～500 μm thick, cortical layer composed of three to four perpendicularly arranged cell-rows, densely pigmented outwards, thickening in old thallus, superficial cells arranged in palisade, almost tetragonal, 5～10 μm high, 6～12 μm wide, inner cells compressed, medullary layer composed of three to five cell-rows, hyaline, outer cells compressed, small and flat outwards, 5～10 μm high, 10～20 μm wide, central cells large, polygonal, 250～450 μm broad, 180～300 μm high ; unicellular hairs dispersed in groups ; tetrasporangia dispersed in sori over whole surfaces except for lower portion, terminal on superficial cortical cell, with stalk cell, elliptical, divided cruciately, 60～75 μm in length, 52～65 μm in width, sterile branches in sorus three to four perpendicularly elongated celled ; spermatangia dispersed in sori similar to tetrasporangia, developed subterminally on spermatangial mother cell, oblong, 9.2 μm high, 3.4 μm wide ; cystocarp not known ; color reddish to brownish purple ; specimens adher to paper except for lower portion. Perennial.

Habitat : Lower tidal zone on rocks.

Distribution : Northern Honshu and Hokkaido, Japan ; Okhotsk Sea ; Japan Sea Coast of Siberia ; Kamchatka ; Pacific Coast of North America ; Atlantic Coast of North and South America and of Europe ; Arctic Ocean ; North Sea and Baltic Sea ; Kuriles ; Saghalien ; and Japan Sea Coast of North Korea.

Phenological Observation

The plants were investigated at Oshoro, Muroran and Akkeshi. They inhabit on rocky substratum in lower tidal zone, where the wave action is not so strong.

At Oshoro Bay, the investigations were carried out from June, 1966 to April, 1968. They were the most commonly encountered algae at the area. In November, 1966, many germlings less than 5 cm high were at rather calm places along the coast of inner Bay, and also many new proliferations from the margin of old plants remaining with basal portion only. The new fronds were quite similar each other in form and size. In February, 1967, the plants became 20～35 cm high and 4～7 cm wide on an average, and bore mostly tetrasporangial or spermatangial sori. The two kinds of sori were found only on the proliferations or new plants. The old thalli bearing the proliferations became thick, firm and dark purple. In March, most of the large branches were broken or half torn away. The remainder, however, bore frequently many proliferations from the margin, while there were many new plants protruded from the same base. One of the large plants remaining

completely was about 40 cm high and 9 cm wide at the broadest part. During the period, the lower firm portion of main branch became more distinct compared with the other part. It was mostly less than 5 cm long from the base, submembranaceous, firm, and dark purple, whereas the upper portion, if remained, bore generally the reproductive organs, and was still tender, membranaceous and purple. A distinct border appeared between the two areas. The plants were so abundant at the time that they covered almost all the areas along the coast of the inner Bay. In April, there were rarely sterile plants. Most of thalli became brownish purple to green, except for the blackish purple lower portion, and were torn or broken irregularly in the upper portion. Almost all the plants collected in May were such remainders with thick, firm and coriaceous lower portion. Frequently the central area became especially thick so that there appeared midrib-like longitudinal stripes on the thallus surface in both sides (Fig. 13 E; cf. OKAMURA 1935, pl. 343, fig. 8). The plants collected in July, August, September and October were also such remainders with firm and whitish green colored thalli except for the midrib-like stripes, which remained with a dark purple color. These remainders refreshed themselves in November when the new germlings began to grow.

In addition, many of the plants collected in December, 1967 had tetrasporangial or spermatangial sori in early stages of development. Some large plants were more than 15 cm high and 3 cm wide, while the plants collected in January, 1968 were grown fully and had reproductive organs rather commonly.

At Muroran, the investigations were carried out from May, 1966 to June, 1967 and in February and March, 1968. Both the germlings and proliferations less than 5 cm high were observed in November. They became about 20～35 cm high and 4～7 cm wide on an average in December, and bore both the tetrasporangial and spermatangial sori in early developmental stages. The plants became most luxuriant in number and height from January to March, showing about 30～40 cm high and 5～8 cm wide. Especially at Denshinhama, about 1 m high thalli covered the substratum so compactly that the other algae were scarcely exposed at low tide. One of the large plants encountered in March was a tetrasporophyte of 125 cm high and 10 cm wide at the broadest part. In February they became firm in lower portion, and decreased in number rapidly until April, though plants bearing the fertile organs remained later than in Oshoro. On the other hand, in May there appeared abundant young plants within 7 cm high, probably originating from spores. These new germlings did not grow so large both in height and

width. In July they were about 10 cm high and 8 mm wide at the broadest part, and protruded frequently numerous slender branches. All thalli collected at the time were submembranaceous, and bearing tetrasporangial or spermatangial sori. In October I could find no other thallus except for the thick and coriaceous remainders less than 5 cm high.

At Akkeshi, the investigations were carried out from June, 1966 to October 1968. When I visited in December, 1966, the thalli were about 10 cm high and bore already tetrasporangial or spermatangial sori in early stages of development. They became most luxuriant from January to March. The fully grown thalli were 15～20～(36) cm high and 3～5～(8) cm wide. At Akkeshi, however, they were not so abundant as in Oshoro and Muroran. The new germlings, as seen in Muroran, appeared in April and bore reproductive organs in June. The old plants with complete upper portion were encountered until June. From June, both the new and old thalli became submembranaceous in texture and yellow-green to brownish purple in color, while the lower portion of old thalli remaining were firm and dark purple. In these areas, the old plants with lots of proliferations were rather common. Especially the plants collected at Daikokujima Isl., or the ones cast ashore at Aikappu in February, April and June bore numerous proliferations on old segments of the thallus. Some of them developed these proliferations five times successively one after another. Such plants seemed to grow at deep and rather calm places, affected scarcely by the wave action, so that the proliferations could remain rather safely. It is not clear whether the times of proliferation accord with the annual nature of the plant, though ROSENVINGE (1931, fig. 566) reported this. However, the proliferations seemed to occur sometimes twice in a year.

Considering the above investigations, these plants reveal almost similar growth phenology at Oshoro, Muroran and Akkeshi, though there are also respective characteristics among them owing to the difference of habitats. It may be summarized that the plants appear in November, mature beginning in December, become most luxuriant in number and height from January to March, and decrease rapidly in number after April. Many of them, however, lose the upper portion bearing the reproductive organs, and remain with the lower portion which becomes thick, firm and reduced in color, but survive throughout summer season. The old remainders refresh and proliferate new fronds beginning in November when the germlings newly appear. In addition, the germlings are found once more in April at Akkeshi and in May at Muroran but not at Oshoro. They grow to produce reporductive organs in June at Akkeshi and in July at Muroran. These plants

are characterized by small and narrow fronds, many branches and submembranaceous texture from the young stage. The plants bearing the complete upper portion remain later at Akkeshi, but rapidly disappear at Oshoro.

Both the tetrasporangia and spermatangia are developed in December, and become abundant from January. They remain until the upper portion of thalli disappear. The tetrasporic plants are more abundant, while the male plants frequent. However, no female thalli were encountered, even though so many plants were investigated for this purpose in every collection.

Morphological Observation

External Appearance

This plant is very variable in outer appearance as mentioned by HARVEY (1849, pl. 217). At the beginning it appears in elongate oblong to lanceolate shape, then the apical portion is divided soon dichotomously or palmately (cf. ROSENVINGE 1931). In several thalli investigated the primary branch appears when they become 1.5～2 cm high (Masuichi, Nov. 1966). Sometimes, they develop no branches for a long while, nor at all but remain with a simple form. From round to irregularly expanding holdfast the frond is erected with simple or branched cylindrical but slightly compressed stipe, which is sometimes scarcely distinguishable (Fig. 13 A). The frond is broadened upward with divergence of 15°～35°, and becomes gradually or abruptly widened near the portion about 2 cm above the base. Some of them expand in divergence more than 120° or mostly 50°～80°. Above the middle portion, however, the frond expands very slowly. Some thalli become almost same in width throughout, except for the basal and apical portions.

Ramifications are repeated once to five times dichotomously and palmately. More often the plant shows an indefinite form by irregular clefts. Even in the same thallus, there are such varying ramifications (TURNER 1809). The plants in luxuriant period show comparatively fewer ramifications than the ones after the period. On the cleft of frond, KILLIAN (1926) mentioned it might take place under the mechanical influence of waves, whereas ROSENVINGE (1931) was dubious about it. At study sites the plants inhabit mostly calm places, and therefore the mechanical influence seems to be doubtful.

As ROSENVINGE noticed, the proliferations of the branches appear from the apex or margin of old thallus. There remains a slight constriction at the base of the proliferates or sometimes none. Some plants encountered after the luxuriant period in Muroran (Charatsunai, July 1966), Oshoro (June 1966), Akkeshi (Aikappu, June 1967) and Rausu (May 1968) accord with var.

sarniensis (MERT.) GREV., known as *Rhodymenia palmata*. They are characteristically slender fronds with many branches as shown by previous investigators (TURNER 1808, pl. 44~5; HARVEY 1849, pl. 218; OKAMURA 1935, pl. 344, figs. 7~8). Some other plants collected at Muroran (Tokkarisho, June 1967) are linear-lanceolate and accord well with f. *ochotensis* NAGAI

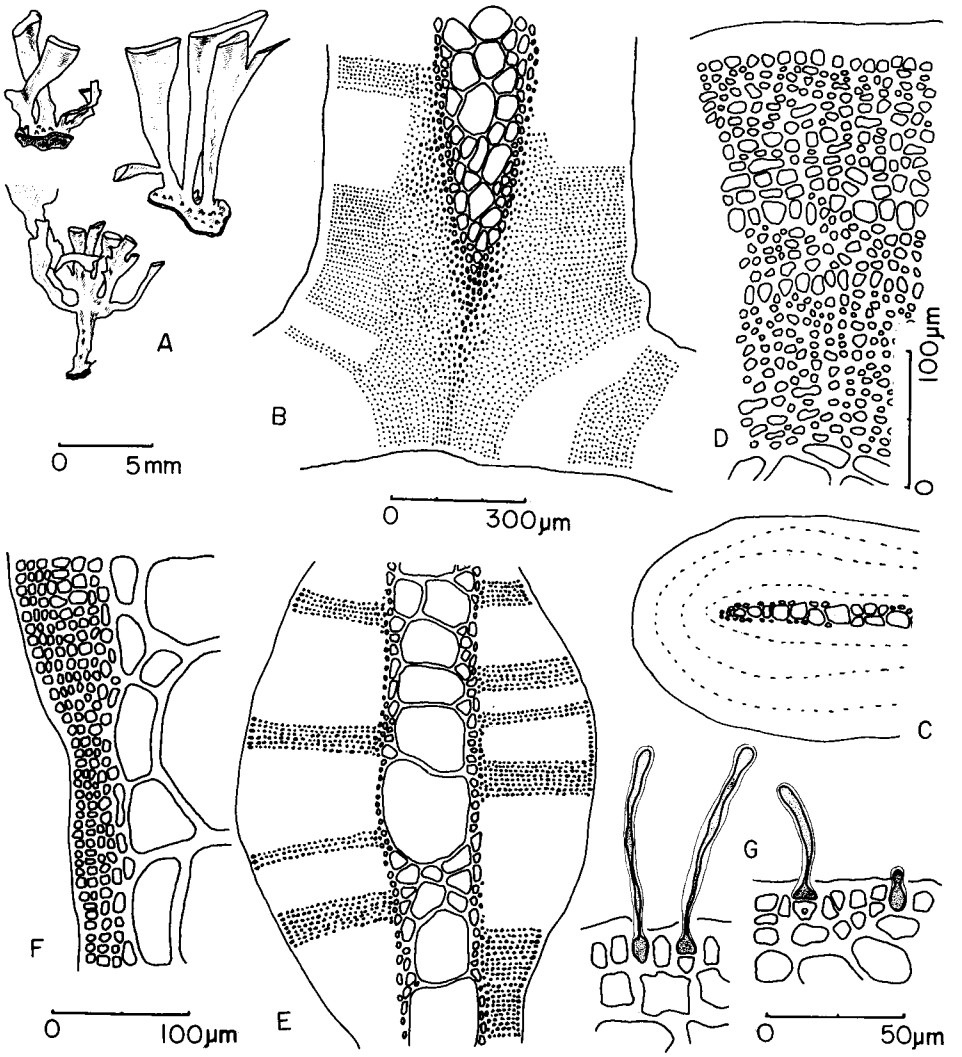

Fig. 13. *Palmaria palmata* (L.) O. KUNTZE

A, basal part showing holdfast; B, holdfast in longitudinal view; C, stipe in transverse view; D, part of the same magnified; E, thickening of cortex in old thallus; F, part of the same magnified; G, development of hairs.

of *R. palmata*. On the other hand, many plants encountered at Aikappu, Tokotan, and especially at Daikokujima Isl., accord with f. *prolifera* (KÜTZ.) KJELLMAN of *R. palmata*, bearing many proliferations.

The margin of the thallus is entire, serrate or irregularly cleft. The entire ones are more common. Sometimes, the serrate or irregularly cleft ones are confined only in the lower portion of the thallus. The apex is obtuse or erose. A broad thallus has an erose apex, but a slender one an obtuse apex. The holdfast erects a single frond at first, and then several ones additionally, so that there are a large and several small fronds afterwards (ROSENVINGE, *l. c.*). Frequently a few bases are piled one upon the other, and expand more than 5 mm in diam.

The plant has dark spots on the thallus surfaces, caused by dense aggregation of the plastids in the superficial cortical cells (ROSENVINGE *l. c.*). These spots expand in longitudinal stripes of a few to several mm long, appearing at random. They appear also in reproductive sori, but not always distinct on the plants collected in winter.

The germination of the tetraspores *in situ* is rather common in these areas (Fig. 16). These germlings are protruded so compactly, that they cover frequently the whole thallus surfaces. Some of them collected at Aikappu grow into plants more than 7 cm high 4 mm wide.

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers. In transverse section the cortical layer consists of three to four rows of cells arranged perpendicularly to the surface (Fig. 14 E-F). The superficial cells are somewhat flat tetragonal with dense plastids and arranged in palisade. They are slightly larger than the other cortical cells below. In young thallus, they are divided obliquely at one upper corner and then at the opposite, so that there are formed two to three upper and one lower cells as shown by SJÖSTEDT (1926, figs. 19 B-C) in *Rhodymenia pertusa*. The cortical layer increases the thickness by repeating such divisions. The inner cortical cells contain plastids poorly, and become more or less compressed (Fig. 14 E).

The medullary layer is composed of three to five rows of cells. The cells of outer one to three rows are thick walled and round to periclinally compressed, while the central one or two cells are very large and elliptical to polygonally rounded. In the marginal portion of the frond the central cell is replaced by a few to several small cells.

When the thallus is old, the cell wall becomes thick in both layers. The superficial cortical cells all around the surfaces are divided repeatedly

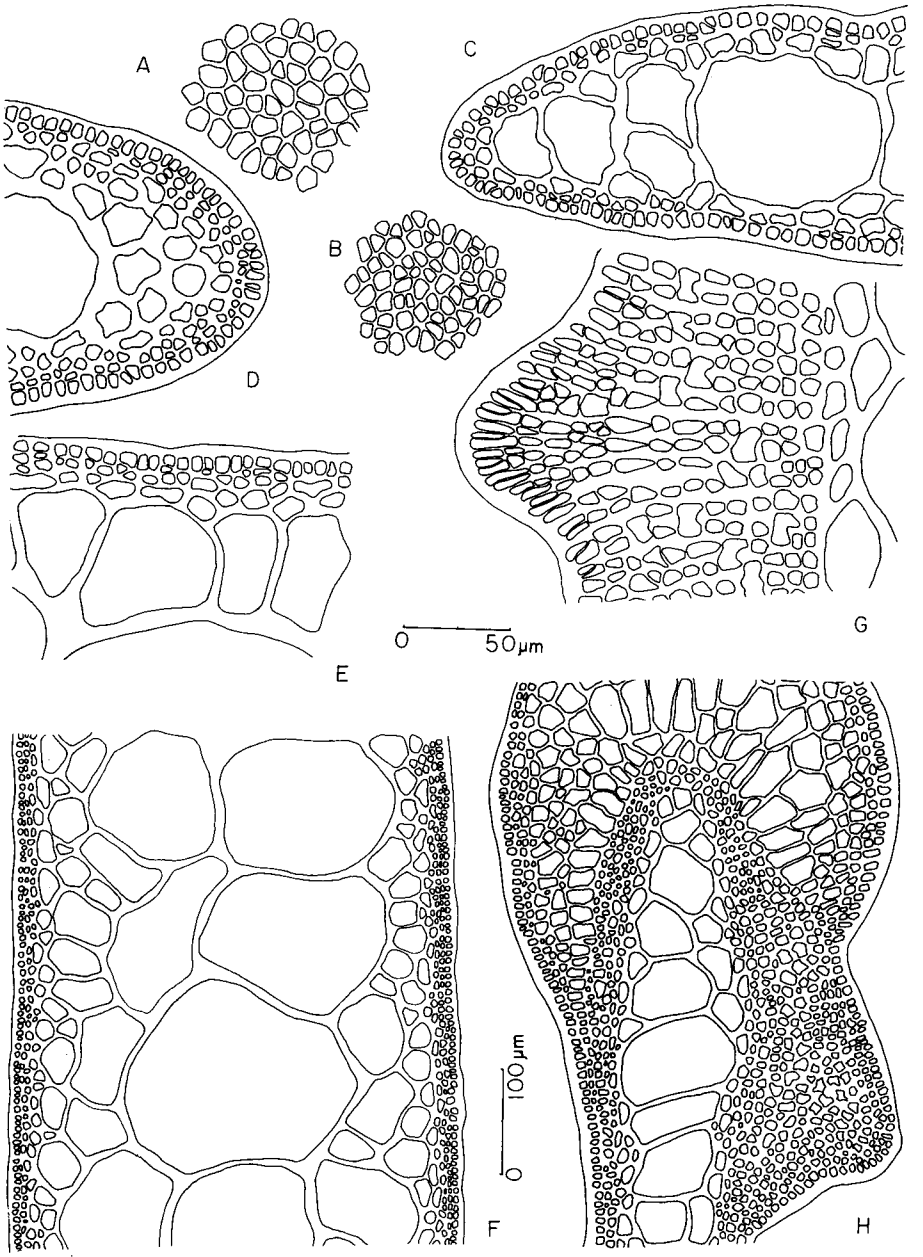

Fig. 14. *Palmaria palmata* (L.) O. KUNTZE

A–B, superficial cortical cells in surface view, A being young; C–E, fronds in transverse view, C being young, D showing margin; F, mature thallus in longitudinal view; G–H, development of proliferations from cortical cells.

and arranged in perpendicular rows, so that the cortical layer becomes specially thick (Fig. 13 E-F). At the beginning, the division occurs only in small areas at random. Then, it extends over the whole surfaces. Sometimes, it occurs only at a definite area successively, where the cortical layer becomes three to four times thicker, appearing as a stripe observed from surface (Fig. 13 E). This thickening occurs intermittently, because the superficial cortical cells are small and densely pigmented when divisions have stopped, while the cells during the division are large and poorly pigmented. One specimen investigated had more than 500 μm thick cortex with four stratifications in the lower segment of old thallus (Fig. 13 C-D). The number of stratifications accords generally with the times of proliferation of new fronds.

In proliferation two different growth patterns are discernible. One is initiated by the divisions of superfical cortical cells in a small area, where the new frond or branch are protruded gradually. There is discernible a typical multiaxial type of growth in the early developmental stage (Fig. 14 G). A constriction remains generally at the base of these new fronds. The other is initiated by the cell divisions in a rather broad area, which is elevated in a round (Fig. 14 H). The medullary cells are formed by the fusion of inner cells with one another. There remains scarcely or slightly the constriction at the base in the latter proliferation. Sometimes, the new proliferated fronds become thicker than the old one.

The holdfast in longitudinal section is composed of thick walled tetragonal cells arranged perpendicularly to the surface (Fig. 13 B). There are also some stratifications owing to the apical growth of the superficial cells as mentioned by ROSENVINGE (1931). When the bases are piled one upon the other, there remains always the contacting border between them. The stipe in transverse section has rather thick cortical and thin medullary layers. In old stipe there are ring like stratifications in the cortex as seen in the frond, and the medullary cell wall becomes much thicker.

Unicellular hairs develope from epidermal cells (Fig. 13 G). It was observed for the first time by WILLE (1891). At the beginning of the development a hair-initial becomes round at top and protrudes out of the thallus surface, leaving a slight constriction at the base. As ROSENVINGE (*l. c.*) reported, the hairs appear on the freckled spots of the thallus. However, the thallus has no distinct places for the occurrence of hairs. They are abundant in young plants and appear as round to longitudinal stripes in aggregation. Sometimes, they occur in the tetrasporangial and also in young spermatangial sori.

There are no fusion of thalli, nor the rhizoid formation in this species.

Reproductive Organs

Tetrasporangia : As mentioned previously, tetrasporangial sori are con-

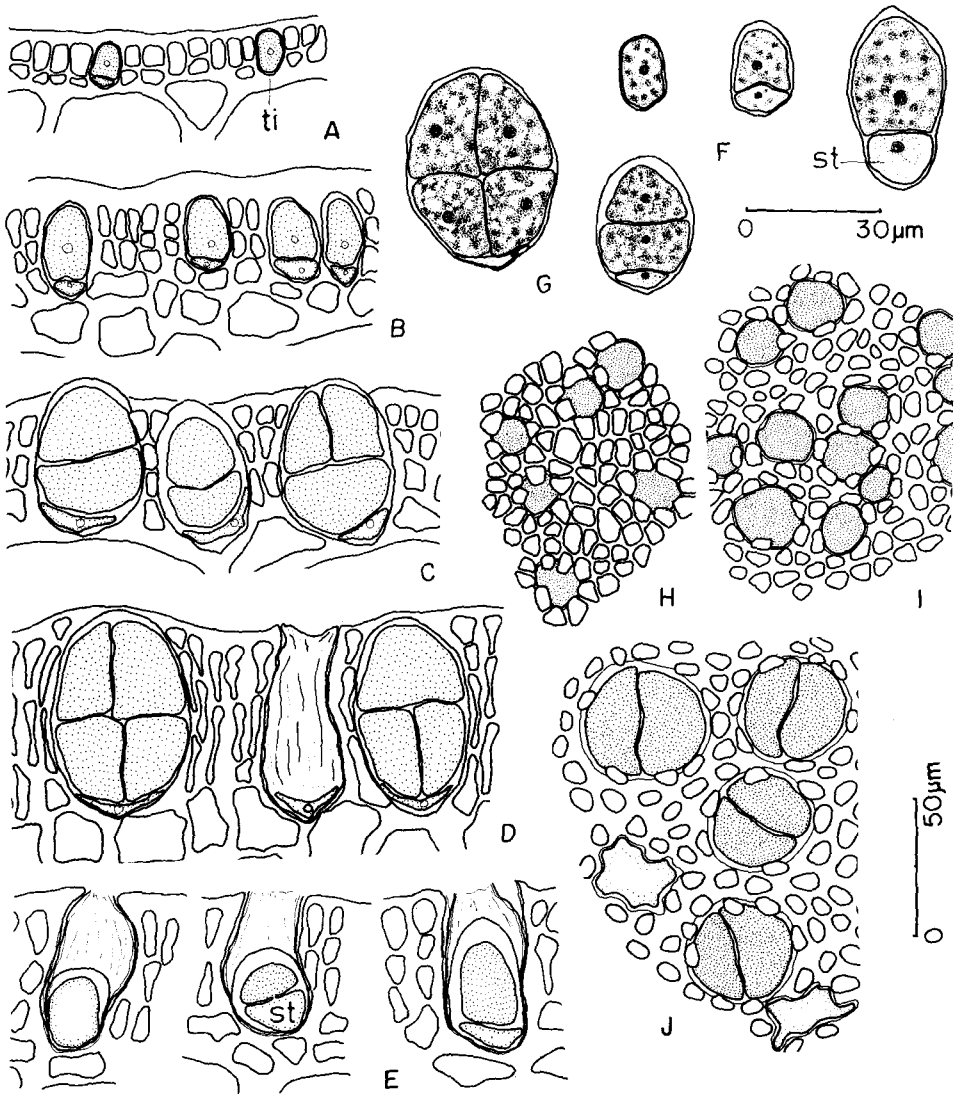

Fig. 15. *Palmaria palmata* (L.) O. KUNTZE

A–D, development of tetrasporangia in transverse view; E, regeneration of secondary tetrasporangia from stalk cells; F–G, growth of tetrasporangia; H–J, same as A–D in surface view.

st : stalk cell.

fined only to first-year fronds or proliferations, though ROSENVINGE (1931) and INAGAKI (1933) reported they appeared in old frond. The tetrasporic plant is easily distinguished from sterile ones owing to its dark purple color and thick frond. Sometimes, its surface becomes uneven as the soral areas are expanded. When a thallus has mature sori, the sporangia are discerned in the field by deeply pigmented spots. The sori are developed at first in the middle portion of the thallus, and extend later to almost all surfaces except for the lower portion and margin (cf. WESTBROOK 1928). There are various stages of development even in a single frond (Fig. 15 H–J).

In cross section, tetrasporangia originate from the superficial cortical cells. In early developmental stage the tetrasporangium-initial is slightly larger and stained more densely than adjacent sterile cells (Fig. 15 A). After slight elongation, it cuts off transversely a stalk cell below. The upper cell is a young sporangium, which is three to four times higher than the stalk cell Both cells are surrounded by the common wall (Fig. 15 B–D, F). When it becomes about 30 μm high, there occur periclinal and anticlinal divisions to form tetraspores cruciately (Fig. 15 C–D, G). A fully mature tetrasporangium is elliptical and 60$\sim$75 μm in length and 52$\sim$65 μm in width. During the time the stalk cell becomes poor in contents and compressed flat.

The sterile superficial cortical cells in sori are elongate and divided once transversely when tetrasporangium-initials cut off a stalk cell. The upper cells become as high as adjacent young sporangia, while the lower cells are somewhat flat at first. Before the sporangia are divided periclinally these upper sterile cells are divided once again periclinally. There occurs frequently an anticlinal division additionally in the superficial cell. As a result, these sterile cells become three rowed with oblong to tetragonal cells. They are elongate and slender as adjacent tetrasporangia are mature, and become almost same in height as the tetrasporangial row. The superficial sterile cell is modified to spatulate form later (Fig. 15 D).

Tetraspores are liberated from the ruptured apical portion of the sporangial wall. The secondary sporangium is developed in a similar manner to the previous one (Fig. 15 E). The wall of the primary tetrasporangium is rather distinct in this species The germination of tetraspores *in situ* is quite similar in development to that of *Halosaccion* mentioned above. The four spores are similarly functional, and the primary division occurs quite independently of one another. However, outer two spores of a sporangium are divided more rapidly. They form a common mass of small cells, which are protruded out of the surface, becoming later of a mushroom shape (Fig. 16 A–D). A single frond is protruded at first from the base and then

a few later. Some times, the first frond is protruded soon after the celll mass is pushed out of the mother thallus, so that it has a rather small base (Fig. 16 E).

Spermatangia : The spermatangial sori are confined to first-year fronds, as seen in tetrasporangia. In the field, the soral areas are distinguished

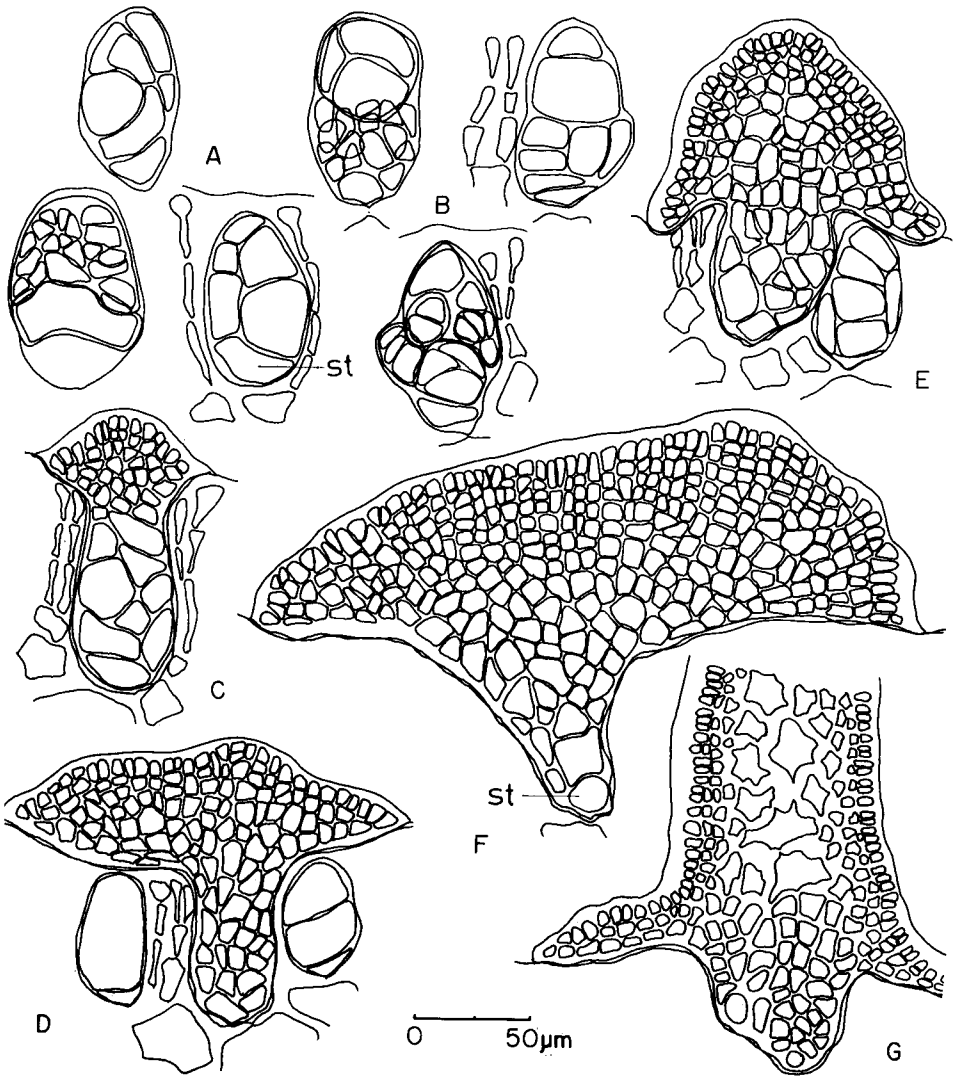

Fig. 16. *Palmaria palmata* (L.) O. KUNTZE
A–G, germination of tetrasporangia *in situ*.
st : stalk cell.

owing to slightly reduced color and uneven surfaces. Sometimes, there appear irregular freckles after drying the specimens (cf. DELF & GRUBB 1924, ROSENVINGE 1931).

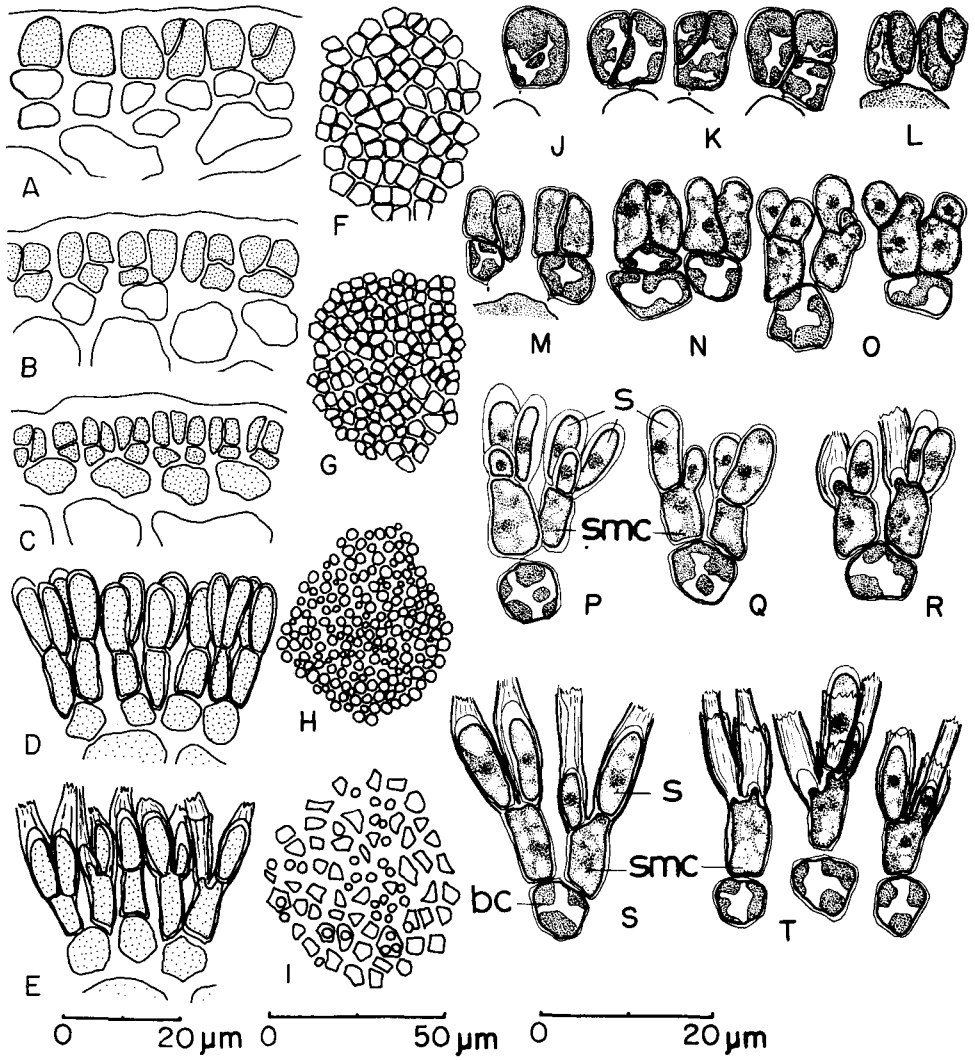

Fig. 17. *Palmaria palmata* (L.) O. KUNTZE

A–E, formation of spermatangia in transverse view; F, superficial cells in surface view; G–I, same as A–E in surface view; J, superficial cortical cell; K–M, formation of spermatangial mother cells; N–Q, development of spermatangia from mother cells subterminally; P, developing third spermatangia; R–T, successive development of spermatangia.

smc: spermatangial mother cell, s: spermatangium, bc: basal cell.

The sori appear and extend on thallus surface in a similar manner to tetrasporangia, except for sterile areas here and there in the fertile portion. Such sterile areas are especially distinct in lower portion of the thallus. Although DELF & GRUBB (*l. c.*) mentioned no sori in the apex, they are found over whole surface except for the margin and lower portion of thallus. Especially in lower portion the border between fertile and sterile zones is so distinct, that it is easily discerned even in the field. On microscopic observation from the surface, the epidermal cell is divided into three to four cells at first, which are divided once again into two cells, respectively. The latter becomes spermatangial mother cells (Fig. 17 F-H).

In cross section, two to three spermatangia are developed subterminally on a mother cell. The spermatangia are originated from the superficial cortical cell. As the cell is enlarged to about 8.5 μm high, it cuts off three to four cells obliquely from the upper corners (Fig. 17 A-B). After some enlargement, these upper cells cut off again two cells subterminally, which become spermatangial mother cells. The lower cell remains as a basal cell of the mother cells (Fig. 17 C, L-M).

The mother cell is elongate anticlinally with almost round apex. When it becomes about 5.9 μm high, it protrudes a spermatangium subterminally from the top. The spermatangium and mother cell are surrounded by a common wall. Sooner or later the second spermatangium as reported by DELF & GRUBB (1924) is protruded from the same mother cell beside the previous one, showing quite a similar developmental manner (Fig. 17 O). Frequently these two spermatangia are mature almost at the same time (Fig. 17 D). A third spermatangium, mentioned by no previous investigators, from the same mother cell may be formed (Fig. 17 P, R, T). The third seems to occur rather frequently.

A mature spermatangium is oblong and 9.2 μm long and 3.4 μm wide, while the mother cell is oblong and 5.7$\sim$8.6 μm high and 3.4$\sim$4.6 μm wide. The liberation of spermatium occurs by the rupture of upper wall of the spermatangium. It conveys all the contents, leaving the wall only. The spermatium has a distinct nucleus and a fine protoplasmic membrane.

In the course of spermatangium formation, there are no plastids in the mother cells, spermatangia and spermatia, but remain in the basal cell. The superficial gelatinous wall of the frond is shed when spermatangia are protruded from the mother cell.

The secondary spermatangium is common in this species (Fig. 17 E, R-S). The developmental manner is quite similar to that of *H. firmum*. After the liberation of spermatium, the secondary spermatangial wall is pro-

truded out of the primary one. In addition, the tertiary spermatangia are found not rarely after the liberation of the previous two spermatia (Fig. 17 T). However, some of them are mature, but the others immature. Finally, the mother cells lose those walls and the inner cortical cells are exposed instead (Fig. 17 I). No recovery of the mother cell into an ordinary vegetative cell, as reported by GRUBB (1925), was observed.

Discussion

The present species was introduced by LINNAEUS (1753) as *Fucus palmatus*, and by GMELIN (1768) as *F. dulcis*. Since then, there appeared many synonyms before GREVILLE (1830), who combined them with *Rhodomenia* (=*Rhodymenia*) as *R. palmata* (cf. C. AGARDH 1817, HARVEY 1849, KÜTZING 1849, J. AGARDH 1852, De TONI 1900, etc.). Comparing with the type species of *Rhodymenia*, GUIRY (1974) transferred this species to *Palmaria* as *P. palmata*, and recently he (1975) combined forma *mollis* (*R. palmata* f. *mollis* SETCHELL et GARDNER 1903) in this species.

The plant possesses so many diverse forms, that there are many infraspecific taxa distinguished by external appearances under the name *R. palmata* (cf. C. AGARDH 1922, KÜTZING 1849, J. AGARDH 1852, KJELLMAN 1883, SETCHELL & GARDNER 1903). Among them I could encounter var. *sarniensis*, var. *sobolifera*, f. *ochotensis* and f. *prolifera* in this area. According to the present investigation, except for the latter, these varieties and forma are seen generally among thalli growing after the luxuriant period, but are linked with intermediate forms with each other. F. *prolifera* is nothing but the old thalli inhabiting specially at calm and deep places where the mechanical interference is not so strong and producing lots of proliferations successively. However, on the f. *grandifolia* OKAMURA (1933), having specially broad blades, I only observed dried specimens including the type specimen. It is not clear how this form is linked with the others in outer appearance.

As reported by KILLIAN (1926) and INOH (1947), germlings of tetraspores *in situ* form a multicellular disc. But no specially large apical cell, mentioned by KILLIAN, is distinguished before the development of frond from the disc. This accords well with INOH's observations.

Spermatangia were recorded for the first time by THURET (1855). They were studied precisely by DELF & GRUBB (1924) and TAZAWA (1975), which are, however, somewhat different from the present investigation. DELF & GRUBB reported a single spermatangial mother cell protruded two primary spermatangia and TAZAWA one to two primary spermatangia, while in this study it protrudes two to three primary spermatangia from a single mother cell.

WESTBROOK (1928) carried out cytological detection on the tetraspore formation, and mentioned "strong evidence for believing that the sporangial divisions are meiotic", while MAGNE (1959) suggested that apomeiosis might well occur in the tetrasporangia. The chromosome number was counted n>20 (WESTBROOK, *l. c.*), n=21 (AUSTIN 1956), n or 2n=c. 14 (SPARLING 1961) (cf. DIXON 1966). Recently, YABU (1972) concluded that reduction division occurred distinctly in the nuclear division of tetrasporangium, since in the somatic division of tetrasporophyte the chromosome number was counted 52 and in tetrasporangium 20 to ca. 26. If there occur sporic meiosis as concluded by YABU, the recovery of chromosome number should be required somewhere during the life history, by true fertilization or more possibly by auto-recovery in early stage of development of tetraspores, as seen in *Chaetomorpha* by KÖHLER (1956).

On the other hand, no one has discovered the female organ of this plant certainly. The trichogyne described by GRUBB (1923) was explained by ROSENVINGE (1931) to be a hair. TOKIDA (1954) reviewed the descriptions of so called "cystocarp-like body" mentioned by several previous investigators, and clarified it had no cystocarpic nature.

PERESTENKO (1973) erected *Rhodymenia stenogona* with the plant known as "*R. palmata*" occurring on the Pacific Coasts of northern Asia including Japan Sea. The characters distinguishing the species from European "*R. palmata*" are the mostly linear shape of thalli and proliferations, the occurrence of proliferations from the surface of thallus as well as the margin, sorus of tetrasporangia aggregating in longitudinally lienar shape or occurring on the whole surface, and other features. As to the relationship of this species to the Japanese plant of *Palmaria palmata*, I cannot resolve it now because of lack of the specimen of the former.

***Palmaria marginicrassa* sp. nov.**

(Text-figs. 18~22: Plate II, D-E)

Japanese Name: *Atsubadarusu* (nom. nov.)
Type Locality : Aikappu, the Pacific Coast of Hokkaido, Japan
Type Specimen: Holotype, SAP No. 032340 (Tetrasporic plant)
Paratype, SAP No. 032341 (Male plant)

Materials

Kushiro District. Aikappu, Akkeshi: June 18, Aug. 26, Dec. 29, 1966; Feb. 8, Apr. 15, June 26, July 7, 1967; Oct. 9~10, 1968. Daikokujima Isl., Akkeshi: June 23, 1967. Tokotan, Akkeshi: June 19, 1966; June 24,

1967. Konbumori: May 7, 1967. *Hidaka District*. Ikantai: Mar. 29, 1967. Horoizumi: Mar. 29, 1967. Higashitoyo: Mar. 29, 1967. Harutachi: Sep. 27, 1966. Erimo: Sep. 28, 1966. Samani: Sep. 28, 1966. Nishihirau: Sep. 28, 1966. Hamatoei: Sep. 28, 1966. Mitsuishi: Nov. 14, 1966. *Nemuro District*. Habomai: May 11, 1968. Nosappu: May 11, 1968.

In Herbarium Specimens (SAP)

No. 022017 Ketoi Isl., Kurile, Aug. 20, 1929 (by M. TATEWAKI & K. TAKAHASHI), No. 022040 Iema, Kurile, Aug. 1933 (by Y. YAMADA).

In Herbarium Specimens (SAPA)

No. 3750～3755, 5378 Sikotan Shima, July 1934 (by M. NAGAI), No. 5380 Kunashiri, Kurile, Aug. 1, 1929 (by M. NAGAI & M. SHIMAMURA), *without number* (12 sheets) Onnekotan, Kurile, Aug. 15, 1935 (by M. NAGAI), (several sheets) Shimushir, Kurile, Aug. 11, 1935 (by M. NAGAI), (one sheet) Ketoi, Kurile (♂), Aug. 20, 1929 (by M. TATEWAKI & K. TAKAHASHI), (two sheets) Urup, Kurile, Jan. 16, 1891 (by FUJIMURA).

Description

Thallus gregarius vel solitarius, planus, oblanceolatus aut spathulatus, interdum linearis, submembranaceus aut coriaceus, crassus, simplex vel in parte media usque raro semel dichotome ramosus, stipitatus vel estipitatus, haptero discoideo adhaerens substrato, 10～20 cm altus, 1.5～2.5 cm latus ad partem latissimam; hapteron 1 mm diam.; stipes teres, simplex vel ramosus, 0.5～1.0 mm diam.; frons basi cuneiformis, sensim sursum in apicem dilatata, apice acuta vel interdum obtusa, margine integra, pagina levis, in vetere planta proliferationibus numerosis, in sectione 350～510 μm crassa, ex stratis corticalibus et medullosis composita, in vetere thallo spissescens, strato corticale composito ex tribus aut quatuor seriebus cellularum perpendiculare ordinatarum, margine seriebus cellularum peculiare crassa, cellulis superficialibus dense pigmentiferis, in vallis disposita, fere quadrangulari, 8.3～11.2 μm alta, 5.6～9.7 μm lata, strato medulloso ex tribus aut quinque seriebus cellularum composita, hyalina, cellula centrali multiangulare rotunda, 120～280 μm diam.; pili absentes; tetrasporangia in soris hieroglyphioidibus supra paginis praeter partem infernam et marginem elevata, e superficiali corticali cellula terminale praesentia, cellula stipitata, cruciate divisa, oblonga, 49～53 μm longa, 21～27 μm. lata, inter paraphyses quatuor aut quinque cellularum posita; spermatangia in soris supra paginis dispersa, subterminale praesentia, oblonga aut elongata elliptica, 8.6 μm longa, 3.4 μm lata; cyatocarpia ignota; color in vivo purpureus aut atropurpureus, in sicco atropurpureus; specimina praeter partem superam thalli juvenis vix papyro adhaerentia. Perennis.

Thallus gregarious or solitary, flat, oblanceolate to spatulate, sometimes linear, submembranaceous to coriaceous, thick, simple or rarely branched once dichotomously in middle to upper portion, with or without stipe, adhering to substratum by means of discoid holdfast, 10～20 cm high, 1.5～2.5 cm wide at the broadest part; holdfast about 1 mm in diam.; stipe terete, simple or branched, 0.5～1.0 mm in diam.; frond cuneate at base, gradually broadened toward apex, acute or sometimes obtuse at apex, entire at margin, smooth at surface, with numerous proliferations in old plant, in section composed of cortical and medullary layers, 350～510 μm thick, cortical layer composed of three to four rows of cells arranged perpendicularly, at margin especially thick cell-rowed, superficial cells densely pigmented, arranged in palisade, almost tetragonal, 8.3～11.2 μm high, 5.6～9.7 μm wide, medullary layer composed of three to five rows of cell, hyaline, central cell polygonally round, 120～280 μm in diam.; hairs absent; tetrasporangia elevated in hieroglyphic sori on surface of thallus except for lower portion and margin, occurring terminally from superficial cortical cell, with stalk cell, cruciately divided, oblong, 49～53 μm in length, 21～27 μm in width, placedam ong paraphyses of four to five cells; spermatangia dispersed in sori similar to tetrasporangia, subterminal on spermatangial mother cell, oblong to elongate elliptical, 8.6 μm in length, 3.4 μm in width; cystocarps not known; color purple to dark purple in fresh, blackish purple in drying; specimens scarcely adhering to paper except for upper portion of young thallus. Perennial.

Habitat : Lower tidal zone on rocks.

Distribution : Pacific Coast of South Eastern Hokkaido (Nemuro et Hidaka Districts), Japan, and Kuriles.

Phenological Observation

This new species occurs along the Pacific Coast of Kushiro, Hidaka and Nemuro Districts of Hokkaido. The phenological observation was carried out at Aikappu at Akkeshi, the type locality of this species, near the Akkeshi Marine Biological Station, Hokkaido University, from June, 1966 to October, 1968. They grew on the rocky substratum in lower tidal zone gregariously or solitarily. The habitat was often covered with sand, and the basal portion of the plants were buried. In February, 1967 there were many germlings mostly 2～3～(4.5) cm high and 0.2～0.3～(0.7) cm wide, and also the old thalli with intact or partly eroded upper portions. The latter proliferated numerous new fronds from the margin as well as surfaces of the lower portion (Fig. 18 B). Both proliferations and germlings were similar in form and nearly equal in size. Most of the intact old plants had mature

tetrasporangial or often spermatangial sori. In April, the new thalli were mostly 3～5～(7) cm high and 0.5～1～(1.5) cm wide at the broadest part. They became gradually firm in substance but not fertile yet. There remained old plants bearing reproductive organs, though their number had decreased. In June the plants were most abundant in number. They were fully grown at about 10 cm high and 2.5 cm wide on an average and became very thick and firm in coriaceous texture. The larger plants collected were 13 cm high and 3.5 cm wide at the broadest part. However, there were no reproductive organs. The old intact plants with reproductive organs were scarce, except for the lower remainders of thalli with numerous proliferations. In August, 1967 and October, 1968, the plants showed no difference in growth to that of June. However, in December, 1967 they became fertile, bearing tetrasporangial or spermatangial sori in comparatively early stages of development. The plants were not so abundant at that time and were frequently eroded or torn partly at the upper portion. These fertile organs were confined only on the first-year fronds, proliferated or germinated. No cystocarpic plants were found through years.

Considering the above investigations, the plants seem to appear in February at Akkeshi area. They become most abundant from June to August and decrease in number before producing any reproductive organs. Both the tetrasporangial and spermatangial sori are produced after the luxuriant period of growth. The sori seem to appear after November, considering their developmental stages shown in December. Since December, however, most of the thalli are eroded from the upper portion. The lower fragments survive as remainders and proliferate new fronds in the next year. The fertile thalli of complete or partly eroded shapes remain until June of the next year. The tetrasporic plants are common but the spermatangial plants are rare in this area.

In Hidaka areas, on the other hand, the plants were encountered as numerous cast ashore thalli in September and November, 1966. They were characteristic in somewhat elongate slender form, showing 15～22 cm high, 1～2 cm wide. The habitats were exposed only in March when the lowest tidal level of the year occurs. At the time many young thalli 6～10～(13) cm high and 1～2 cm wide were growing in aggregation on rocky substratum stretched rather evenly. There were also lots of proliferations developed from the lower remainders of old thalli. The tetrasporangial and spermatangial sori were found on large intact thalli at the time. Young sori were encountered in September. In Hidaka areas they seem to appear in or earlier than February and grow in height rather rapidly during summer.

The reproductive organs, both sporangia and spermatangia, appear in late August or September (about 1～2 month earlier than in Akkeshi) and remain until the next year when the old intact thalli survive.

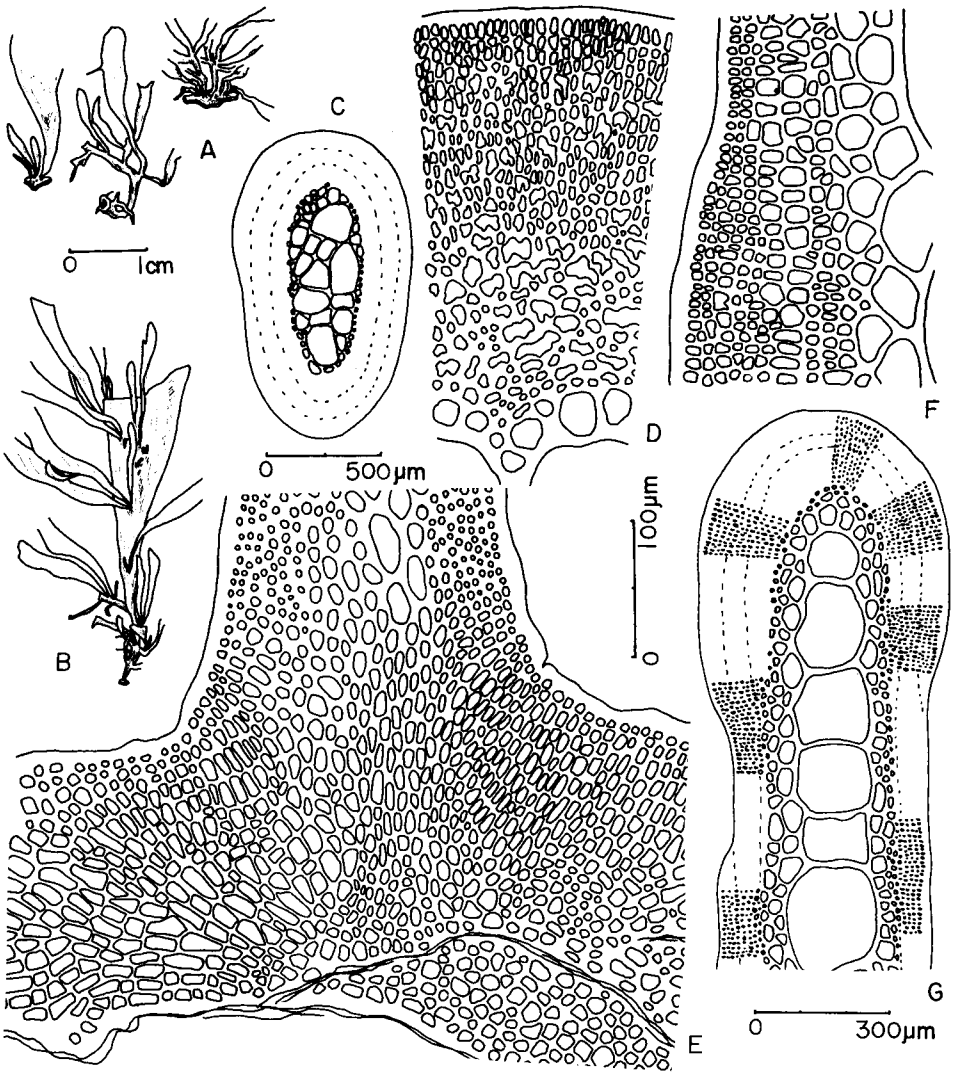

Fig. 18. *Palmaria marginicrassa* I. K. LEE

A, basal part showing holdfasts; B, proliferation of new fronds; C, stipe in transverse view; D, part of the same magnified; E, base in longitudinal view; G, thickening of cortex; F, part of the same magnified.

Morphological Observation

External Appearance

The plant is oblanceolate to spatulate or sometimes linear in shape. They do not vary the shape during the growth. The ramification occurs infrequently once dichotomously at the middle to upper portion of thallus. The branches extend with the divergence of 20°～40°, and are quite similar in shape to a simple thallus.

The apex is obtuse to acute. In young thallus less than 7 cm high, it is frequently round. The frond attenuates gradually to the stipe, which is scarcely discernible in first-year thalli but becomes cylindrical to slightly compressed in old thalli. The discoid holdfast erects a single frond at first, and several ones later. More often a few bases are piled one upon the other, extending more than 1 cm in diam.

The erosion or decay of thalli begin with the appearance of irregular pores on the upper portion of thallus where the reproductive organs were developed. The lower sterile portion less than 1 cm long survives through years, and becomes very thick. It proliferates numerous new fronds from the margin and surfaces. No proliferations are visible on soral areas of tetrasporangia and spermatangia. One old basal fragment, 1.3 cm long and 7 mm wide at the upper broadest part, bore 123 proliferations on both surfaces. About 75 of them were more than 3 cm long (Aikappu, June 1967). Four successive proliferations repeated one after another in the same plant (Aikappu, Apr. 1967). However, it is not clear whether the number of successive proliferations accords with the age of plant or not.

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers (Fig. 19 J, K). The cortical layer is composed of three to four rows of cells arranged perpendicularly to the surface. The superficial cortical cells are almost tetragonal with poor plastids and are somewhat compressed. They become thick walled as the thallus grows old.

The cortical layer at the margin of mature thallus is especially thick (Fig. 19 C). They become more than ten rows perpendicularly and four to five times thicker than the other cortical layer of the same plant. This is one of the important character of this species. In young plant, however, the cortical layer consists of a single row of polygonal cells arranged compactly (Fig. 19 A, D). There are annual ring-like stratifications in the cortical layer of old thallus as seen in *P. palmata*. One of them at lower portion of the thallus has four stratifications in the cortex which is more than 560 μm thick (Fig. 18 F, G).

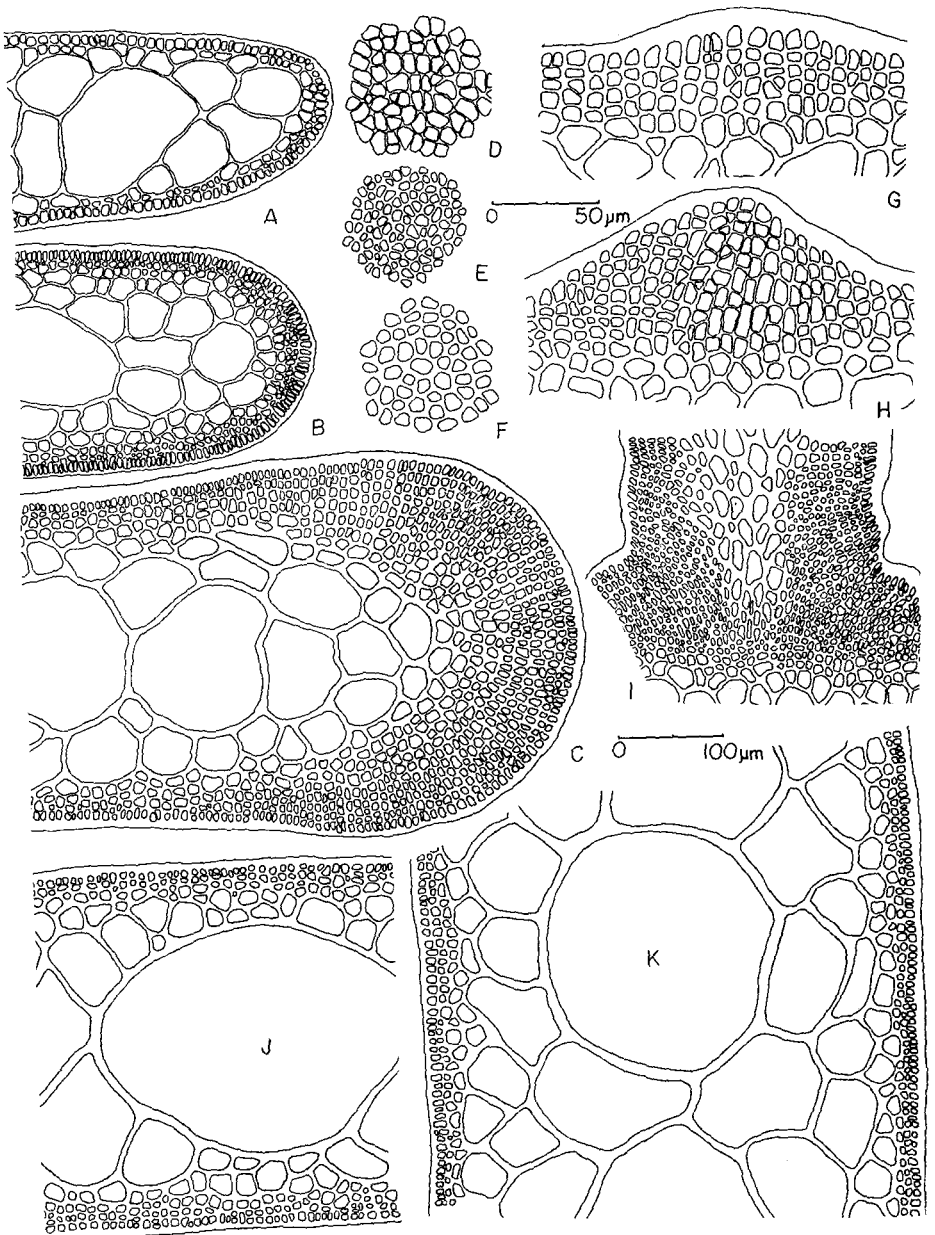

Fig. 19. *Palmaria marginicrassa* I. K. LEE

A–C, marginal portions of thalli in transverse view, being mature alphabetically; D–F, superficial cortical cells in surface view, being mature alphabetically; G–I, development of proliferation; J, mature thallus in transverse view; K, the same in longitudinal view.

The medullary layer is composed of three to five rows of cells. The cells in outer one to three rows are variable in size and slightly compressed. The outermost cells are scarcely distinguishable from the innermost cortical cells except for the latter containing comparatively poor plastids. The central one or two cells are very large, hyaline, polygonal to rounded and thick walled. Sometimes, they are replaced by a few small cells especially in the marginal portion. There is no difference in cell shape between transverse and longitudinal views (Fig. 19 J, K).

The discoid holdfast in longitudinal section is composed of perpendicularly arranged oblong to tetragonal cells. When it is piled one on the other, there remains the contacting border distinctly (Fig. 18 E). These bases extend broadly and protrude lots of fronds by transverse divisions of superficial cells in definite areas.

The hairs and rhizoid formation, or fusion of thalli were not found in this species.

Reproductive Organs

Tetrasporangia: It is also characteristic of this species that the soral area of tetrasporangia is elevated conspicuously and sterile branches of cells in the sorus are developed into paraphyses. Tetrasporangial sori are confined only to the first-year fronds. They are easily distinguished in the field owing to the soral areas pigmented with a blackish purple color. The tetrasporangia appear at first in middle to upper portion of the thallus and form hieroglyphic sori on both surfaces (Fig. 20 A). After maturation they extend over whole surfaces except for the margin and basal portion of the thallus. There remains a distinct boundary between the fertile and sterile parts (Fig. 20 B).

In cross section the tetrasporangia are developed terminally from the superficial cortical cell among sterile cell rows modified into paraphyses, and bear a stalk cell below. In early developmental stages the tetrasporangium-initial is elongated anticlinally and contains abundant protoplasmic substances compared with adjacent sterile cells. When it becomes about 20 μm high, it is divided periclinally into a young sporangium and stalk cell. The two are surrounded by a common wall. There is a large distinct nucleus in the sporangium. When the sporangium becomes about 25 μm high and 17 μm wide, it is divided periclinally and anticlinally, so that four tetraspores are formed cruciately (Figs. 20 E–G, 21 D–F). During the time the stalk cell becomes reverse pyramidal in form. A fully mature tetrasporangium is oblong and 49–53 μm in length and 21–27 μm in width, while the stalk cell is 7.0–9.7 μm high and 18–21 μm wide.

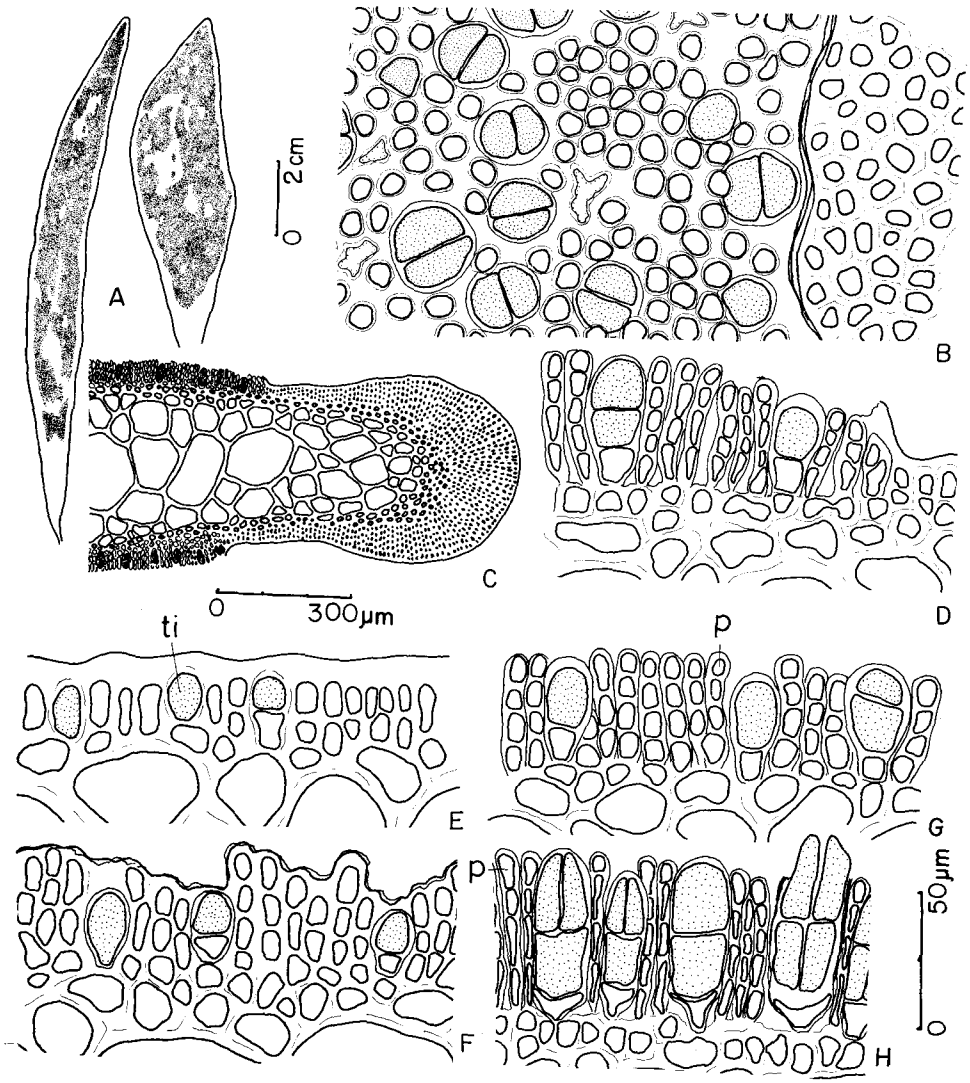

Fig. 20. *Palmaria marginicrassa* I. K. LEE

A, parts of tetrasporic plants bearing tetrasporangial sori; B, marginal portion of the sori in surface view, right being sterile cortex; C, the same in transverse view; D, part of the same magnified; E–H, development of tetrasporangia in transverse view.

ti: tetrasporangium initial, p: paraphysis.

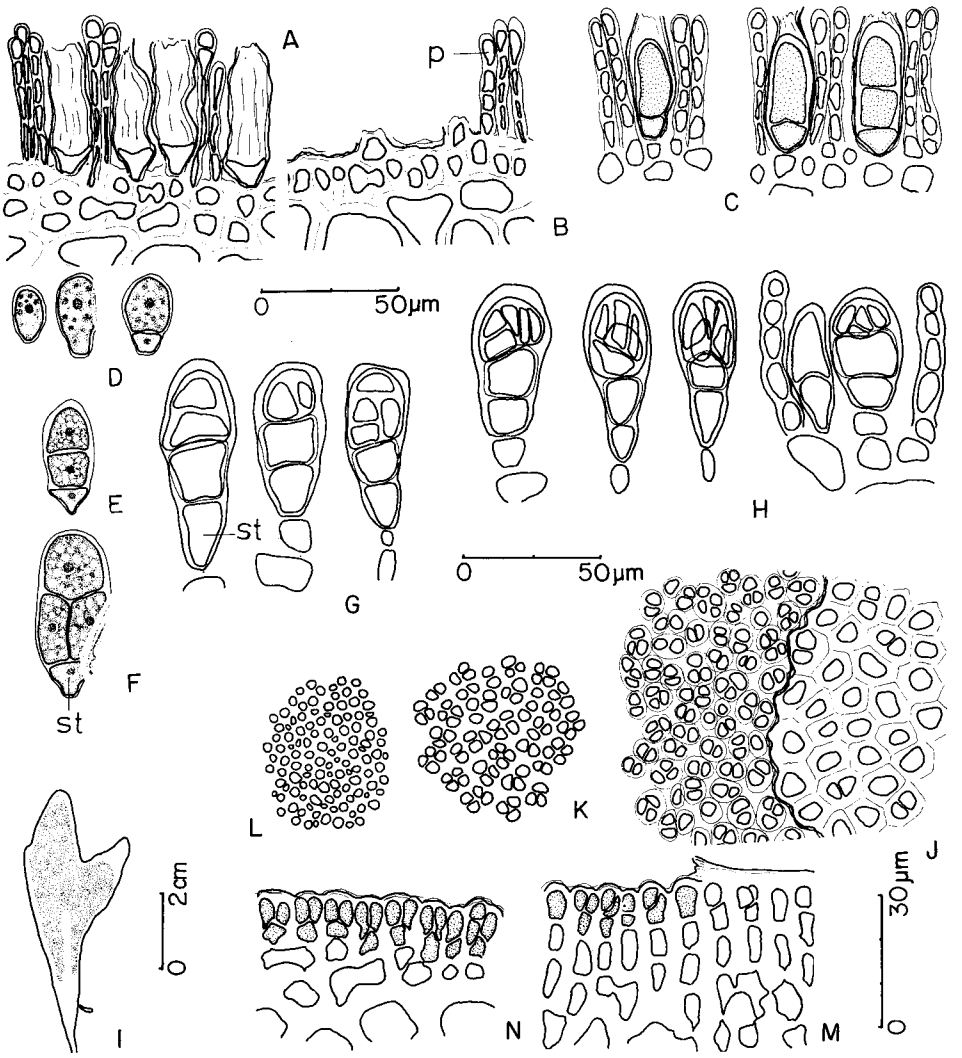

Fig. 21. *Palmaria marginicrassa* I. K. LEE

A–B, later stages in tetrasporangium formation, showing empty cavity and paraphyses; C, regeneration of secondary sporangia from stalk cell; D–F, development of tetrasporangia; G–H, germination of tetraspores *in situ*; I, part of male plant bearing spermatangial sori; J, marginal portion of the sori in surface view, right being sterile cortex; K–L, development of spermatangia in surface view; M, same as J in transverse view; N, formation of mother cells from superficial cortical cells.

st: stalk cell, p: paraphysis.

In the course of tetrasporangium formation the sterile superficial cortical cells in sori are elongated anticlinally and divided periclinally into two when the young sporangium and stalk cell are formed. Sometimes, there occur oblique divisions in the sterile cells so as to form two cells upwards. These superficial cells elongate more rapidly and repeat periclinal divisions to form four to five oblong cell-branches, which become paraphyses. All the cells of paraphyses are surrounded by a common wall, and plastids are not distinct in the cells.

The sterile branches are somewhat irregular in height at the beginning, and elongate more rapidly compared with adjacent tetrasporangial branches (Fig. 20 F). After the full growth, however, they become uniform in height (Fig. 20 G, H). In mature sorus the paraphyses become very slender except for their uppermost cells, and are 56~62 μm high. The superficial wall in soral area is ruptured and shed when these sterile branches are modified into paraphyses.

After the liberation of spores, a new sporangium is developed not rarely from the stalk cell (Fig. 21 C). When the regenerated sporangium formation is discontinued, the stalk cells and tetrasporangial walls are shed before the erosion of thallus (Fig. 21 B).

Germination of tetraspores *in situ* was frequent in the materials collected from Hidaka areas (Fig. 21 G, H). However, all of them were in early developmental stages. The division is repeated only from the two upper spores, showing four- to rarely eight-celled stages. One of the plants investigated shows that of 1,350 tetrasporangia only 1% remain without division *in situ*.

Spermatangia: Spermatangial sori are also confined to the first-year fronds. They appear and extend on thallus surfaces similar to tetrasporangial sori (Fig. 21 I). When the thallus develops spermatangia, the soral area becomes brownish purple in color. On microscopic observation from the surface, a distinct border between the fertile and sterile areas is formed (Fig. 21 J). All the superficial cells in the sorus are converted into fertile ones.

In cross section two spermatangia are developed subterminally on a mother cell. The spermatangia originate from the superficial cortical cell. As the cell is elongated about two times as high as wide, it cuts off obliquely two upper cells, which become spermatangial mother cells. The lower cell remains as a basal cell of the mother cells (Fig. 22 E). Frequently one or both of the mother cell cut off again two cells upwards which become also the mother cells (Fig. 22 I).

As the spermatangial mother cell becomes about 6.3 μm high, a spermatangium is protruded from its top modified into narrow and round shape (Fig. 22 G). The spermatangium and mother cell are surrounded by a common wall. A fully mature spermatangium is oblong to elongate elliptical and 8.6 μm long and 3.4 μm wide, while the mother cell is oblong and 6.8 μm high and 2.8 μm wide. The second spermatangium is protruded sooner or later on the same mother cell beside the first (Fig. 22 H, I). Sometimes,

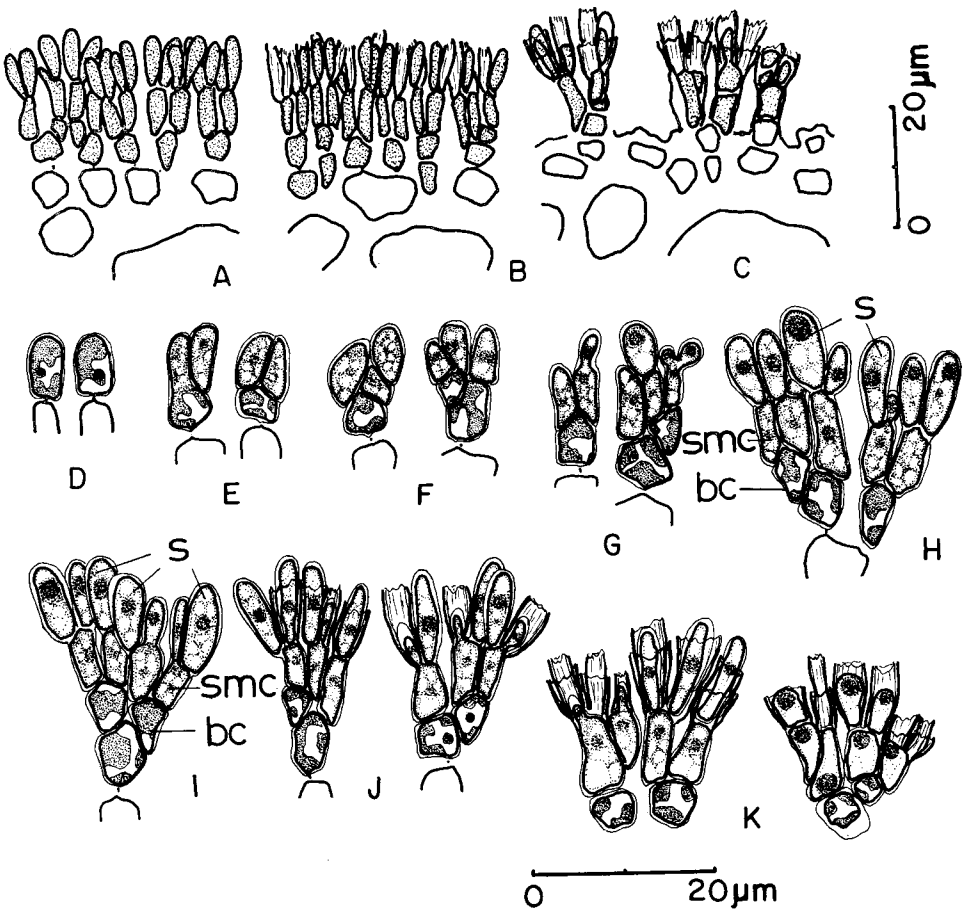

Fig. 22. *Palmaria marginicrassa* I. K. LEE

A–C, development of spermatangia from mother cells; D, superficial cortical cells; E–F, formations of mother cells from cortical cells; G–I, development of spermatangia from mother cells; J, formation of secondary spermatangia; K, later stage in spermatangium formation.

s: spermatangium, smc: spermatangial mother cell, bc: basal cell.

these two primary spermatangia become almost the same size. The mature spermatia are liberated, conveying all the contents, leaving behind an empty cavity. The spermatium is surrounded by a fine protoplasmic membrane and has a large nucleus and vacuoles.

The secondary spermatangium is formed within the cavity of previous wall. It is generally slender especially in the early stage of development. In addition there is formed a tertiary spermatangium within the previous two cavities (Fig. 22 K). There are no plastids in the mother cells, spermatangia and spermatia, but plastids are observed in basal cells rather distinctly.

During the formation of spermatangial mother cells, the superficial wall of the thallus in soral area is shed, leaving a distinct border (Fig. 21 M). The mother cell becomes poorer in contents as it protrudes more spermatangia. When spermatangium formation is discontinued, the mother cells become hyaline in contents. Frequently the inner cortical cells are exposed by losing these mother cells and basal cells (Fig. 22 C).

Discussion

This new species is a well defined taxon of *Palmaria* because of a stalk cell formation of tetrasporangia and lack of the female thallus in life history, as defined by GUIRY (1974). It approximates very much *P. palmata* (L.) O. KUNTZE, not only in outer appearance but in anatomical character of the thallus. Especially when the cortical layer is thickened as the thallus becomes old, it is very difficult to discern *P. marginicrassa* from *P. palmata* only by the vegetative structure. The development of proliferations is similar in both. However, compared with *P. palmata*, this species is distinguished by a cortical layer thickened specially at the margin. The formation of paraphyses in tetrasporangial sori and two subterminal spermatangia on a mother cell are also characteristic of the plant.

At present this plant was found in Japan only along the Pacific coast of Hokkaido from Hidaka to Nemuro Districts. However, according to herbarium specimens in both SAP and SAPA, it seems to be distributed from middle to southern Kuriles, too. Especially in SAPA, lots of herbarium specimens collected from Kuriles and determined as *H. firmum* by NAGAI are this new species.

Rhodymenia GREVILLE (1830)

GREVILLE (1830) erected the genus *Rhodomenia* with sixteen species known mostly as members of *Sphaerococcus* and *Halymenia*. The generic

name was corrected later orthographically as *Rhodymenia* by J. AGARDH (1852), accepting the suggestion of MONTAGNE (1839).

The genus is characterized by flat, branched and sometimes proliferated fronds, two to four rowed small cortical cells outwards and large medullary cells inwards. Cystocarps are elevated from the thallus surface and have a surrounding pericarp. The carposporangia are converted from almost all the gonimoblast cells. Tetrasporangia occur terminally in the cortical layer and are divided cruciately.

J. AGARDH (*l. c.*) divided this genus into two sections, *Palmatae* and *Palmettae* (=*Rhodymenia*), based on the occurrence of tetrasporangia scattered or aggregated, and then (1876) into three, adding a new section *Clinophora* with the character of sterile cells in tetrasporangial sori. DAWSON (1941), in his monographic study, divided this genus into two subgenera, *Eurhodymenia* (=*Rhodymenia*) and *Dendrymenia*, and five sections, *Pertusae*, *Palmatae*, *Palmettae* (=*Rhodymenia*), *Clinophora* and *Dendrymenia*, with about 46 species. He revised J. AGARDH's key to the sections adding the character of the modification of the cortex in tetrasporangial sori, and adopted newly the branching habit of stipe and the occurrence of stolons for the separation of subgenera. According to him, *Dendrymenia* SKOTTSBERG (1923) was reduced to a subgenus of *Rhodymenia*, which was accepted by SPARLING (1957), but not by TAYLOR (1945, 1960) and KYLIN (1956).

Some important further investigations on the genus under discussion were carried out by several workers, such as SJÖSTEDT (1926), KYLIN (1930, 1931), SPARLING (1957), and TOKIDA & MASAKI (1959).

Rhodymenia intricata (OKAMURA) OKAMURA

(Text-figs. 23～29 : Plate III, A-C)

(1930 a) Icon. Jap. Alg. VI, p. 23, pl. 267. OKAMURA (1930 b) p. 96 ; (1934) p. 16 ; (1936) p. 677 ; INAGAKI (1933) p. 48 ; SEGAWA (1938) p. 147 ; TAKAMATSU (1939) p. 66 ; DAWSON (1941) p. 138 ; OHSHIMA (1950) p. 116 ; KANG (1966) p. 86 ; FUNAHASHI (1967) p. 31 ; LEE & KUROGI (1968 b) p. 285, figs. 1～3.

Phyllophora intricata OKAMURA (1921) p. 129, pl. 182, figs. 1～8.

Phyllophora palmettoides J. AGARDH, YENDO (1916) p. 59 (as to material only).

?*Fauchea repens* (J. AG.) Mont., OKAMURA (1916) p. 47 (as to material only).

Japanese Name : *Masagoshibari* (OKAMURA)

Type Locality : Izu, Pacific Coast of Honshu, Japan.

Materials

Shiribeshi District. Oshoro : June 13, July 11, Sep. 11, Oct. 7, Nov. 10, 1966. Feb. 11, June 16, July 7, 16, Aug. 3, 17, Sep. 18, Nov. 14, Dec. 18, 1967. Jan. 24, Mar. 28, Apr. 14, Sep. 3, 1968.

Description

Thallus procumbent to decumbent, flabellate, forming intricate semicircular to circular mass, flat, membranaceous, entire, branched three to five times dichotomously or subpalmately, stipitate, attaching to substratum by means of stoloniferous holdfast, 2.5～4 cm high, 2～6 mm wide at the broadest part ; holdfast discoid, 1～2 cm in diam. ; stipe cylindrical, branched frequently 0.5～1.2 mm in diam. ; branches gradually or abruptly expanding upward, sometimes almost broadly linear, 5～12 mm long, 2～6 mm wide at the broadest part, spatulate to obcordate and 2～4 mm wide in terminal segment, sometimes protruding branchlets at margin, attaching to each other at contacting portion ; stolons protruding from holdfast, stipe or frond margin, intricate ; rhizoids developed at stolon and frond irregularly ; frond in section composed of cortical and medullary layers, 120～150 μm thick, cortical layer composed of one to three rows of cells, densely pigmented, superficial cells small, round to anticlinally elliptical, not arranged in palisade, connected obliquely with inner cells, 4.2～5.6 μm high, 2.8～4.2 μm wide, inner cells almost round, medullary layer composed of four to eight rows of cells, hyaline, medullary cells gradually increasing in size inwards, round to elliptical, elongate longitudinally, central cells 28～30 μm high, 35～42 μm wide, 70～90 μm long ; tetrasporangia occurring on both surfaces of apical portion of terminal branch, forming round to semicircular sorus, developing from inner cortical cells intercalarily or terminally, without stalk cell, divided cruciately, elliptical to oblong, 34～39 μm in length, 15～18 μm in width ; spermatangia occurring in sorus similar to tetrasporangia, developed terminally or subterminally on mother cells, almost elliptical, 3.1 μm in length, 2.3 μm in width ; cystocarps scattered solitary or occurring together but not so many on both surfaces of upper margin of branches, elevated, mammiform, sessile, 680～770 μm high, 600～690 μm wide, carpogonial branch two-celled, carposporangia round to polygonal, 19～23 μm in diam. ; color bright red when fresh, dark red in drying ; specimens scarcely adhering to paper. Perennial.

Habitat : Lower tidal zone on rocks.

Distribution : Pacific Coast of Japan, Japan Sea Coast of Hokkaido and Korea.

Phenological Observation

The plant was investigated in Oshoro Bay. The periodic observation

was performed at the plain rocky substratum shadowed by the cliff in the lower tidal zone. The plants inhabited a small pool of about 1 m diam. and 50 cm depth, and grew gregariously all around the declining margin of the pool, in stratified layers, overlapping and intricate. There were no plants at the bottom. The stipe and stolons were immersed sponges covering the substratum.

The investigations were carried out monthly from June, 1966 to September, 1968. In June, 1967 there appeared germlings less than 1.0 (max. 1.5) cm high from discoid bases or intricate thread-like filamentous stolons. A few large plants had already secondary branches and often undulated margin. A few male thalli had already spermatangial sori in early developmental stages. Some old plants, remainders of previous year, were a dark purple color. They protruded lots of stolons and broadly linear proliferations at the margin. In July the plants were mostly 2～3 mm wide and 1.2 cm high and had occasional secondary branches. Some thalli collected in mid-July issued tertiary branches. Most branches became elongate and almost uniform in width throughout. They issued stolons rather frequently. Male thalli had fully mature spermatangial sori, while tetrasporic plants bore the sori in early developmental stages. In August they were fully grown and expanded in semicircular to circular form to 3.5～4 cm diam. They formed intricate mass with radially issued stolons and overlapping fronds. The rhizoid formation from the frond surfaces, margin and stolons made them more intricate. Fully mature spermatangia and tetrasporangia were rather common, while young cystocarps began to appear in early August. Several thalli encountered in mid-August had roundly ruptured pores beneath the apex where spermatangial or tetrasporangial sori occurred. In September there was no special difference in growth from that of August, except for the appearance of mature cytocarps. In November they were worn away or eroded from the margin of outer branches. Especially the apical portion developing tetrasporangial or spermatangial sori were eroded more rapidly. The spermatangial sori were scarcely found after that time. In December most of them had only lower fragments with dark purple color. No fertile thalli were found from that time. The plants collected in January and March, 1968 were these remainders. During the winter time they were olive green in color.

Considering the above investigations, this plant in Oshoro Bay seems to appear in late May to June and becomes luxuriant from July to September. After October they decrease gradually in number, and remain with lower segments through the winter. However, many of them survive until next

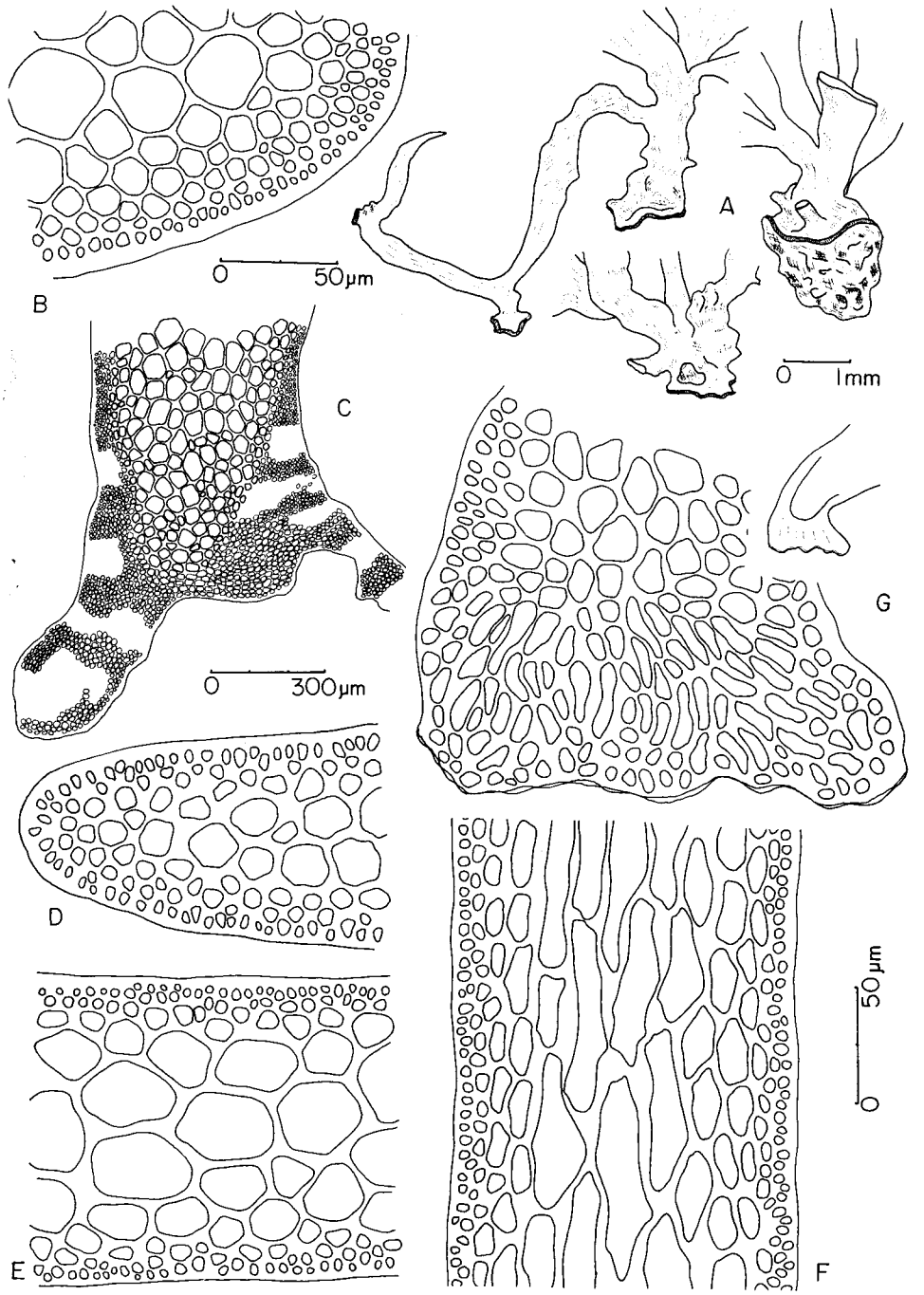

Fig. 23. *Rhodymenia intricata* (OKAMURA) OKAMURA

A, basal part showing holdfast, upper left developing stolon and rhizoids; B, part of stipe in transverse view; C, base in longitudinal view; D-E, fronds in transverse view, D being margin; F, the same in longitudinal view; G, rhizoid in longitudinal view.

year when the new germlings appear, and refresh themselves protruding stolons and proliferations. The tetrasporangia appear after July and remain until November, while spermatangia appear in June, soon after the appearance of new fronds, and remain until October. Cystocarps appear after August and remain until October. Tetrasporic plants are most common among the fertile thalli, and female plants considerably more rare.

Morphological Observation

External Appearance

The plant appears in oblanceolate to spatulate form at first. The frond is developed from discoid base or intricate filamentous stolons. The primary branches are issued dichotomously from the upper portion. The secondary

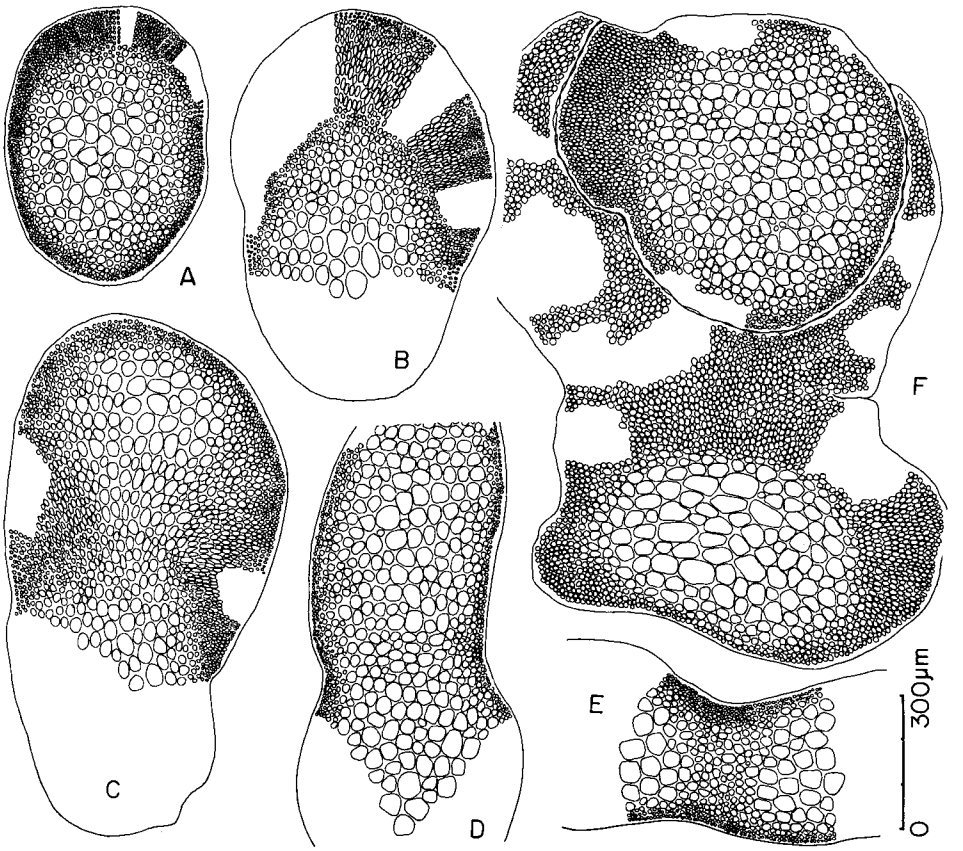

Fig. 24. *Rhodymenia intricata* (OKAMURA) OKAMURA
A–E, stipe in successive transverse views at ramified portion; F, attachment of stolons mutually, cortex developed from one part.

and tertiary branches are dichotomous, trichotomous or subpamlate and expand rather widely, and the further branches, not so common, remain as small ramuli. The branches are constricted slightly below the ramification. The basal segment expands upwards with divergence of 45°~90°, or almost horizontally. The branch axil is round to acute, or mostly obtuse. The primary branches are short, and reverse pyramidal in shape, but the others are elongated and uniform in width throughout. In mature thalli, these branches overlap and form a semicircular to circular plane. There occurs commonly the attachment of fronds at contacting portions, so that they become more intricate (Fig. 25 B-C).

The stipe is cylindrical and simple in young thallus. There appear later lots of stolons from the holdfast directly or from the margin of old fronds. They develop rhizoids in various intervals at attaching portions to the substratum or to the frond surfaces (Fig. 25 A). The terminal portion of the changes frequently into a frond (Fig. 23 A). The holdfast is large and complicated by producing such stolons. Sometimes, it is difficult to discern the orginal base from the disc of rhizoids in mature thallus.

Structure of Thallus

The thallus consists of outer cortical and inner medullary layers (Fig. 23 E). The cortical layer is composed of irregularly arranged one to three rows of small cells pigmented densely. The superficial cells are arranged not in palisade, nor compactly. They are round to anticlinally elliptical and connected with inner cells obliquely. On microscopic observation from the surface, they are longitudinally elliptical, and provide wide intercellular spaces (Fig. 26 B). The inner cortical cells are round and arranged sparsely. Some of them are not connected with superficial cortical cells, and exposed to the surface. They are about two times as large as the superficial cells. In longitudinal section, these inner cells are elongated periclinally, about two times as long as broad.

The medullary layer is composed of four to eight rows of hyaline and somewhat thick walled cells, which are polygonally round to elliptical and increase in size rapidly inwards. Central cells in two to three rows are hyaline and large. In longitudinal section, medullary cells are elongated periclinally in various lengths. The central cells are about five to six times as long as broad, while the outer cells about two times (Fig. 23 F). There occurs no thickening of the medullary layer when the thallus becomes old.

The discoid holdfast in longitudinal section is composed of slightly compressed tetragonal to polygonal cells arranged compactly in perpendicular

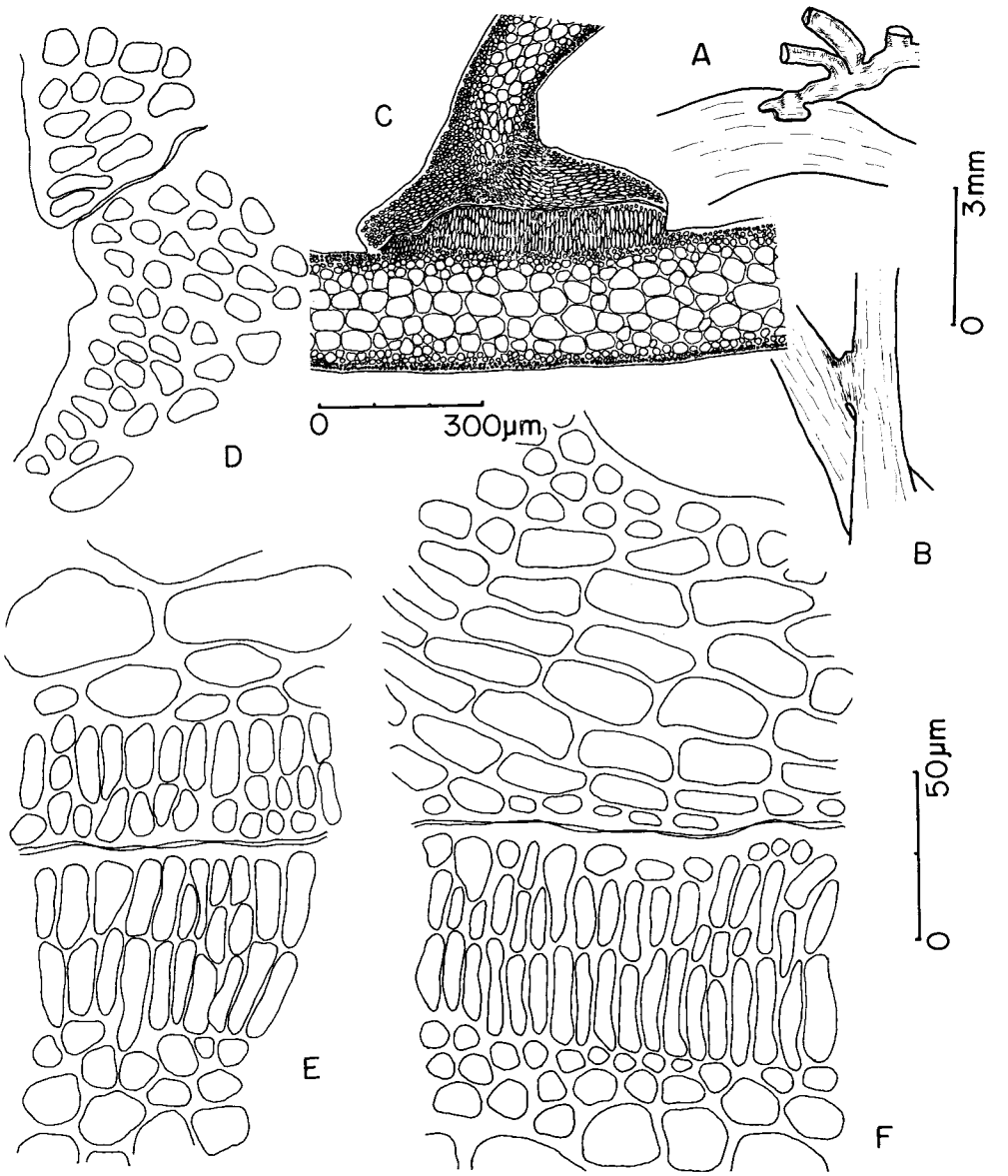

Fig. 25. *Rhodymenia intricata* (OKAMURA) OKAMURA

A–C, attachment between two fronds, C being longitudinally sectioned upper and transversely sectioned lower fronds; D–F, parts of the same magnified, D being margin, E and F being inner portions.

rows to the surface. The medullary layer expands upward parabolically in outline from the central portion soon above the base (Fig. 23 C).

When the stipes and stolons contact one another, the cortical cells at the areas are divided perpendicularly in order to attach mutually. Sometimes, the divisions occur only on one side, and the divided cells envelop opposite ones (Fig. 24 F). No protoplasmic connections are formed between them. When the attachment occurs between two fronds, mostly between margin and surface, the cortical cells of one of the tissues at the contacting margin are divided successively and arranged in perpendicular rows to the surface of opposite frond of which cortical cells are divided only once or twice (Fig. 25 C–F).

The formation of rhizoids is essentially similar in anatomy to the attachment of fronds (Fig. 23 G). In this case, however, the cortical cells are divided and arranged in irregular rows. Then, they are elongated to various lengths, expanding roundly on the substratum. The cells of rhizoids lose pigments and become pale.

The stipe becomes thicker as the thallus grows. In old thallus there appear stratifications in cortical layers formed by intermittent cell divisions, as seen in *Palmaria palmata* and *P. marginicrassa*. One stipe of 600 μm diam. had three ring-like stratifications consisting of three to five or more rows of cells. It is not clear whether these stratifications represent survival years of the plants or not.

No hairs are observed in this species.

Reproductive Organs

Tetrasporangia : The tetrasporangial sorus appears almost at the same time on both surfaces of apical portions of ultimate branches, and becomes round to oblong in outline. After full maturation the sorus extends all over the apical area except for the margin. A large sorus examined was 4.5 mm in diam. Sori are similar in shape and size on both surfaces of the same apex, or sometimes different from each other (Fig. 26 A right). The soral area is discerned easily by a dark purple color and slightly swollen feature.

The tetrasporangium is homologous to an inner cortical cell. It occurs intercalarily to terminally in the cortical cell rows. In cross section, the tetrasporangium-initials are discernible by densely stained contents, a large nucleus and an elliptical to oblong shape. Frequently they bear obliquely divided small terminal cells corresponding to superficial cortical cells (Fig. 26 I, J). When they are elongated to about 25 μm high, periclinal division occurs centripetally at the middle portion, followed by the anticlinal division before the completion of the previous division. Thus, the tetraspores are formed

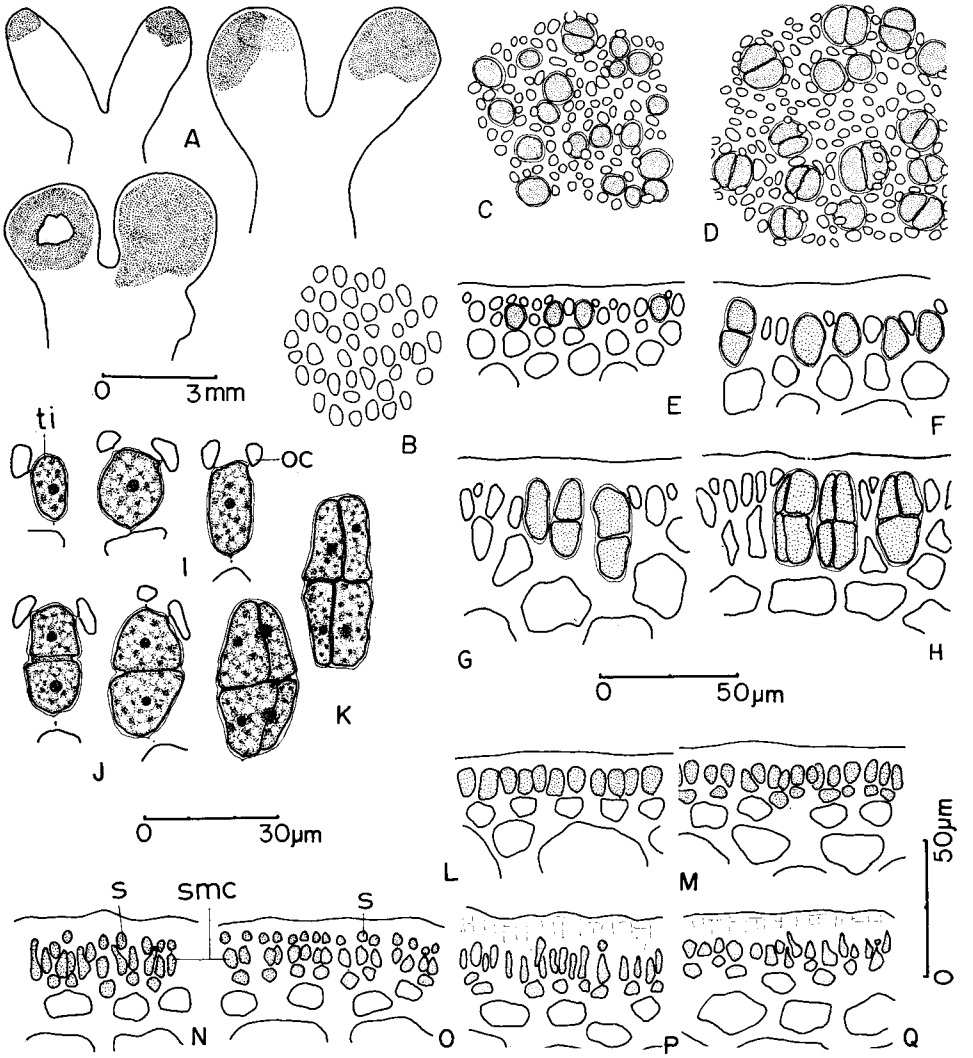

Fig. 26. *Rhodymenia intricata* (OKAMURA) OKAMURA

A, part of fronds with tetrasporangial sori, right showing not coincident development of sori on both surfaces; B, sterile cortex in surface view; C–D, development of tetrasporangia in surface view; E–H, the same in transverse view; I–J, some intercalary tetrasporangia, bearing pit-connections with outer cortical cells; K, mature tetrasporangia; L, elongation of superficial cortical cells; M, formation of spermatangial mother cells; N–O, development of spermatangia terminally or subterminally on mother cell; P–Q, later stages of spermatangium formation.

oc: outer cortical cell, ti: tetrasporangium-initial, s: spermatangium, smc: spermatangial mother cell.

cruciately. A mature tetrasporangium is elliptical to oblong, and 34～39 μm in length and 15～18 μm in width. When the sporangium is mature fully, the pit-connections with outer terminal cortical cells become very difficult to discern.

There is no stalk cell of the sporangium. In sporangium formation the sterile cortical cells in the sorus are elongated anticlinally. The inner cells become irregularly angled oblong, while the outer cells are elongate oblong to oblanceolate in form (Fig. 26 E-H). As a result, the cortical layer in soral area becomes thick but almost even.

Spermatangia: The spermatangium formation was reported by LEE & KUROGI (1968 b). Spermatangia are developed early before the thallus becomes large. The smallest spermatangial plant was 7 mm high and 1.5 mm wide (July 1967). The sori appear and extend quite similarly in the manner of the tetrasporangial sori. The soral area becomes somewhat reduced in color.

In cross section, one or two spermatangia are protruded on a mother cell terminally or subterminally. They originate from superficial cortical cells. When the cortical cell is enlarged to about 7.4 μm high, it is divided obliquely into two to three spermatangial mother cells upwards and a basal cell below. The mother cells, however, cut off frequently a secondary mother cell obliquely upwards. Thus, the primary and secondary mother cells are seriate side by side with pit-connection. Sometimes, the primary is divided into two secondary mother cells upwards and a basal cell below.

The spermatangium is protruded from the top of mother cell by a centripetal constriction, leaving a pit-connection with the mother cell. There is no common wall to surround the two cells. In addition, some mother cells protrude a second spermatangium beside the first. A mature spermatangium is ovate to elliptical, and about 3.1 μm in length and 2.3 μm in width, while the mother cell is about 5.2 μm high and 2.3 μm wide. During the spermatangium formation, the mother cell loses plastids before the protrusion of spermatangium. No plastids are observed in spermatangia and spermatia. When the spermatangium is fully mature, the pit-connection with mother cell is cut. The spermatangium migrates through the superficial wall of the thallus, where the spermatangial wall seems to be ruptured. The superficial gelatinous wall of the thallus is not shed in this species.

The secondary spermatangium is developed from the top of the same mother cell after the liberation of primary one. It is distinguished from the previous spermatangium by the presence of a trace of the previous pit-connection. The tertiary spermatangium formation is not rare. Sometimes,

two or three spermatangia are arranged in a row within the superficial wall. The mother cells become poorer in contents and slenderer in form

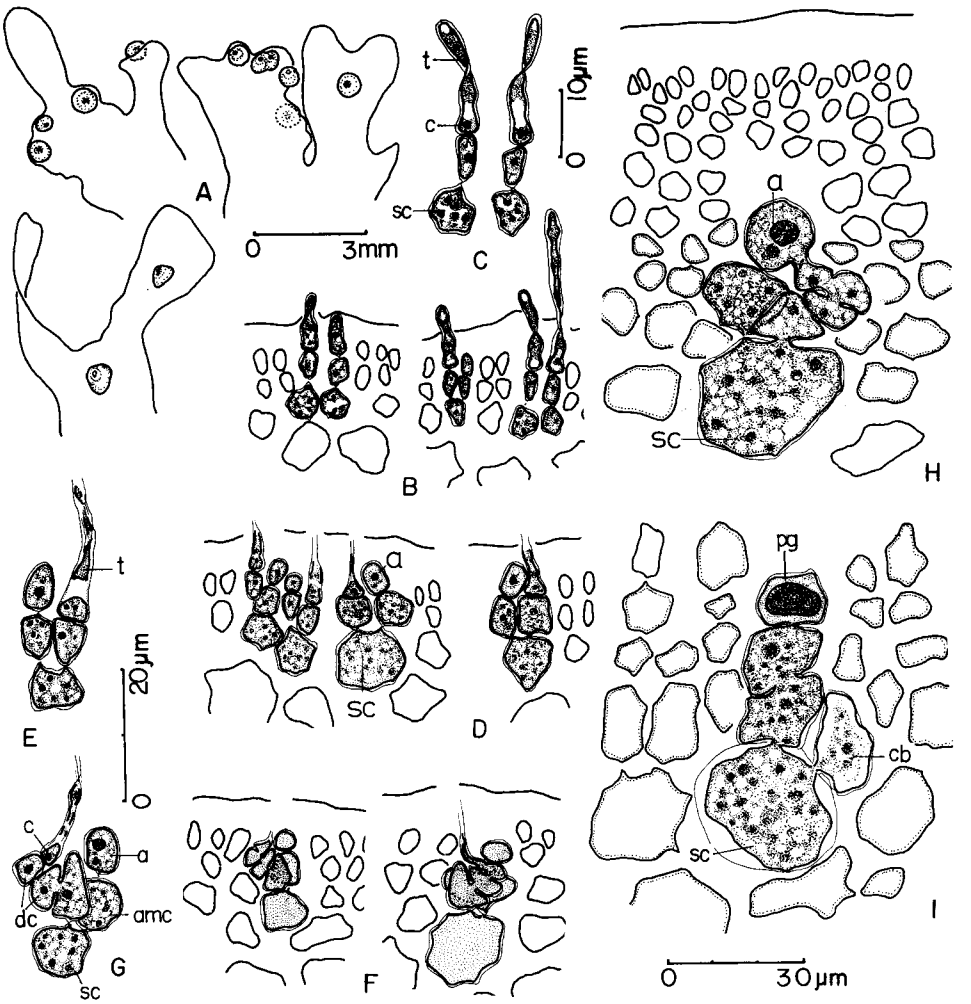

Fig. 27. *Rhodymenia intricata* (OKAMURA) OKAMURA

A, part of female thalli with cystocarps; B–C, carpogonial branches and supporting cells; D–E, degeneration of trichogyne, showing auxiliary cell branch; F–G, cutting off two cells between carpogonium and hypogynous cell; H, fusion between auxiliary cell and carpogonial branch; I, cutting off primary gonimoblast cell containing large protein body.

c: carpogonium, t: trichogyne, cb: carpogonial branch, sc: supporting cell, a: auxiliary cell, amc: auxiliary mother cell, cc: cells divided from carpogonium and hypogynous cell, pg: primary gonimoblast cell.

as they protrude more spermatangia. Spermatangial mother cells remain empty after final discharge of spermatangia. The soral area is later eroded and shed. There remains only a round hole.

Cystocarps: As mentioned previously, the cystocarpic plants appear rarely at Oshoro. A female thallus produces several cystocarps only. Almost all the cystocarpic plants encountered were small (1 to 2.5 cm) in height. Cystocarps are confined to the upper portion of branches, as described by OKAMURA (1930) and INAGAKI (1933). They appear solitarily or often together. The cystocarp is sessile, elevated mammiform. It is 680~770 μm high and 600~690 μm wide and bears a carpostome of 60~100 μm diam.

As seen in transverse section of the thallus, the carpogonial branch at first consists of two cells, which are anticlinally straight to the surface (Fig. 27 B-C). They are abundant at the margin of branchlets in groups of more than twenty. Only one or rarely two of them develop cystocarps. The supporting cell is homologous to inner cortical cells. It is quite similar in size to the adjacent sterile cells, except for its dense and homogeneous contents and multi-nuclei. The first cell of the carpogonium is almost oblong. It is a half to two third times as large as the supporting cell, and contains also dense and homogeneous cytoplasmic substances but a single nucleus. The carpogonium is reverse wedge-shaped, and similar in width to hypogynous cell. The trichogyne protruded is without constriction at the base. It is somewhat flat and twisted once or twice. A long trichogyne is more than 40 μm.

The two-celled auxiliary-cell branch is not discernible until the trichogyne disappears. The auxiliary mother cell is connected with the supporting cell. Except for containing a few nuclei, it is similar in shape to the hypogynous cell at first. The auxiliary cell divided from the mother cell is elliptical to oblong with a large nucleus and almost same in size to the mother cell at first (Fig. 27 D-E). A round protein body (cf. KYLIN 1930, p. 33) is observed in the auxiliary cell.

After the presumed fertilization, the cytoplasm between carpogonium and the trichogyne is separated. The trichogyne begins to disappear. During this period, the supporting cell, auxiliary mother cell and hypogynous cell are enlarged rapidly, while the auxiliary cell and the carpogonium enlarge more slowly. The supporting cell contains many nuclei and sinks inward to the medullary layer. The hypogynous cell and the auxiliary mother cell become almost round (sometimes the former is tetragonal). Then, the hypogynous cell is divided into two. The carpogonium is divided transversely also into two after the elongation. There is one nucleus in each of these

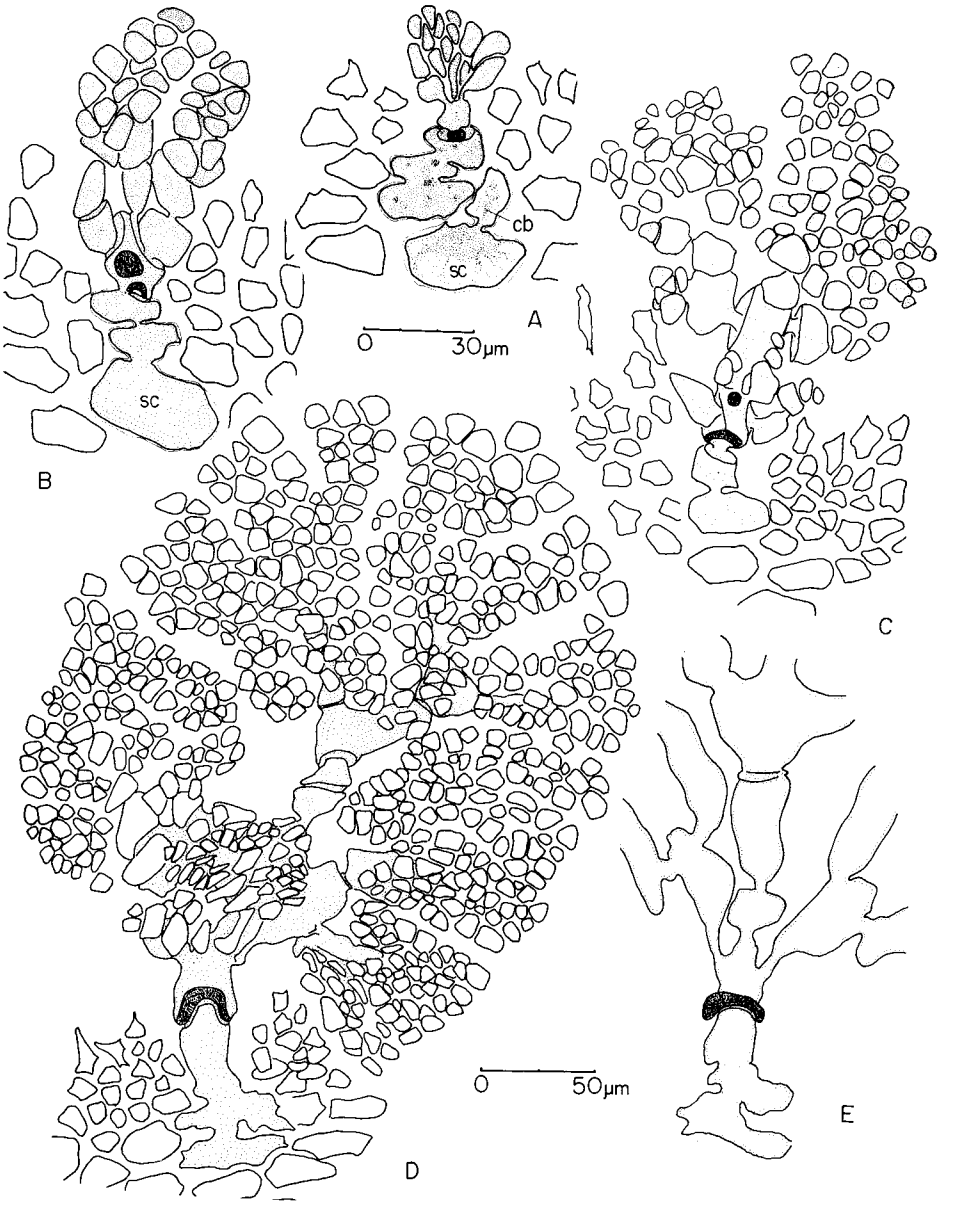

Fig. 28. *Rhodymenia intricata* (OKAMURA) OKAMURA

A–C, development of gonimoblast in early stage; D, young carposporophyte; E, fusion cell of a mature cystocarp.

sc: supporting cell, cb: carpogoninal branch.

cells. As a result, the carpogonial branch becomes four-celled and is curved slightly (Fig. 27 F-G).

The cells of the carpogonial branch enlarge pit-areas gradually. The carpogonium coalesces with the auxiliary cell. The presumed diploid nucleus seems to migrate to the latter. In this pose, these fertile cells remain for a long while, enlarging the volume more (Fig. 27 H). Then, the cells of carpogonial branch form an irregularly shaped single fusion cell, whose contents gradually disappear. There occurs no fusion, however, between this fusion cell and the supporting cell.

The primary cell of the gonimoblast is cut off transversely from the distal end of the auxiliary cell and its contents contain the protein body. This body becomes so large as to occupy whole the space of the cell (Fig. 27 I). About three secondary cells of the gonimoblast are cut off obliquely from the upper corners of the primary gonimoblast, in turn. The succeeding cells of gonimoblast are developed from these cells, so that they form a young carposporophyte (Fig. 28 A-B). In this stage the protein body is always in the primary gonimoblast cell. The supporting cell and the auxiliary mother cell are somewhat compressed and surround by a thick wall. The auxiliary mother cell develops many secondary pit-connections with adjacent sterile cells around it.

The young carposporophyte is generally obovate in outline. Early cells of the gonimoblast become very large, and widen the pit-areas. Carposporangia are formed from outer cells of the goimoblast one by one. Later, almost all the cells of gonimoblast are converted into carosporangia. The carposporangium is somewhat small and almost round of 19～23 μm diam. In a fully mature carposporophyte, the supporting cell, auxiliary mother cell, auxiliary cell and the primary gonimoblast cell form a large column-like fusion cell. The joining areas of these cells, especially in early gonimoblast cells are constricted very much (Fig. 28 E). The protein body disappears during the maturation of the carposporophyte, however there appears a deeply stained pectinaceous ring (cf. KYLIN 1940) at the basal margin of the primary cell of the gonimoblast.

In the carposporophyte formation the sterile cortical cells near by have abundant contents and begin to divide transversely when the carpogonial branch becomes four-celled after fertilization. Then, they are arranged perpendicularly to increase cell rows. The cortical layer increases gradually. When the primary cell of the gonimoblast is cut off, a dome shaped pericarp and pericarpic cavity are formed by the rupture between lower nutritive cells and upper cells forming the pericarp. The cystocarp becomes spherical

to hemispherical. The rostrum is protruded slightly after maturation.

A mature pericarp consists of cortical and medullary layers (Fig. 29 C). The cortical cells are pigmented and arranged loosely in two rows, while the medullary cells are hyaline and arranged in five to seven irregular rows and bear pit-connections radially. The medullary cells are somewhat modified and increase in size inwardly. The pericarp around the carpostome is composed of very small and round cells. The pulvinus is poor at the base of cystocarp (Fig. 29 A).

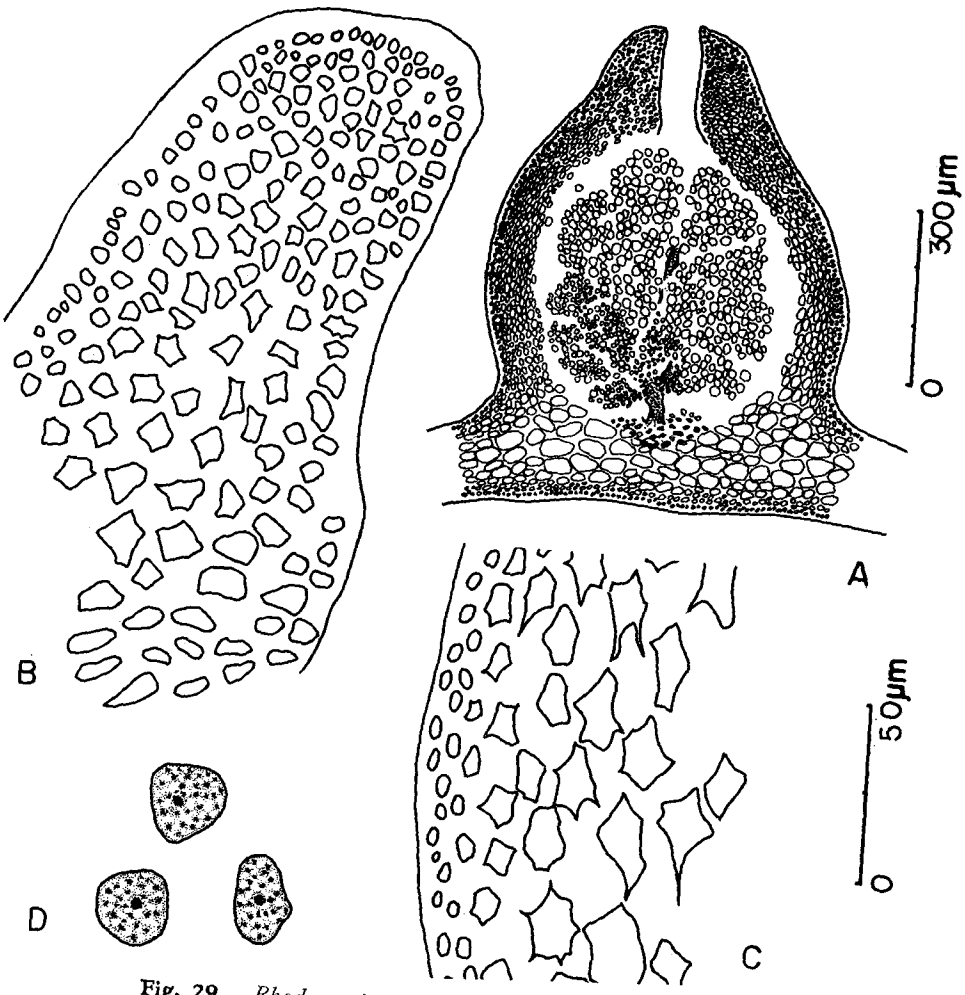

Fig. 29. *Rhodymenia intricata* OKAMURA (OKAMURA)
A, mature cystocarp; B–C, parts of pericarp in mature cystocarp, B being part of rostrum; D, carposporangia.

Discussion

For many years this species, found rather commonly in the Pacific coast of middle Japan, was mis-identified because of lack of knowledge of reproductive structures. OKAMURA (1920), giving the basionym *Phyllophora intricata*, described it with sterile plants only and pointed out that intricate and creeping segments were characteristic of this plant. According to him, *P. palmettoides* sensu YENDO (1916) and (?) *Fauchea repens* sensu OKAMURA (1916) were also mis-interpretations of this species.

By finding both tetrasporangia and cystocarps, however, OKAMURA (1930) transferred it to *Rhodymenia*, as *R. intricata*, because of the cystocarpic character of the genus. Afterward, OKAMURA (1936) noticed once again YENDO's plant, which was preserved in Herb. of Botanical Institute, University of Tokyo, that it was to be identified with this species.

Reviewing the genus *Rhodymenia* monographically, DAWSON (1941) classified this species under the section *Clinophora* owing to the character of the dispersion of tetrasporangial sori.

In Oshoro Bay the plant is much smaller in size compared with the ones commonly encountered in the Pacific coast of Honshu, Japan (OKAMURA 1921, 1930). However, it is interesting that cystocarpic and spermatangial thalli are not rare in this area, though they are known to be scarce in other areas.

Since the tetrasporangia originate from inner cortical cells, many tetrasporangia occurring intercalarily in cortical cell rows are thought to be one of the important characters of this species. No previous investigators mentioned such an occurrence of sporangium in the members of *Rhodymenia*. The spermatangium formation is characterized by terminal and subterminal occurrences on the mother cells, having no common wall between the spermatangium and mother cell, and by the mother cells connected seriately.

The two-celled carpogonial branch is a remarkable character of this species. It becomes four-celled after fertilization when both the carpogonium and hypogynous cell are divided transversely to form the four-celled carpogonial branch. SPARLING (1957) reported the formation of a connecting cell, cut off laterally from the carpogonial branch of *R. pseudopalmata* (LAMOUR.) SILVA. In this species no connecting cell is formed. No two-celled carpogonial branch has been reported in any of the members of Rhodymeniales.

Rhodymenia pertusa (POSTELS et RUPRECHT) J. AGARDH

(Text-figs. 30～37 : Plate III, D-F)

(1852) Spec. Alg. II (2) p. 376. J. AGARDH (1876) p. 329 ; HARVEY (1853) p. 147 ; KJELLMAN (1883) p. 150 ; De TONI (1900) p. 511 ; (1924) p. 289 ; OKAMURA (1907) p. 93, pl. 21, figs. 1～7 ; (1916) p. 48 ; (1936) p. 673, fig. 322 (2～3) ; SETCHELL & GARDNER (1903) p. 313 ; SJÖSTEDT (1926) p. 30, figs. 18 (B)～21 ; KYLIN (1925) p. 41 ; (1930) p. 35, figs. 22～23 ; (1931) p. 21 ; TOKIDA (1932) p. 17 ; (1954) p. 186 ; INAGAKI (1933) p. 46 ; KAWABATA (1936) p. 209 ; TAKAMATSU (1938) p. 53, pl. 9, fig. 1 ; DAWSON (1941) p. 129 ; NAGAI (1941) p. 200 ; YAMADA & TANAKA (1944) p. 72 ; SPARLING (1957) p. 361, pl. 56, fig. 12, d ; TOKIDA & MASAKI (1959) p. 91, pl. 3, figs. 19～25 ; KANG (1966) p. 86 ; FUNAHASHI (1966) p. 140.

Porphyra pertusa POSTELS et RUPRECHT (1840) p. 20, pl. 36 ; KÜTZING (1849) p. 693.

Japanese Name : *Anadarusu* (OKAMURA)

Type Locality : Kamchatka

Materials

Iburi District. Etomo, Muroran : May 23, 1966. Mar. 2, 30 ; Apr. 1, 27 ; May 26 ; June 25, 1967. Feb. 21, 1968. Charatsunai, Muroran : Aug. 1, 1966. Mar. 2, 1967. *Shiribeshi District*. Oshoro : Aug. 3, 1967. Apr. 14, 1968. *Kushiro District*. Aikappu, Akkeshi : Apr. 15, 1967. Daikoku-jima Isl., Akkeshi : June 23, 1967. Tokotan ; Akkeshi : June 19, 1966. June 24, 1967. Kakijima, Akkeshi : June 25, 1967. *Nemuro District*. Rausu : May 13～4, 1968. Nemuro : June, July, Aug., Oct., Dec., 1969 and June, 1970 (by M. KUROGI).

Description

Thallus solitary or few together, flat, obovate to elliptical, membranaceous, perforated over whole surface, simple or branched once dichotomously in lower portion, stipitate, attaching to substratum by means of discoid holdfast, 15～40～(100) cm high, 7～20～(50) cm wide at the broadest part ; holdfast 0.5～1.5 mm in diam., erecting one or a few fronds ; stipe cylindrical or par tly compressed, simple or branched, 0.5～1.2 mm in diam. ; frond gradually or abruptly attenuate to base, round to obtuse at apex, entire, sometimes undulate at margin, frequently laciniate, with branches similar to simple frond in shape, in section composed of cortical and medullary layers, 200～230 μm thick, cortical layer composed of one to two irregularly arranged cell-

rows, densely pigmented, superficial cells round to elliptical, irregularly arranged, 5.6～8.3 μm high and wide, medullary layer composed of three to five cell-rows, increasing in cell size inwards, central cells large, hyaline, almost round to elliptical, thick walled, 70～100 μm high, 50～140 μm wide; tetrasporangia dispersed in sori over whole surfaces except for lower portion, developing intercalarily to terminally in cortical rows, without stalk cell, elliptical to ovate, divided cruciately, 63～77 μm in length, 42～49 μm in width, sterile cells in sori scarcely modified; spermatangia dispersed similar to tetrasporangia, terminal or subterminal on mother cell, elliptical, 5.1 μm long, 3.4 μm wide, mother cells seriate side by side; cystocarps scattered abundantly over whole surfaces uniformly, elevated, peach-shaped, sessile, with pericarp and carpostome, 1200～1350 μm high, 1400～1670 μm wide, carpogonial branch four-celled, carposporangia rounded, 48～58 μm in diam.; color bright reddish purple; specimens adhere to paper. Perennial.

Habitat : Lower tidal to subtidal zone on rocks.

Distribution : Honshu and Hokkaido, Japan; Kamchatka; Arctic Ocean; Greenland; Bering Island; Pacific Coast of North America; Okhotsk Sea; and Japan Sea Coast of Korea.

Phenological Observation

The plants were investigated at Muroran. They were encountered mostly as drift specimens. A few places where they were growing were found at Charatsunai and Etomo, Muroran. They grew rather sparsely on shady bottom of the rock in lower to subtidal zone.

The investigations were carried out from May, 1966 to February, 1968. In March, 1967 at Charatsunai several young thalli of 6～7 cm (max. 12.5 cm) high and 2～3 cm (max. 4 cm) wide were in lower tidal zone. They were simple and without perforation. However, some of them already bore spermatangial sori in early developmental stage. At the same time there were numerous plants cast ashore at Etomo. They were mostly 20～30 cm high and 10～15 cm wide, and bore mostly spermatangia, tetrasporangia or cystocarps in mature stages. Their habitats, however, were not exposed even at the lowest spring tide. In April at some places of Etomo, there were several plants less than 10～(15) cm high and 6～(8) cm wide. Tetrasporangial sori were in early stage of development, but spermatangial sori mature. Perforations were common. Such attached plants did not become very large. On the other hand, the plants cast ashore decreased in number gradually until April. In May at Etomo, the plants attached were encountered more frequently. Most of them about 10 cm high were fertile, bearing spermatangia, tetrasporangia or young cystocarps. They were rarely ramified, but

frequently with fissures of frond, or mostly ruptured from upper portion. Cast ashore plants were not abundant. In June, the plants decreased rapidly in number, and cast ashore ones were lacking. At Etomo in February, 1968 the plants cast ashore were 14～23 cm high and 5～10 cm wide at the broadest part. Some of them had already spermatangial or tetrasporangial sori in early developmental stages. In August, 1966 at Charatsunai such cast ashore plants were found as fragments of lower portion where the upper portion was eroded and shed away. They had commonly tetrasporangia or cystocarps.

Considering the above investigations, at Muroran in lower tidal zone these plants appear in February and become most luxuriant during April and May. After that period, they decrease in number rapidly but remain until July to August. However, the plants cast ashore, from deeper subtidal zone seem to appear from February or probably more earlier and continue until August or later in the area. Spermatangial sori are developed from March in attached thalli at lower tidal zone and remain until June. Tetrasporangial sori appear from April and remain until the plants disappear. Cystocarps occur from May and remain until the plants disappear.

On the other hand, the plants at Akkeshi were mostly attached in the lower tidal zone. In June, 1966 and 1967 they were on the rocky bottom facing the open sea but being protected from wave action, and about 17 cm high and 6 cm wide, bearing mostly tetrasporangia, spermatangia or cystocarps. However, the plants collected in June at Kakijima, which is a shallow inlet, were commonly many centimeters in height. The largest one was about 1 m high and 50 cm wide at the broadest part. Besides, the ones dredged in 5～6 m depths at the Bay of Akkeshi were commonly more than 120 cm. They had a distinct and thick stipe branching once or more.

After the investigations, I had fortunately a chance to compare again the growth of this plant with the materials collected from the Nemuro area during 1969～1970 by the kindness of Prof. M. KUROGI. According to him and his materials, the plants are most luxuriant and fertile from late spring to summer. They are up to 50 cm or more high, characteristic in having long and branched stipes as seen in Kakijima and the Bay of Akkeshi. From August they decrease in number, but some of them survive with the lower portion or stipe. The proliferation of new fronds less than 2 to 5 cm high from the remainder of stipes was seen in the collections of late October and December. New plants probably originating from spores were not collected, although there seems to be the possibility of such occurrence. On the other hand, in June new plants about 1 cm high and considered to be

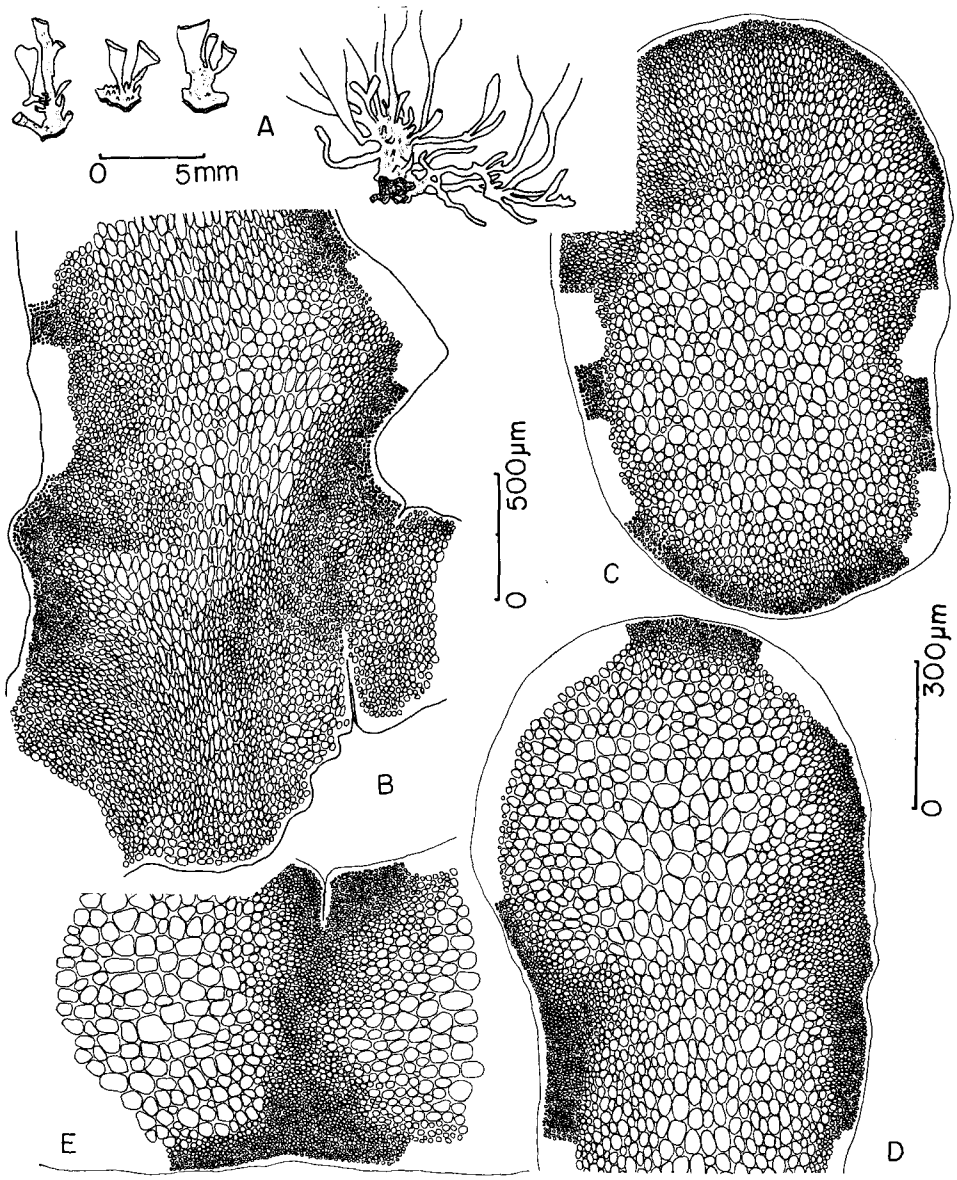

Fig. 30. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH
A, basal part showing holdfast; B, longitudinal section of base; C–E, successive transverse sections of stipe at ramified portion.

originated directly from spores were collected. From this investigation, the plants in Nemuro area are confirmed to be perennial, although the proliferation of new fronds and the occurrence of new plants in June were not found in the Muroran area.

Morphological Observation

External Appearance

The plant is obovate to elliptical. The young thallus less than 10 cm high is oblong to spatulate. As the thallus grows, it ramifies frequently once or a few times dichotomously at the apical portion. Frequently the thallus is laciniate into two or more lobes from upper margin to middle or lower portions. The margin becomes thick and frequently undulate and the apex is mostly obtuse.

Perforations appear in various stages of the growth. They appear at first in the middle to lower center of the frond, where several blackish purple spots begin to show at random. The spots become whitish yellow in color before the destruction of cells. In mature plants the perforations of various diameters are scattered over the whole surfaces. The margin of the pore is curved to one side of the surfaces, so that the thallus frequently becomes uneven.

The discoid holdfast is not so large. It is mostly less than 10 mm in diam., and frequently bears more than two stipes (Fig. 30 A). The stipe is cylindrical and variable in length or sometimes scarcely discernible. It remifies once or a few times and develops frond terminally. The long and complicated stipes (max. 5 cm long) were encountered among the materials collected at Kakijima. Daikokujima Isl., and Nemuro area. Some of them are immersed in sponges covering the substratum.

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers (Fig. 31 E). The cortical layer consists of one or two rows of cells pigmented densely. The superficial cells are round to elliptical and not arranged palisadelike. In the young thallus, cortical cells are single rowed. The rows are increased by oblique divisions of the superficial cells, as mentioned by SJÖSTEDT (1926, fig. 19 B-C). Some of them, however, remain without division as inner cortical cells.

The medullary layer is composed of three to five rows of cells. One or two central cells are very large, hyaline, thick walled and almost round to periclinally elliptical. Sometimes, they are about two times as long as wide in longitudinal section. Outer two to three cells of the medulla are

poorly pigmented and variable in size. They become smaller outwards, and are distinguishable from inner cortical cells owing to poorer plastids and about two to three times larger size of the inner cells.

The margin is filled with rather small cells in the young frond (Fig. 31 C). It becomes thick by increasing numbers of cells, and curves to either side of surfaces, so that it is undulate in a mature thallus.

The perforation of frond begins with the destruction of the cells at a definite area. After then, both the cortical and medullary cells around the pore cut off numerous small and irregularly shaped cells outwards. The new cells divided cover the poral margin, so the cortical layer of the portion is formed. Later, this poral margin becomes thick and elevated to either side of the thallus surfaces (Fig. 32 E-L).

The holdfast in longitudinal section is filled with round to longitudinally

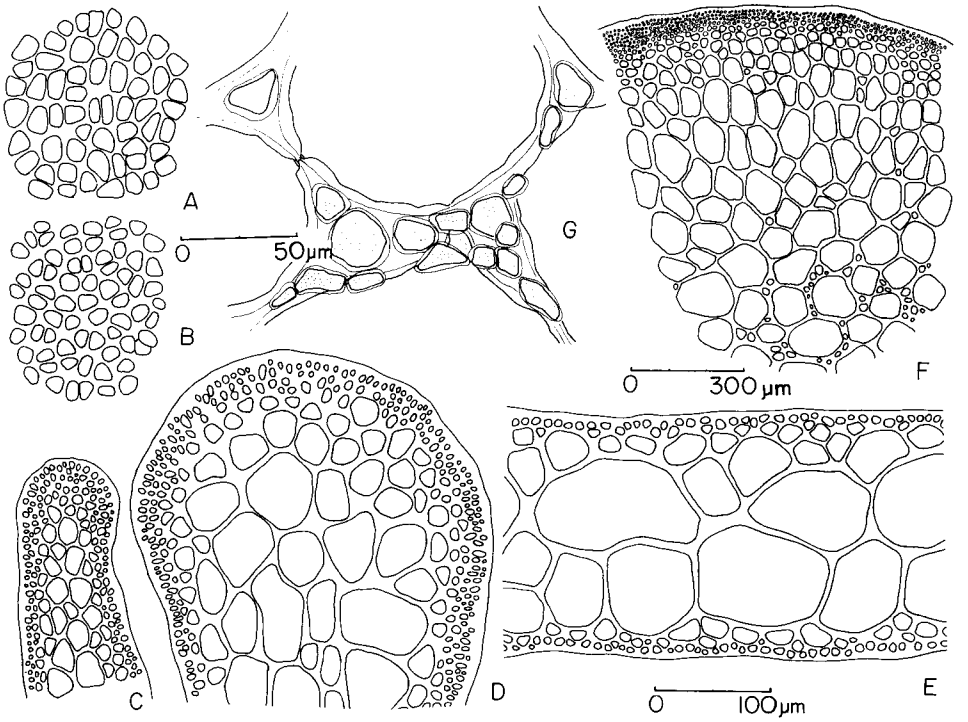

Fig. 31. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH

A-B, superficial cortical cells in surface view, A being young; C-D, transverse sections of thallus in margin, C being young; E, transverse section of mature thallus; F, part of stipe in transverse view, smaller cells occurring in central medulla; G, the same smaller cells magnified.

elliptical cells. In central portion there are developed large and longitudinally oblong cells, which extend in transverse rows upwards to form the medullary layer of stipe (Fig. 30 B). In the lower portion of stipe, on the other hand, many small cells of almost same size as the cortical cells are scattered among

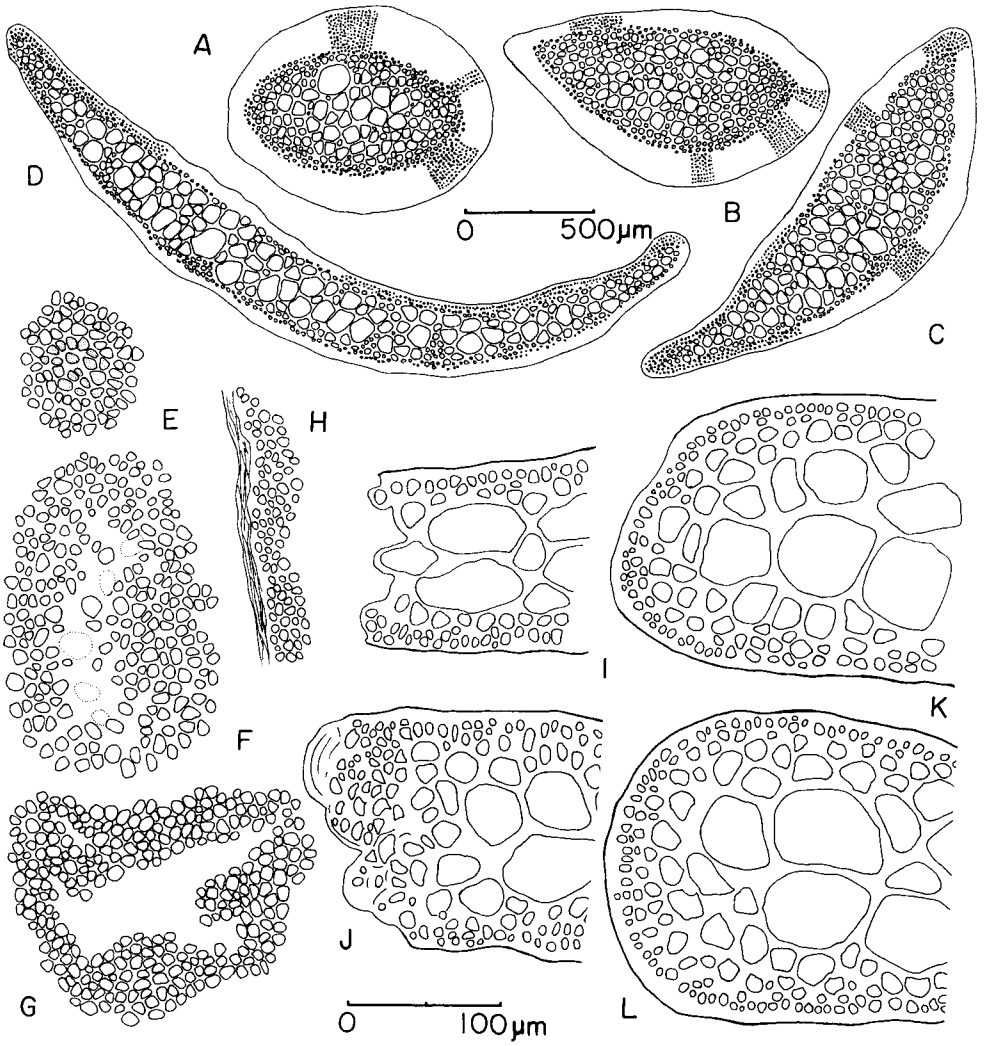

Fig. 32. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH
A-D, successive transverse sections of transitional portion from stipe to frond; E-H, development of pore in surface view, H showing poral margin; I-L, regeneration of cortical layer in poral margin after perforation, shown transversely.

the intercellular spaces of the medullary cells (Fig. 31 F-G). They disappear gradually towards the upper portion of stipe. The serial transverse sections of the transitional portion from stipe to frond is somewhat peculiar in anatomical feature. The frond is formed by the compression and elongation of the stipe transversely, not by changing the cellular constitution as seen in the other species. The basal portion of the frond is slightly concave to one side (Fig. 32 A-D).

In this species there are no rhizoids and hairs, nor the lateral fusion of thalli.

Reproductive Organs

Tetrasporangia: The tetrasporangial plants are variable in size from 2.2 cm to more than 1 m high. They are of equal size range compared with cystocarpic plants. Tetrasporangia appear in numerous dark purple spots on thallus surfaces discernible easily in the field (cf. SJÖSTEDT 1926, DAWSON 1941, TOKIDA 1954, SPARLING 1957). They appear at first as indefinite sori with sparsely aggregated sporangia on the upper middle portion of thallus. In the mature thallus these sori coalesce and extend over the whole surfaces except for the lower portion. Various developmental stages of tetrasporangial sori are generally seen in a single thallus.

The tetrasporangium is homologous to inner cortical cells. As seen in *R. intricata*, sporangium-initials occur intercalarily to terminally in the cortical cell rows (Fig. 33 E, F). They are distinctive by containing abundant protoplasmic substances and a large nucleus. The sporangium is divided periclinally and then anticlinally before the completion of previous division. It becomes elliptical to ovate as it is mature (Fig. 33 D, G), and sinks inwards to the medullary layer, where the medullary cells are compressed. A mature tetrasporangium is 63~77 μm long and 42~49 μm wide. The pit-connection with outer cortical cells becomes very difficult to discern as the sporangium is mature fully. A stalk cell is not found.

The modification of sterile cortical cells in the sori is not remarkable during the maturation of tetrasporangia. These sterile cells are enlarged anticlinally and become elliptical to oblong when the sporangia are divided periclinally. However, the outer cortical cells are scarcely changed in form even after the full maturation of the sporangium. The soral area is plane though the cortical layer becomes slightly thicker.

Spermatangia: Almost all the spermatangial plants are very small in size. The largest one encountered was only 7 cm high and 2 cm wide at the broadest part. In fresh material male plants bearing mature sori show a pink-red color. Spermatangial sori appear and extend like the sporangial

sori (Fig. 34 Q). From the beginning of development, all the superficial cells in a sorus are converted into fertile cells (Fig. 34 A–C, G).

In transverse section one or two spermatangia are developed on a mother cell terminally or subterminally. They originate from superficial cortical cells. The superficial cell is elongated at first slightly in elliptical to oblong

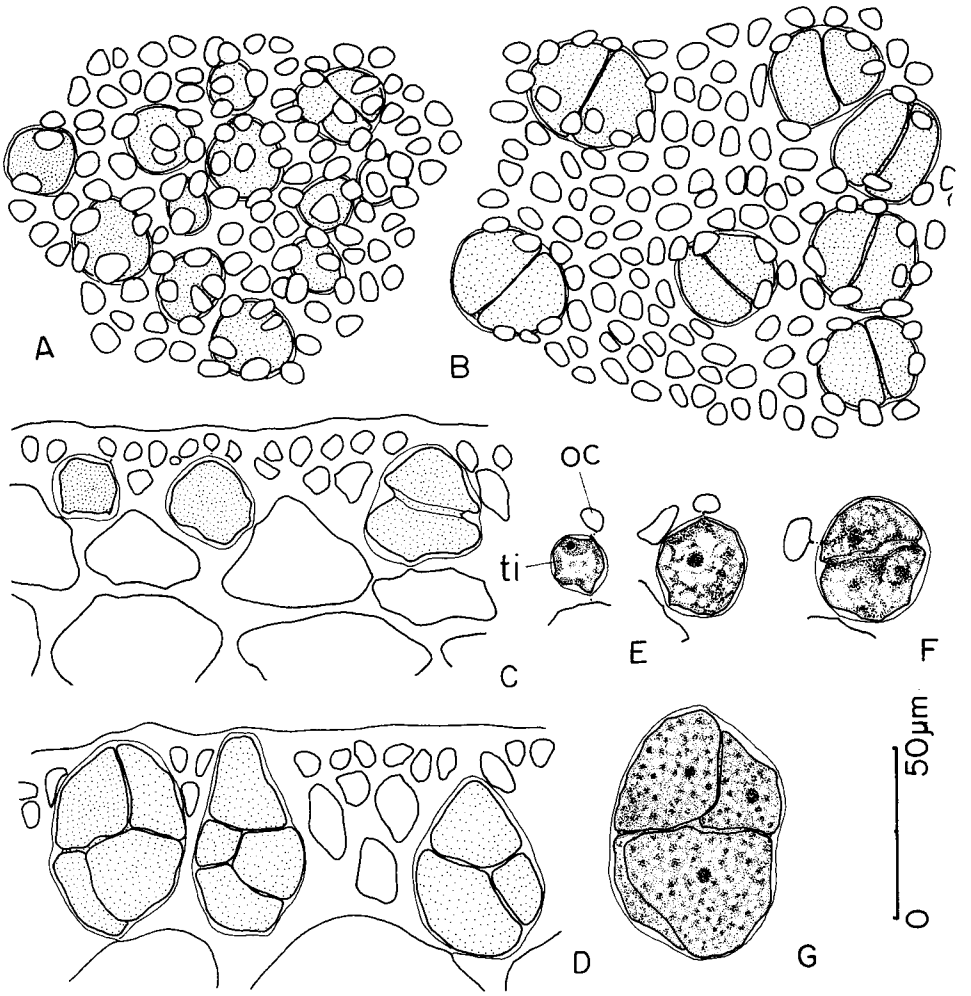

Fig. 33. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH

A–B, development of tetrasporangia in surface view; C–D, the same in transverse view, C being intercalary occurrence in cortex; E–F, growth of young sporangia bearing pit-connections with outer cortical cells; G, mature tetrasporongium.

oc: outer cortical cell, ti: tetrasporangium-initial.

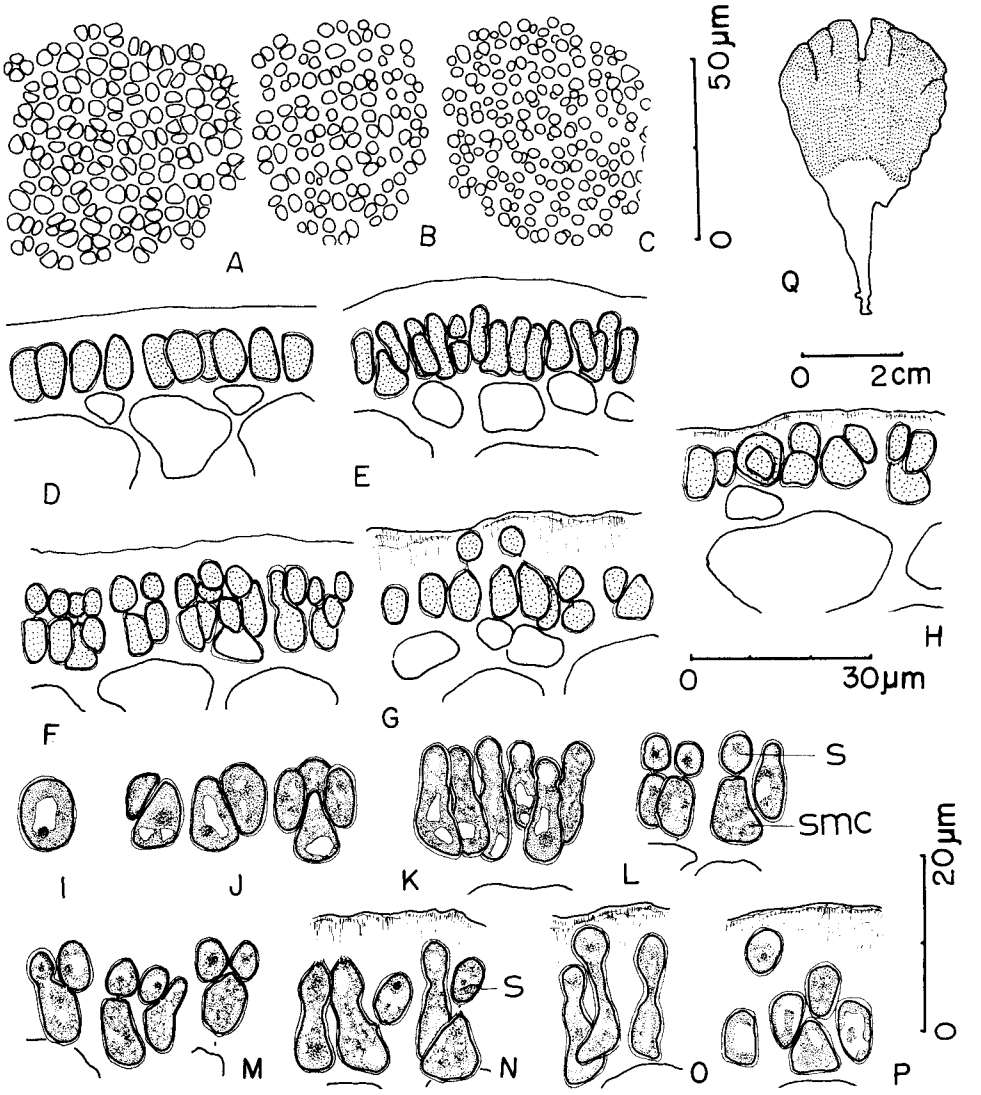

Fig. 34. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH

A–C, development of spermatangia in surface view; D–H, the same in transverse view; I, elongate outer cortical cell; J, formation of spermatangial mother cells; K–L, development of spermatangia from mother cells terminally; M, subterminal formation of spermatangia; N–O, successive development of spermatangia; P, later stage of development; Q, male thallus.

s: spermatangium, smc: spermatangial mother cell.

form. Then, it is divided longitudinally or obliquely into three to four cells (Fig. 34 D-E, I-J), all of which become spermatangial mother cells. The mother cells are side by side. Sometimes, the division plane is much curved, and one mother cell is put upon a corner of another. There are no basal cells of the mother cells as seen in *R. intricata*.

When the mother cell becomes about 13 μm high, it cuts off a spermatangium transversely at the roundly modified top (Fig. 34 K). There is no common wall between the spermatangium and the mother cell. Some mother cells cut off second spermatangium beside the first. Thus, two spermatangia are protruded subterminally on a single mother cell (Fig. 34 M). A mature spermatangium is round to elliptical, and 5.1 μm long and 3.4 μm wide, while the mother cell is almost oblong, and 8.9 μm high and 4.3 μm wide.

The mother cells lose plastids before the protrusion of spermatangia. No plastids are in spermatangia and spermatia. The superficial gelatinous wall of the thallus is not shed during the spermatangium formation.

A spermatium is liberated in a similar manner to that of *R. intricata*. After the primary spermatangium is released, a secondary one is protruded again from the top of the same mother cell (Fig. 34 N), and a tertiary one is observed rarely. The spermatangial mother cell becomes poorer in contents, as it protrudes more spermatangia successively. In the later stage of spermatangium formation the mother cell and spermatangia become slender and elongate columnar in shape (Fig. 34 O). When the spermatangium formation is discontinued, the mother cells return mostly to ordinary cortical cells, which closely resemble other sterile cells (Fig. 34 H, P). Such male plants with discontinued spermatangium formation are scarcely distinguishable from sterile plants. However, it is not clear that male plants grow continuously to become as large as tetrasporangial or cystocarpic plants. In the areas investigated no sterile plants of large size are encountered through the year.

Cystocarps: Cystocarpic plants are also variable in size, as large as the tetrasporangial plants. Cystocarps appear at first in the uppermost portion of thallus, and are dispersed over the whole surfaces later. They are sessile, elevated on surface in peach-shape, and 1200$\sim$1350 μm high and 1400$\sim$1670 μm wide. The carpostome is 70$\sim$85 μm in outer diam.

The carpogonial branch is four-celled. It is somewhat different in cell composition from the reports of previous workers (SJÖSTEDT 1926, KYLIN 1930, TOKIDA & MASAKI 1959). SJÖSTEDT and KYLIN reported it was three-celled, whereas SPARLING (1957) mentioned it as four distinct units though the fourth was not clear whether it was a separated trichogyne or an actual

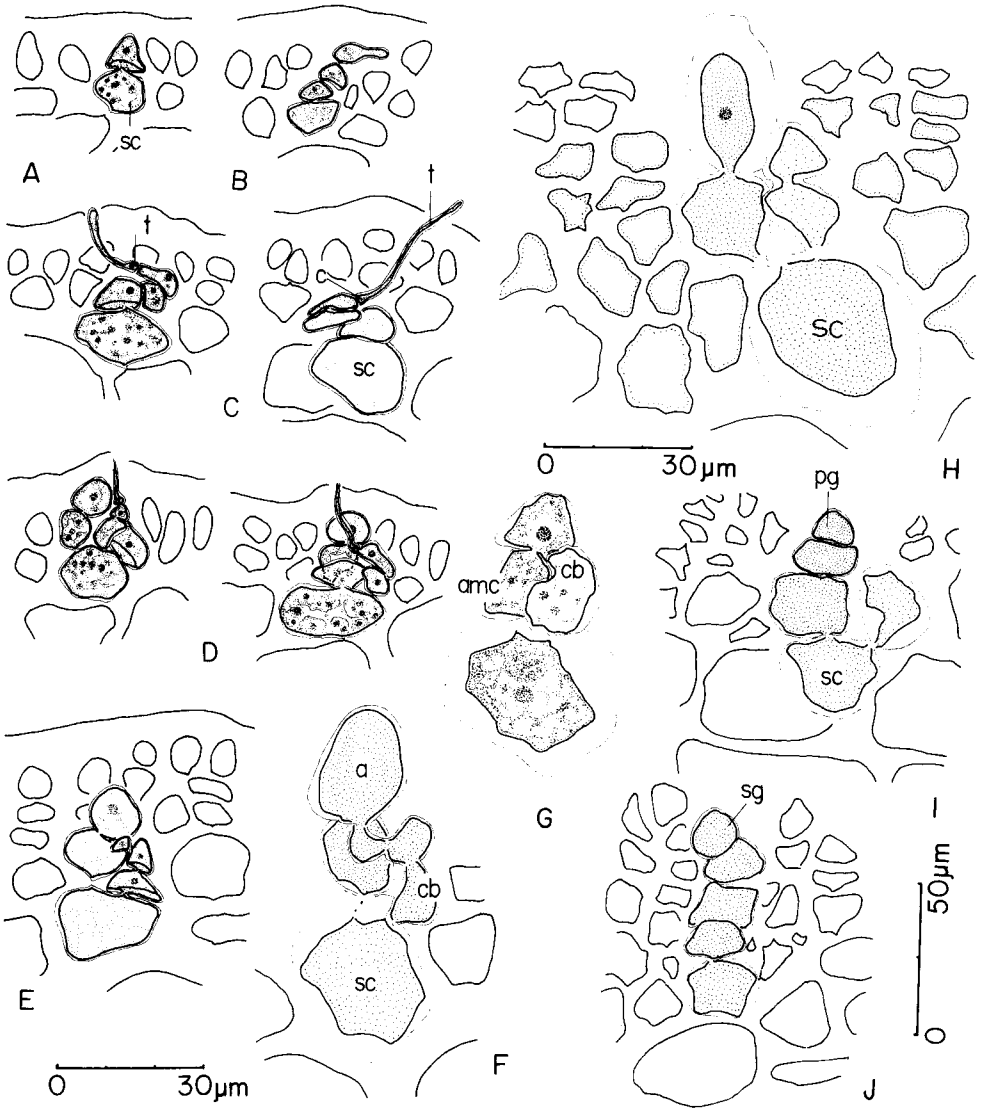

Fig. 35. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH

A–B, development of carpogonial branch; C, carpogonial branch and supporting cell; D, degeneration of trichogyne, showing auxiliary cell branch; E–F, fusion between auxiliary cell and carpogonial branch; G–H, fusion cell of carpogonial branch; I–J, cutting off primary or secondary cells of gonimoblast.

sc: supporting cell, t: trichogyne, c: carpogonium, a: auxiliary cell, amc: auxiliary mother cell, cb: carpogonial branch, pg: primary gonimoblast cell, sg: secondary gonimoblast cell.

carpogonium. TOKIDA & MASAKI reported it consisted of three or four cells. The carpogonial branches are common in the thallus bearing young cystocarps. The supporting cell is homologous to inner cortical cells. Even when the supporting cell bears only one cell outwards, it is distinguishable owing to a round and slightly larger shape and densely stained protoplasmic substances (Fig. 35 A). The supporting cell is enlarged more than two times in diameter compared with the adjacent sterile cells, and has many nuclei when the carpogonial branch is developed. The first cell of the carpogonial branch is one third to fourth of the size of supporting cell and almost pyramidal in form. A single nucleus is in it. The second cell is flat and about a half of the size of the first. It is connected laterally with the first

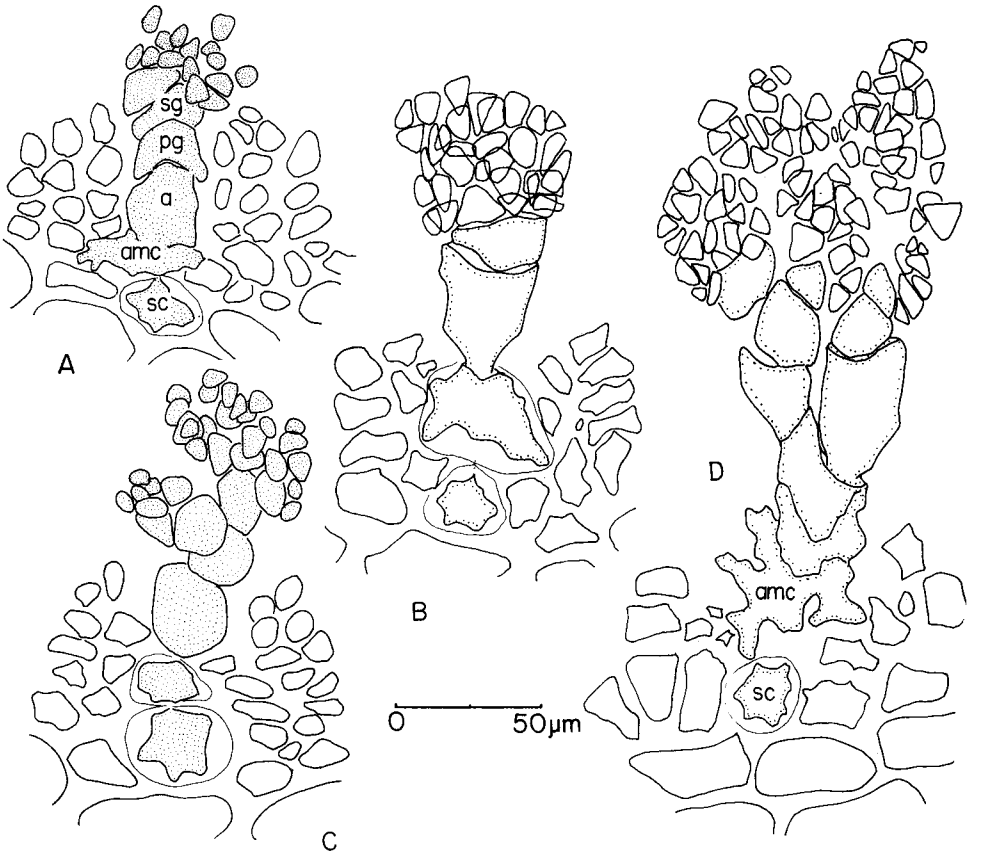

Fig. 36. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH
A–D, development of embryonic cells of gonimoblast, D forming fusion cell. sc: supporting cell, amc: auxiliary mother cell, a: auxiliary cell, pg: primary gonimoblast cell, sg: secondary gonimoblast cell.

and contains one or two nuclei (cf. SJÖSTEDT 1926). The third cell, the hypogynous cell, is similar in shape and size to the second. A single nucleus is observed in it. The fourth, the carpogonium, is very small and triangular in shape. It is connected laterally with the third and placed close to the first owing to the curvature. The trichogyne is protruded from one corner of the carpogonium. It is very slender and uniformly thick, curving gently toward the thallus surface. The carpogonial branch is curved and biphasic inasrangement (Fig. 35 C).

The auxiliary-cell branch is two-celled. It is distinguishable after the presumed fertilization. The auxiliary mother cell is multi-nucleate and oblong to elliptical at first. It is connected with the supporting cell. The auxiliary cell is almost round with a single large nucleus. It is slightly larger than the mother cell below. After the presumed fertilization, the trichogyne disappears rapidly. The carpogonium, probably containing a diploid nucleus, coalesces with the auxiliary cell (Fig. 35 D). The nucleus seems to migrate into the auxiliary cell through this fusion area. The carpogonium disappears soon, but the hypogynous cell continues the fusion instead (Fig. 35 E-F). In this relationship the fertile cells, especially the auxiliary cell, auxiliary mother cell and supporting cell become thick walled. After a while, the first and second cells make an irregularly shaped fusion cell, which disappears also later (Fig. 35 G-H). No connecting cell is formed in this development (cf. SPARLING 1957).

The primary cell of the gonimoblast is cut off transversely at nearly the middle portion of the auxiliary cell. The secondary is cut off transversely or obliquely from the primary gonimoblast cell (Figs. 35 I-J, 36 A, D). The two tertiary cells of the gonimoblast are cut off obliquely from upper corners of the secondary cell. These embryonic cells of the gonimoblast, the auxiliary cell and the auxiliary mother cell are enlarged very much later and fused with each other by enlarging pit-areas. They form a single column-like fusion cell. The tertiary and fourth cells of the gonimoblast remain as main axes and support upper cells of the gonimoblast (Fig. 36). Further cells of the gonimoblast are developed from the upper cells successively. In early stages of the development, these gonimoblast cells are variously angled, and become smaller outwards, forming a young carposporophyte of elliptical outline (Fig. 37 A). Later, almost all the cells of the gonimoblast are converted into carposporangia successively in groups from the outer cells. They are immersed in a gelatinous matrix. A mature carposporangium is almost round $48\sim58\ \mu$m diam., and has a nucleus and pigments. The central fusion cell is rather slender and simple.

During the carposporophyte formation, sterile cortical cells around the procarp begin divisions transversely when the carpogonium coalesces with the auxiliary cell. They are divided successively and arranged in perpendicular rows, which increase rapidly in number during the enlargement of the auxiliary cell. At the same time the auxiliary mother cell cuts off new sterile cells around it and forms secondary pit-connections with other sur-

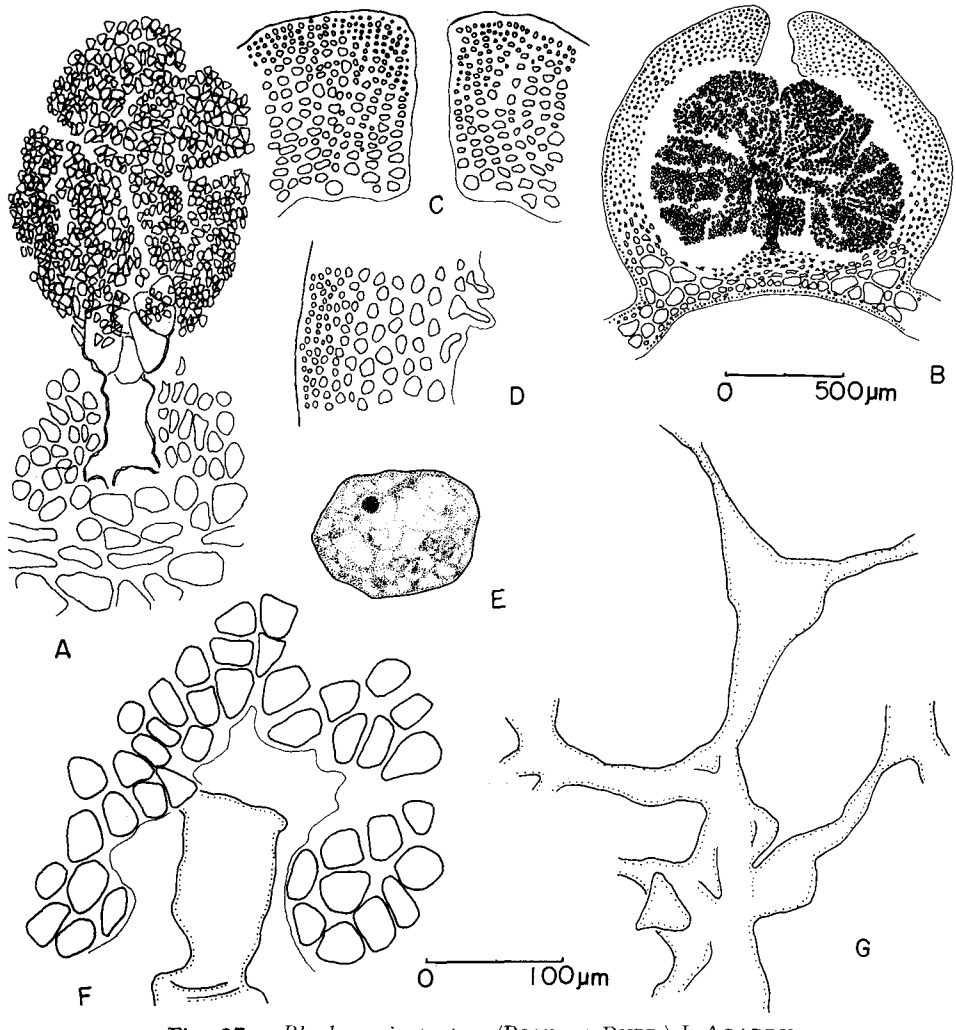

Fig. 37. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH

A, young carposporophyte; B, mature cystocarp; C, part of rostrum; D, part of pericarp; E, carposporangium; F, gonimoblast with young carposporangia; G, part of fusion cell.

rounding sterile cells, which become rich in content accordingly. The outer surface of the area is elevated hemispherically. When the primary cell of the gonimoblast is formed, a dome shaped pericarp and the pericarpic cavity are formed sooner or later by the rupture of connection between lower nutritive cells and upper cells forming pericarp. The cystocarpic pore is opened afterwards.

In a mature cystocarp the pericarp is composed of two layers of irregularly arranged cells. The outer layer is similar to the cortex of thallus, and the inner layer is composed of more than five rows of cells, which are not modified in cell shape but bear secondary pit-connections radially (Fig. 37 D). The cells around the carpostome are very small and arranged regularly. The carpostome is narrower outwards, showing 70~85 μm in outer diam., and 120~140 μm in inner diam. The rostrum is not protruded but the pulvinus at the base of cystocarp is considerable in development.

Discussion

POSTELS & RUPRECHT (1840) introduced this alga from Kamchatka, as *Porphyra pertusa*, which was removed to *Rhodymenia* by J. AGARDH (1852). The plant was reported to be common from the Arctic, Pacific and Atlantic Oceans (J. AGARDH *l. c.*). The structure of thallus and reproductive organs were described and illustrated by SJÖSTEDT (1926) and KYLIN (1930). The cystocarpic nature was investigated again by SPARLING (1957) and TOKIDA & MASAKI (1959).

In spite of such detailed investigations several interesting observations were obtained in this study. The tetrasporangium originates from an inner cortical cell, and is frequently intercalary in the cortex, as seen in *R. intricata*. The previous investigators mentioned above reported that tetrasporangial plants were ampler than cystocarpic ones. However, on many more specimens than these researches had, there is no difference between the sizes of the two kinds plants. Moreover, tetrasporangia were reported to be scattered over the thallus surfaces (SJÖSTEDT *l. c.*, DAWSON 1944, TOKIDA 1954, SPARLING *l. c.*), but I have found them in sori that extend broadly along the marginal portions of the thallus. The sori coalesce as they become mature.

The carpogonial branch was also explained variously by the above workers. In this study, however, among 60 carpogonial branches investigated, 57 were four-celled, and the remaining three; two of them were still young so that no trichogyne was formed, and one was not clear at the connecting area between the trichogyne and third cell. Thus, it is considered that no three-

celled carpogonial branch (SJÖSTEDT *l. c.*, KYLIN *l. c.*, TOKIDA & MASAKI *l. c.*) exists in this species.

The male organ was reported by TAZAWA (1975) for the first time. As mentioned by TOKIDA (*l. c.*), SJÖSTEDT's remark on the male organ is nothing but a review on that of *P. palmata*. The important character in spermatangium formation is the lack of the basal cell of the mother cells. The other characters of the development are very similar to those of *R. intricata*.

Chrysymenia J. AGARDH (1942)

The genus *Chrysymenia* was established by J. AGARDH (1842) with six species transferred from *Halymenia* and *Chondria*, and two newly nominated. In 1851, he divided the genus into three sections, *Chrysymenia*, *Halichrysis* and *Botryocladia*, which were revised by HARVEY (1853) as *Chrysymenia* (including J. AGARDH's *Halichrysis* and *Chrysymenia*), *Botryocladia* and *Cryptarachne* (newly established). Once again J. AGARDH (1876) revised them as *Leptosomia*, *Halichrysis*, *Cryptarachne*, and *Botryocladia*. All the sections, however, were elevated later to generic ranks as *Halichrysis* SCHMITZ (1889, *nomen nudum*), *Leptosomia* J. AGARDH (1892), *Cryptarachne* KYLIN (1931) and *Botryocladia* KYLIN (1931).

OKAMURA (1936) however disagreed with KYLIN's elevation of *Cryptarachne*. The most important character mentioned by KYLIN was that it had a somewhat compressed frond and filamentous cells in the inner cavity of the thallus. However, OKAMURA indicated that these features were not suitable because some species of the *Chrysymenia* showed both of these characters also.

Indicating OKAMURA's interpretation, *Chrysymenia* is characterized currently by cylindrical or often flat and branched thalli consisting of cortical and medullary layers, bearing gland cells, cruciately divided tetrasporangia occurring terminally in cortex, and by hemispherically elevated cystocarps with carpostome.

Chrysymenia wrightii (HARVEY) YAMADA

(Text-figs. 38～44 : Plate IV, A-C)

(1932) Not. Some Jap. Alg. III, p. 118, pl. 25, fig. 4. INAGAKI (1933) p. 43 ; OKAMURA (1936) p. 667, fig. 318 ; TAKAMATSU (1939) p. 65 ; INOH (1947) p. 166, figs. 160～166 ; OSHIMA (1950) p. 115 ; KAWASHIMA (1955) p. 33 ; KANG (1966) p. 85 ; FUNAHASHI (1966) p. 140 ; (1967) p. 31.

Halosaccion wrightii HARVEY (1859) p. 332; J. AGARDH (1876) p. 260; HARIOT (1891) p. 230, De TONI (1895) p. 42; (1900) p. 608.
Chylocladia wrightii OKAMURA (1916) p. 51.
Chrysymenia enteromorpha HARVEY (1853) sensu YENDO (1917) p. 85.
Japanese Name: *Taoyagiso* (OKAMURA)
Type Locality : Hakodate, Japan

Materials

Shiribeshi District. Oshoro: June 13; July 11, 27; Aug. 19; Oct. 7, 1966. May 16, 27; June 3; July 7, 16; Aug. 3, 17; Sep. 18, 1967. Sep. 3, 1968.

Description

Thallus solitary or few together, cylindrical, gelatinous, tender, branched three to four times repeatedly, shortly stipitate, 15~18 cm high, 2~3 mm wide at the broadest part, attaching to substratum by means of discoid holdfast; holdfast small, 1~2.5 mm in diam., erecting single frond generally; stipe terete, simple, 0.5~1.0 mm in diam.; frond smooth, gradually or abruptly constricted at base, similarly broad in middle portion, attenuate gently upwards, tapering at apex, branches radial, alternate, opposite or irregular, constricted at base, decreasing in length upwards, primary branches 1.5~2 mm wide, ultimate branchlets about 2 cm long, 1 mm wide in max., slightly curved inwards; frond in section composed of cortical and medullary layers and central cavity, 120~180 μm thick, central cavity septate at base of branches, cortical layer composed of one to three irregularly arranged rows of cells, densely pigmented, superficial cortical cells in irregularly arranged rows, vertically elliptical to ovoid, 5.5~7.0 μm high, 3.5~4.2 μm wide, medullary layer composed of three to five rows of cells, arranged loosely and irregularly, inner two to three cells elongate longitudinally, thick walled, 45~70 μm high, 35~83 μm wide, 150~500 μm long; gland cells and hyphae-like filaments issuing from innermost medullary cells within central cavity; unicellular hairs scattered uniformly; tetrasporangia developed over whole branches in sori except for uppermost and lower parts of main axis, originating from inner cortical cell intercalarily or terminally in cortex, without stalk cell, round to elliptical, divided cruciately, 48~53 μm in length, 38~42 μm in width; spermatangia occurring over whole branches in sori except for middle to lower portion of main axis, terminal on mother cell, elliptical to elongate hemispherical, 4.0 μm long, 2.9 μm wide; cystocarps sparsely scattered over whole thallus except for basal portion of main axis, sessile, elevated, peach-shaped, with carpostome, 750~850 μm high, 850~950 μm wide, carpogonial branch four-celled, carposporangia round to polygonal,

32～38 μm in diam.; color yellow to bright red; specimens adhere to paper firmly except for lower portion of main axes. Annual.

Habitat : Low tidal zone on rocks.

Distribution : Pacific Coast and Japan Sea Coasts of Honshu, and Hokkaido of Japan; Vladivostok; and Korea.

Phenological Observation

The investigation was carried out from June, 1966 to September, 1968 in Oshoro Bay. The plants occur not so many in this Bay, as mentioned by INAGAKI (1933). They grow on rocky substratum of shady pool or calm places affected almost by no wave action. One of the habitats used for this periodic observation is a calm tidal pool at the inner Bay, which is not exposed even at low spring tide. The plants are solitary and sparse.

In Oshoro Bay the plants appear for a short period, compared with other members of Rhodymeniales investigated. In mid May, 1967, several thalli became 1～2 cm high. They were very slender and had no branches. By the end of May to early June the plants appeared more frequently and were about 4 cm high and 1 mm wide. They commonly bore a few primary branches. The largest one collected in early June was 8.5 cm high and 2 mm wide at the broadest part and had long primary branches of 4 cm max., and also many secondary ones 2 cm max. Both spermatangial and tetrasporangial plants bearing sori in early developmental stages were among them. In July they were rather abundant and became 10～12 cm high on an average but not much wider. The largest one was 20 cm high and 3 mm wide. They protruded lots of branches and branchlets around the main axis. Female plants bearing comparatively young cystocarps were common, and male and tetrasporic plants with mature sori were abundant. Several thalli collected at 7～8 m depth however had fewer branches, though they bore tetrasporangia or cystocarps. In August the plants became mostly more than 15 cm high and 2～3 mm wide at the broadest part. After July, they did not increase in number, nor became more prosperous in branching. Almost all thalli were fertile with mature tetrasporangia or cystocarps, while spermatangial plants were rare. After September, the plants decrease in number rapidly. Most of them were eroded or shed away from upper portion or branches, and disappeared rapidly. In October a few thalli remained with lower portion of main axes. They disappeared completely soon after.

Considering the above investigations, the plants at Oshoro Bay appear in May and become most luxuriant in July and August. They decrease in number rather rapidly after September, and remain with basal fragments until early October. Spermatangial and tetrasporangial plants appear since

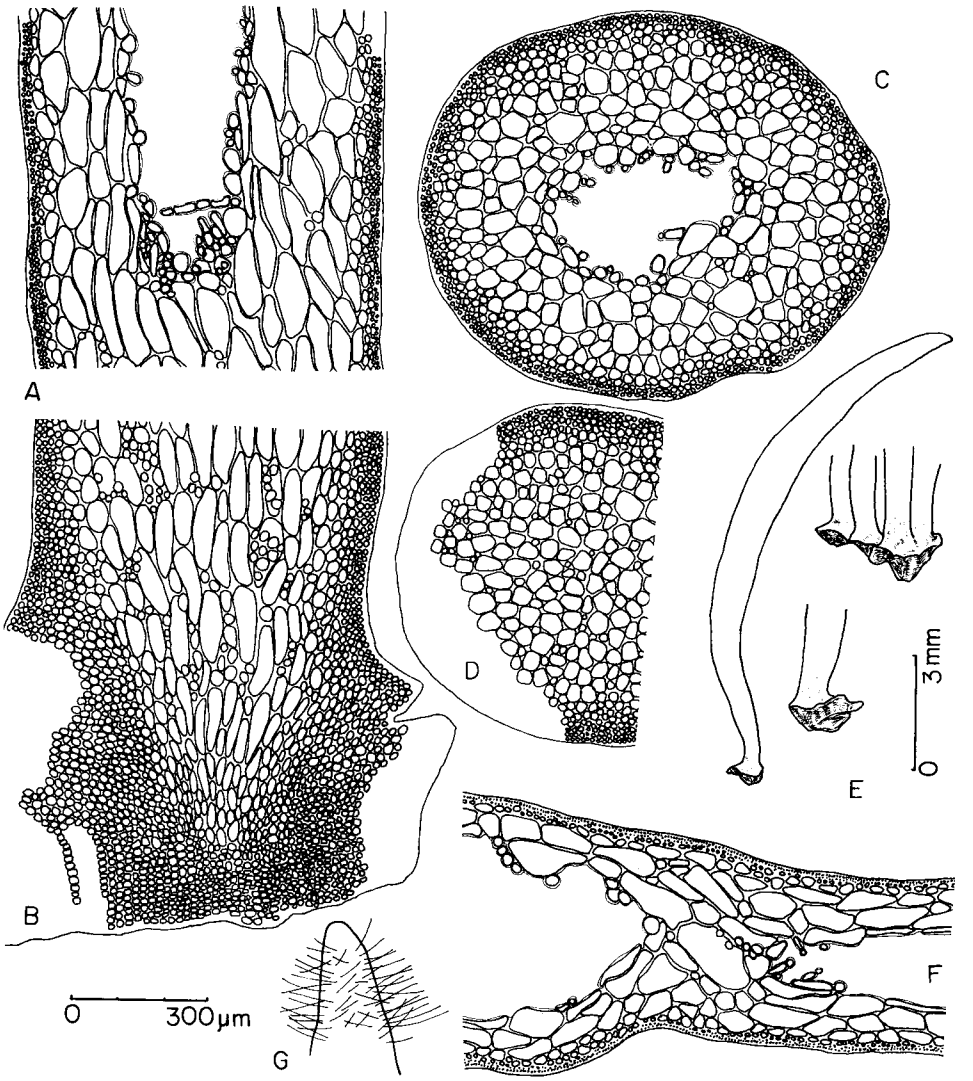

Fig. 38. *Chrysymenia wrightii* (HARVEY) YAMADA

A, part of stipe in longitudinal view, showing central cavity, hyphae-like filaments and gland cells aggregated abundantly; B, longitudinal section of base, showing small cells in medulla; C–D, part of stipe in transverse view, D being lower portion; E, holdfasts and young thallus; F, ramified portion, left being main axis sectioned transversely and right a branch sectioned longitudinally; G, apex bearing hairs.

June, and become luxuriant during July. The former disappears in August, and the latter remains until the plants disappear from the area. Cystocarps appear since July and remain until early October or so, when the plants disappear from the area.

Morphological Observation

External Appearance

The plant grows monopodially and branched three to four times. The primary branch appears when the plant becomes about 2～3 cm or sometimes more than 4 cm high. As decribed by YAMADA (1932), the mode of ramification is similar in all branches. They are protruded alternately, oppositely, or rather irregularly around the main axis. All branches are constricted at the base, gradually widened in the lower to middle portion, atenuate in the upper portion, and tapering off at the apex. Sometimes, the main axis ends bluntly, so that the plant becomes corymbose in form. Most of the mature thalli are naked in the middle to lower portion of main axis. The branchlets are curved slightly inwards.

The discoid holdfast is comparatively small. It is scarcely larger than the stipe in diam. Sometimes, more than two bases are piled one on the other (Fig. 38 E). The stipe is very short or frequently not distinguishable.

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers and central cavity (Fig. 39 C). The cavity is septated with multi-rowed cells at the base of ramifications. The cortical layer is composed of one to three rows of cells. The superficial cortical cells are small and vertically elliptical to ovoid. They are connected obliquely with inner cells and not arranged in palisade-like row. The surface of thallus is smooth or frequently microscopically uneven. Sometimes, outer cells are very closer to the inner cortical cell, whereas some inner cells have no outer superficial cortical cells. The inner cell is about one and a half times the size of outer cells and also vertically elliptical to ovoid.

The medullary layer is composed of three to five rows of cells. The cells become gradually larger inwards. Outer one or two cells are arranged very irregularly and are far apart. They are round, poorly pigmented and about two times as large as inner cortical cells. The inner medullary cells are large, hyaline, almost round, and thick walled. In longitudinal section, they are elongated very much longitudinally, e. g. the innermost cell may be seven to eight times as long as the transverse width. Sometimes, the elongate ends become slender and sharp (Fig. 39 A). In addition, there are longitudinally

slender cells attaching to the innermost medullary cells inwards. In transverse section of the thallus they are slightly larger than inner cortical cells, but longitudinally they are elongated almost as long as inner medullary cells.

The gland cells and hyphae-like filaments are protruded into the central cavity (Fig. 39 G, B). They are especially abundant on the multi-rowed cellular septa at the base of branches (Fig. 38 F). The gland cell is ovoid

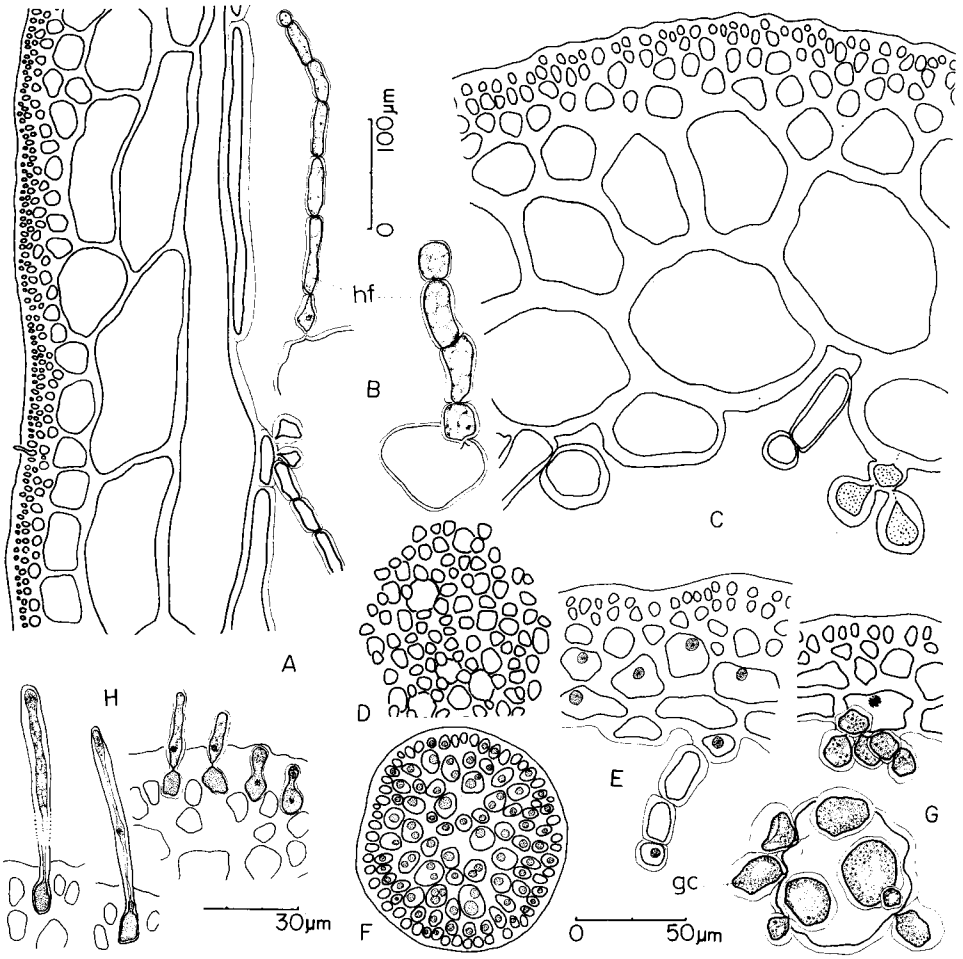

Fig. 39. *Chrysymenia wrightii* (HARVEY) YAMADA

A, longitudinal section of mature thallus; B, hyphae-like filaments; C. transverse section of mature thallus; D, cortex in surface view; E–F, transverse sections at apex, showing granules in cells; G, gland cells aggregated; H, development of hairs.

hf: hyphae-like filament, gc: gland cell.

to pear-shaped or irregular in form and about 35 μm in max. diam. They appear solitarily or more frequently in aggregation. More than eight gland cells may be aggregated (cf. YAMADA 1932). They are produced on innermost medullary cells and more often innermost slender cells or other gland cells. Homogeneously stained contents occupy the outer space of the cell, while the central portion is filled with vacuoles. Small granules are dispersed frequently in the cell. The nucleus is not discernible.

The hyphae-like filaments (YAMADA *l. c.*) appear solitarily or in aggregation (Fig. 39 B). They consist of two to seven (mostly two to four) cells covered with gelatinous wall. The basal cell becomes often pear-shaped, and the terminal one is round. The rest are oblong, 27~70 μm long and 14~19 μm wide on an average. There are no pigments in the cells. The ramified filaments, mentioned by YAMADA (*l. c.*), were not found in this investigation.

The holdfast in longitudinal section is solid and filled with small cells similar to cortex. The cells are somewhat compressed tetragonal and arranged in perpendicular rows. In the central portion, they are gradually elongate longitudinally toward the stipe in parabolic outline (Fig. 38 B). There are lost of small and globular cells aggregated among the medullary cells in stipe, as seen in *R. pertusa* (Fig. 31 F-G) and also in *Botryocladia microphysa* (HAUCK) KYLIN (as *Chysymenia microphysa*) by KUCKUCK (1912). It is not clear whether they are undeveloped large medullary cells, or the new cells formed secondarily after medullary cells are developed, though KUCKUCK mentioned they were formed secondarily. The central cavity is opened above the stipe. It widens gradually upwards (Fig. 38 A, C). The gland cells and hyphae-like filaments are aggregated abundantly at the base of this cavity. The small cells embedded in the medullary layer of the stipe are not seen in other portions.

Granules (oil droplets ?), stained deeply and homogeneously with cotton blue solution, are frequent in the inner cortical and outer medullary cells. They are abundant in young thalli, especially in the apical portion of branches or in the pericarp around the carpostome. In the apex of the thallus almost all cells contain these droplets (Fig. 39 E-F). The large one is about 7.0 μm in diam. Unicellular hairs are scattered uniformly over all thallus surface except for the lower portion of main axis. They are especially abundant in branchlets within 1 mm long below the apex or in young thalli (Fig. 38 G). The hair is developed from superficial cortical cell and protruded out of the gelatinous wall, leaving a slight constriction at the base (Fig. 39 H).

Reproductive Organs

Tetrasporangia : Tetrasporangial sori appear at first in the lower portion of primary or secondary branches, and extend uniformly over the frond

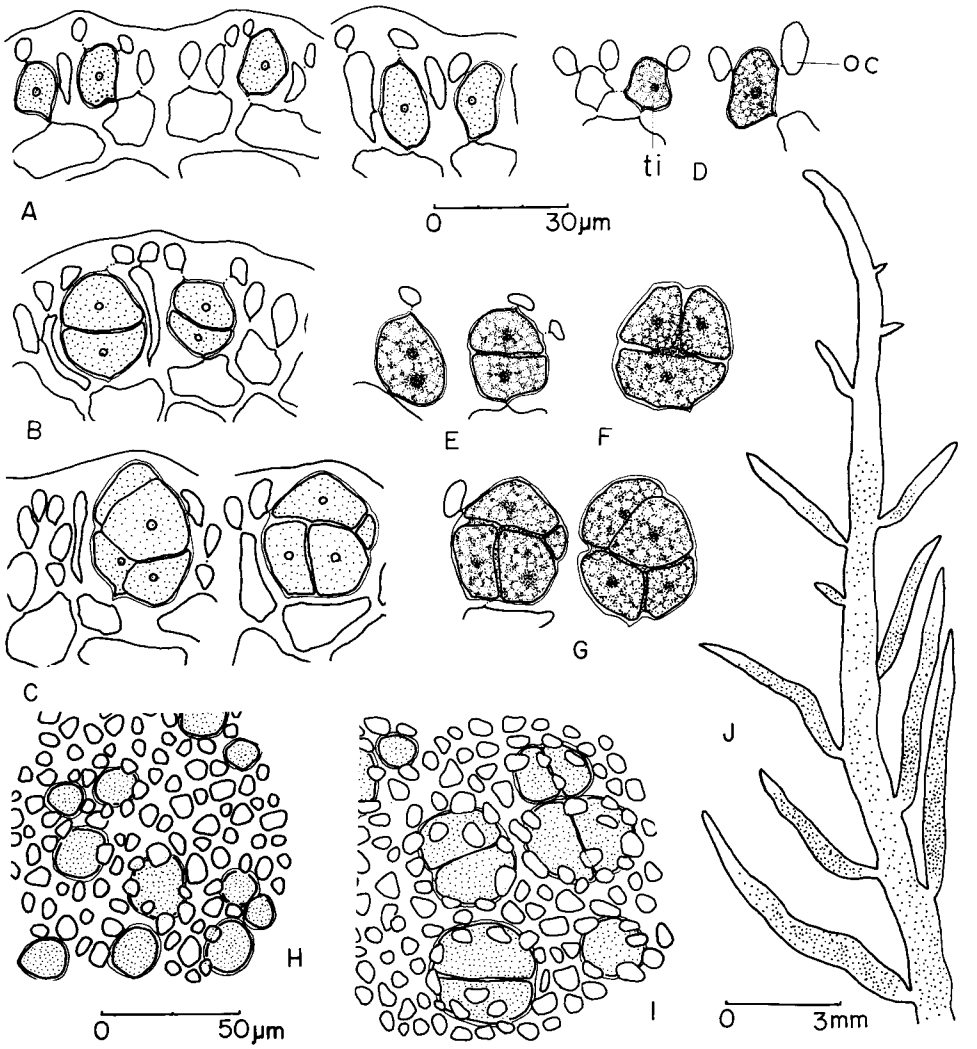

Fig. 40. *Chrysymenia wrightii* (HARVEY) YAMADA

A–C, development of some intercalary tetrasporangia in transverse view; D–F, growth of tetrasporangia, showing pit-connections with outer cortical cells; G, mature tetrasporangia; H–I, development of tetrasporangia in surface view; J, part of tetrasporangial thallus.

oc : outer cortical cell, ti : tetrasporangium-initial.

surface except for the base of branch and the lower and uppermost portions of main axis (Fig. 40 J). The plants bearing young sporangia are scarcely distinguishable from sterile ones in the field. However, as the sori are mature, they coalesce and the thallus surface becomes dark red.

Tetrasporangia originate from inner cortical cell. Like other adjacent inner cortical cells, the tetrasporangium-initial frequently has outer cortical cells, so that it occurs intercalarily in cortex. It has dense cytoplasmic substances and a distinct nucleus, so is discernible rather easily from the early developmental stage (Fig. 40 A, D). In early stage it becomes elliptical to ovoid. The pit-areas with outer cortical cells are protruded slightly. As the cell is enlarged to about 35 μm high, it is divided cruciately. The primary division occurs frequently somewhat obliquely to the surface and secondary ones anticlinally to the first before the completion of previous division. The central portion is undivided for a long while in young sporangium (Fig. 40 F). After maturation, the outer pit connection becomes difficult to discern. A mature tetrasporangium is almost round to elliptical and 48$\sim$53 μm long and 38$\sim$42 μm wide. There is no stalk cell of the sporangium.

Modification of adjacent sterile cells occurs in the sori. When the sporangium-initials are elongate, the sterile cells adjacent are modified into elongate slender forms without division. They become almost the same in height as the mature tetrasporangia. The thallus surface is uneven, as seen in sterile frond.

Spermatangia : Spermatangial sori appear and disperse over the thallus surface except for the middle to lower portion of main axis (Fig. 42 F). Spermatangial plants are scarcely distinguishable from sterile plants, except that they become somewhat pale in color.

As seen in cross section, the spermatangium is developed terminally on the mother cell. It originates from superficial cortical cell. When the cell is enlarged, it cuts off obliquely three to four mother cells on its upper corners. The mother cells are difficult to discern from the sterile cells in the early developmental stage (Fig. 41 A, E). The mother cells, especially larger ones, cut off one or two secondary spermatangial mother cells from the upper corners obliquely. Some of the secondary mother cells cut off again one tertiary cell in a similar manner. As a result, the spermatangial mother cells, originating from a single cortical cell, are seriate.

While the later mother cells are formed, the early ones develop spermatangia from the round top. The spermatangium and the mother cell do not have a common wall (Fig. 41 N). A mature spermatangium is elliptical to elongate-hemispherical and 4.0 μm high and 2.9 μm wide, while the

mother cell is oblong and 4.5~5.7 μm high and 2.8~3.1 μm wide. The mature spermatangium is released in a similar manner to the ones seen in the species of *Rhodymenia*.

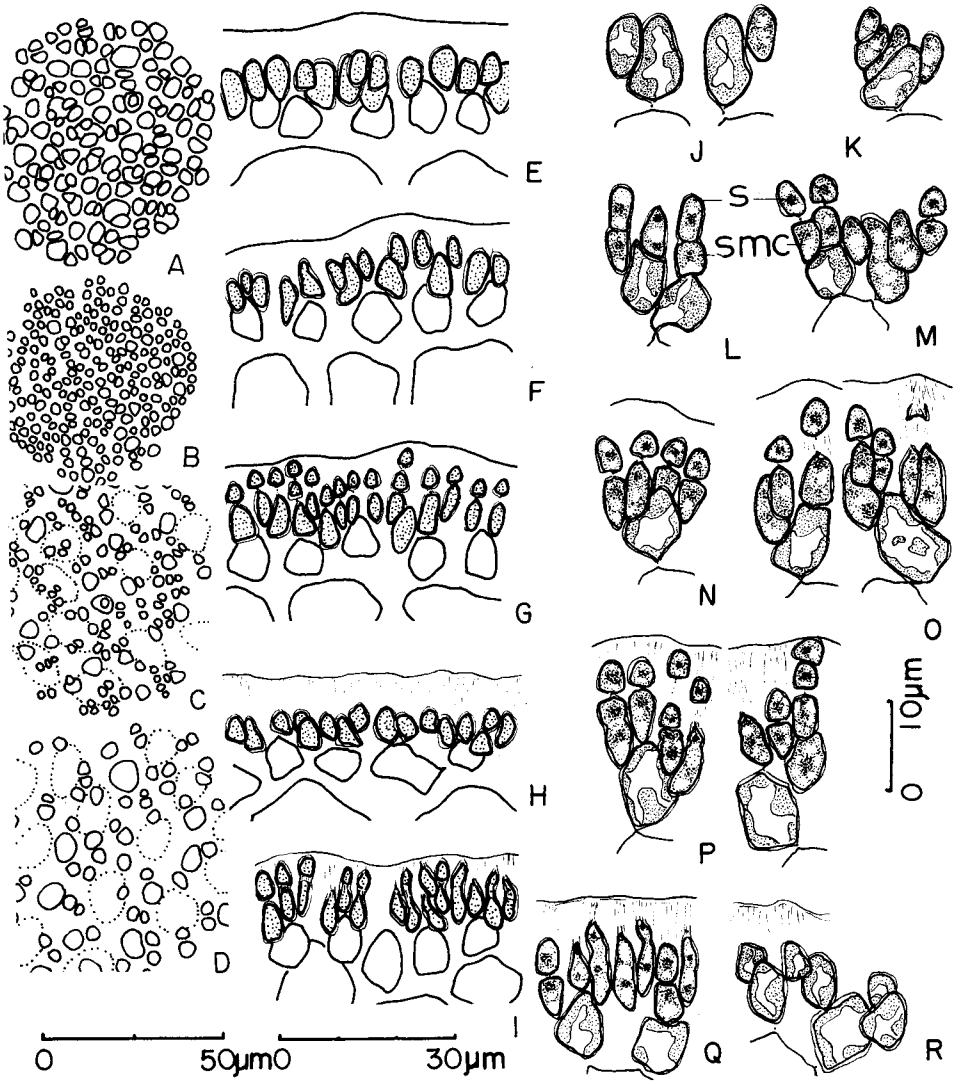

Fig. 41. *Chrysymenia wrightii* (HARVEY) YAMADA

A–D, development of spermatangia in surface view; E–I, the same in transverse view; J–K, formation of spermatangial mother cells; L–N, development of spermatangia terminally on mother cells; O–Q, successive development of spermatangia; R, later stage of development.

s: spermatangium, smc: spermatangial mother cell.

The secondary spermatangium is formed commonly on the same mother cell, as mentioned by TAZAWA (1975). Sometimes, it is developed while the primary one is still in the superficial wall of the thallus, so the two spermatangia are arranged in vertical row (Fig. 41 P). The tertiary sperma-

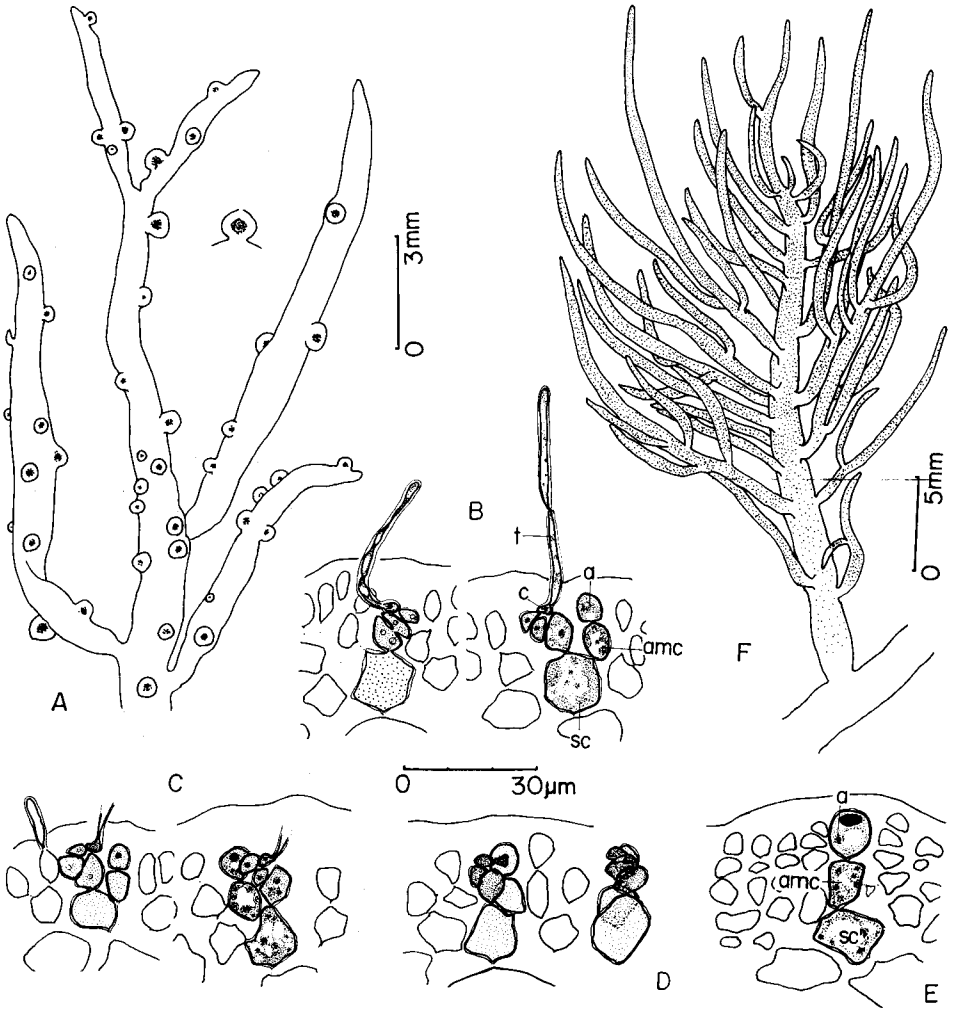

Fig. 42. *Chrysymenia wrightii* (HARVEY) YAMADA

A, part of cystocarpic thallus; B, supporting cell and carpogonial branch; C, degeneration of trichogyne; D, post-fertilization stage; E, enlargement of auxiliary cell branch, showing protein body in auxiliary cell; F, part of male thallus with spermatangial sori.

t: trichogyne, c: carpogonium, sc; supporting cell, a: auxiliary cell, amc: auxiliary mother cell.

tangium is also not rare. The mother cells become slenderer and make a protoplasmic continuation with later spermatangia instead of the pit-connection (Fig. 40 Q).

During spermatangium formation, the mother cells lose plastids before they develop primary spermatangia. The secondary and tertiary mother cells are formed without plastids from the beginning. The plastids are not seen in spermatangia and spermatia, while they are in the basal cell of the mother cells. The superficial wall of the sorus always remains during the spermatangium formation. When the spermatangial mother cells discontinue producing spermatangia, most of them recover cell contents as well as plastids and return to ordinary cortical cells. There remains, however, traces of liberation in the outer wall of the thallus, which is irregularly undulated over these areas.

Cystocarps: Most of the cystocarpic plants are less branched, though they become as large as the other thalli collected at the same time (Fig. 42 A). Cystocarps appear at first in middle to lower portion of primary branches issued at the middle to upper portion of main axis. In fully mature thalli, they are abundant in solitary or rarely together over whole the surface except for the lower portion of main axis. The cystocarp is sessile and elevated peach-shaped on the thallus surface, 750～850 μm high and 850～950 μm wide. The carpostome is 86～100 μm in diam. The rostrum is poorly developed (Fig. 44 B).

The carpogonial branch is four-celled. They are scattered sparsely in the cortical layer. The supporting cell is homologous to an inner cortical cell and is slightly larger than the adjacent sterile cells. It is polygonal, multinucleate and dense in contents. The first cell of carpogonial branch is almost similar in size and form to upper cortical cells. The second and third are semicircular and of almost the same in size, about a half to one third times the size of the first. The fourth cell, the carpogonium, is pyramidal in shape and about a half the size of the hypogynous cell. The carpogonium is connected laterally with the hypogynous cell, being curved while the other cells of the carpogonial branch are straight. A single nucleus is discernible in each cell of carpogonial branch, or sometimes two in the first (Fig. 42 B). The trichogyne is protruded at the top of carpogonium and elongates as a long flattened filament curved at the basal portion and twisted once or twice. The protoplasm is articulated with small vacuoles.

The two-celled auxiliary-cell branch is distinguishable after presumed fertilization. The auxiliary cell is round and has a protein body (cf. KYLIN 1930) at an early developmental stage, while the auxiliary mother cell has

many nuclei and densely stained contents. Both cells are enlarged almost similarly at first. When the auxiliary cell becomes nearly same in size as the first cell of carpogonial branch, the carpogonium, having lost the trichogyne, coalesces with it (Fig. 42 D). The presumed diploid nucleus of the carpogonium seems to migrate to the auxiliary cell. After the coalescence, the carpogonium becomes indiscernible soon, but the hypogynous cell maintains this coalescence with the auxiliary cell. The cells of carpogonial branch englarge pit-areas. In this stage, these fertile cells remain together and en-

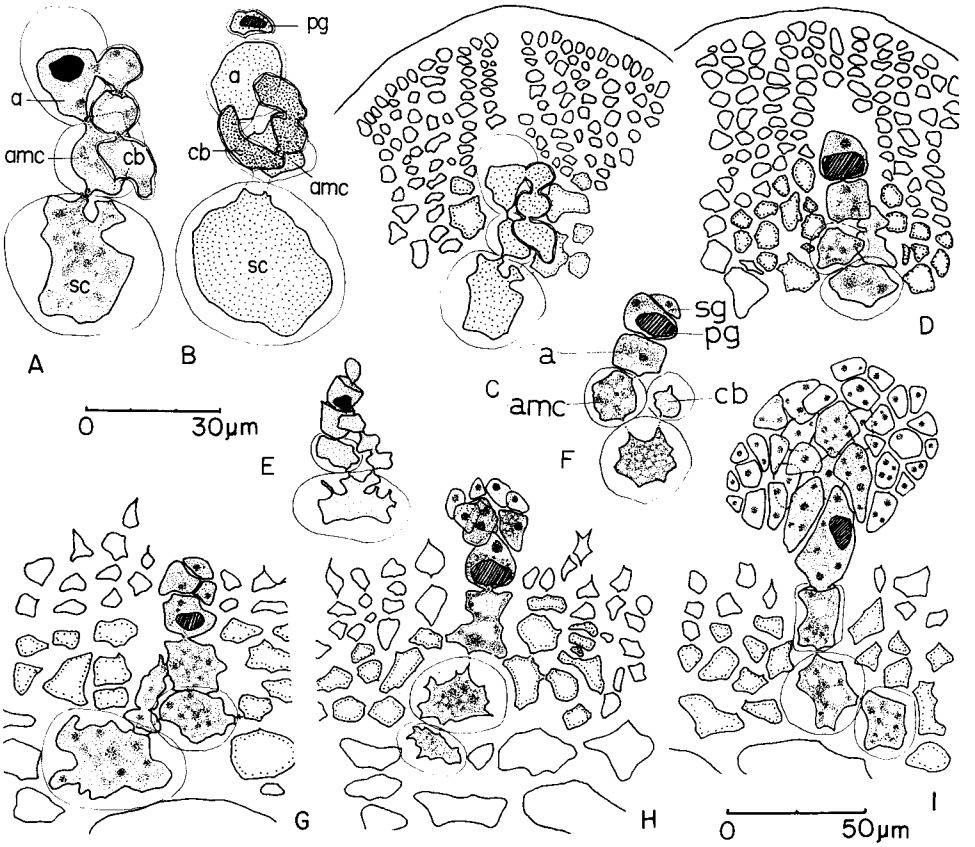

Fig. 43. *Chrysymenia wrightii* (HARVEY) YAMADA

A, C, fusion between auxiliary cell and carpogonial branch; B, D, cutting off primary gonimoblast cell, cells of carpogonial branch coalescing; E-F, cutting off secondary cell of gonimoblast; G-I, development of embryonic cells of gonimoblast.

a: auxiliary cell, amc: auxiliary mother cell, sc: supporting cell, cb: carpogonial branch, pg: primary gonimoblast cell, sg: secondary gonimoblast ell.

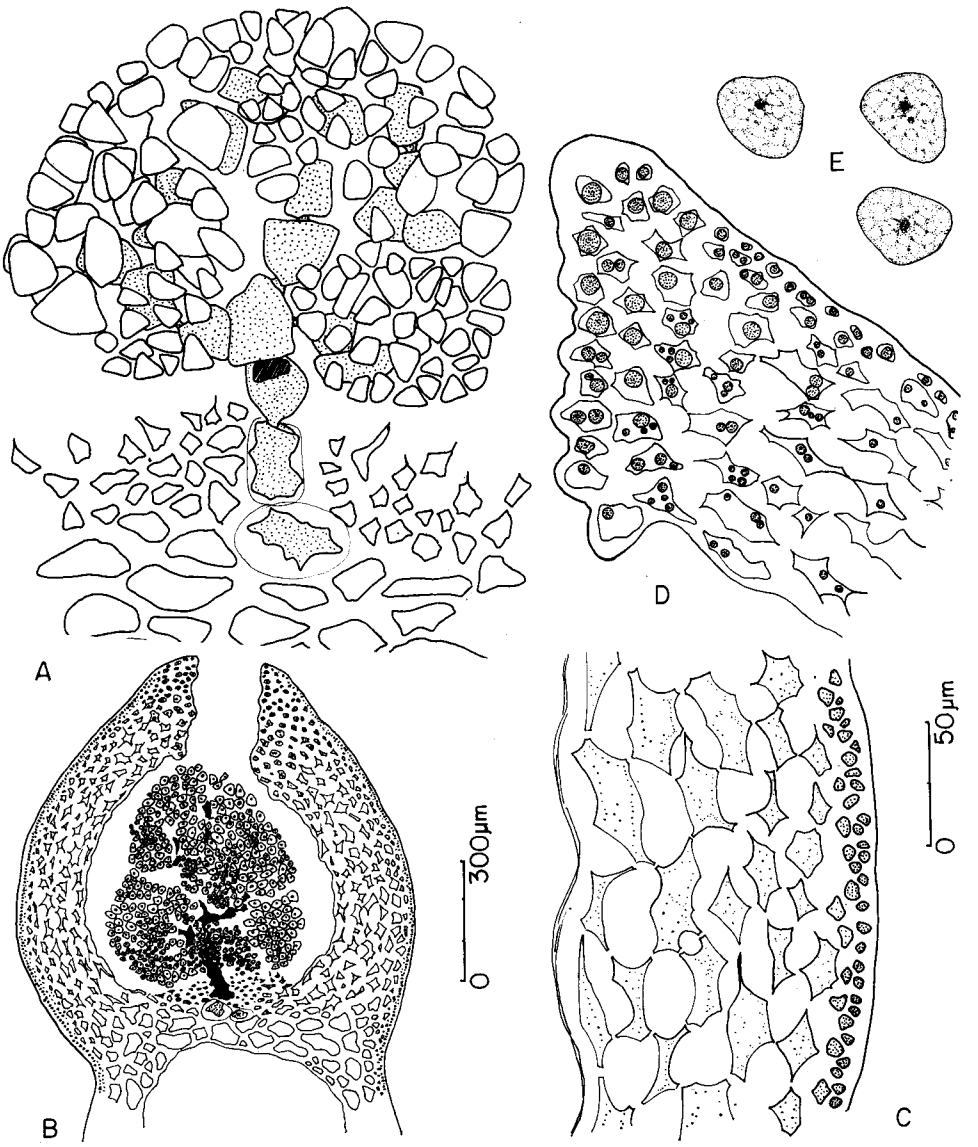

Fig. 44. *Chrysymenia wrightii* (HARVEY) YAMADA

A, young carposporophyte; B, mature cystocarp; C, part of pericarp, inner cells becoming stellate; D, part of rostrum, containing granules in cells; E, carposporangia.

large slowly. The cells of carpogonial branch, losing the contents, disappear gradually without fusing. The supporting cell and the auxiliary mother cell become thick walled (Fig. 43 A, C). The auxiliary cell is covered with a thick gelatinous coat.

The primary cell of the gonimoblast is cut off transversely from the upper portion of the auxiliary cell. It contains a large protein body which was in the auxiliary cell (Fig. 43 B). A large nucleus is located generally upon the protein body. The secondary gonimoblast cell is cut off obliquely from upper side of the primary gonimoblast cell (Fig. 43 F). The further cells of the gonimoblast are cut off successively from the outer ones to form a young carposporophyte almost round in shape (Figs. 43 I, 44 A).

As the carposporophyte grows, carposporangia are developed from the outer cells of the gonimoblast successively, so that almost all the cells of gonimoblast are changed into carposporangia. In mature cystocarp the auxiliary mother cell, auxiliary cell and early gonimoblast cells make a fusion cell. The carposporophyte is immersed in gelatinous substances. A mature carposporangium is polygonal to round and 32～38 μm in diam. It is oblong during the maturation.

The vegetative cells around the procarp modify before or soon after the coalescence between the carpogonial branch and auxiliary cell. The cortical cells around the procarp are divided periclinally into flat cells and arranged in perpendicular rows to the surface. Many secondary pit-connections are formed between the auxiliary mother cell and adjacent sterile cells. The latter becomes rich in nutrition accordingly. The auxiliary mother cell cuts off also vegetative cells around it. Further developmental pattern of the pericarp is similar to the ones seen in the species of *Rhodymenia*.

The mature pericarp is composed of two layers. The outer one is similar to cortex, and the inner one consists of six to eight rows of hyaline cells, which become stellate in form owing to radial protoplasmic connections (Fig. 44 C). The pulvinus at the base of cystocarp is not conspicuous in this species.

Discussion

This plant was first named by HARVEY (1859) as *Halosaccion wrightii*. The diagnosis was short, describing with a sterile plant of only a few centimeters, and mentioned the type locality, Hakodate, Japan. Later, it was transferred by OKAMURA (1916) to *Chylocladia* without referring to the reason. YENDO (1917), however, treated it as a synonym of *Chrysymenia enteromorpha* HARVEY, and mentioned the type specimen was nothing but a young and small form of this.

In 1932 the plant was investigated by YAMADA, who concluded YENDO's treatment was rather doubtful. He pointed out that the existence of hyphae-like filaments in the cavity inside of the frond of this species was the most important difference compared with *C. enteromorpha*. Accordingly, he nominated it as *C. wrightii*.

INAGAKI (1933) and OKAMURA (1936) added to YAMADA's description with reference to vegetative structure or the female organ. INOH (1947) investigated the early developmental features of carpospore and tetraspore, and mentioned that the both spores germinated and formed a "tetraprotocell" from which discoid base was formed and the frond erected later. Recently, TAZAWA (1975) reported the male organ for the first time.

As seen in the members of *Rhodymenia*, the tetrasporangium is homologous to inner cortical cells, and occurs frequently as an intercalary cell among cortical cells. Although no one has mentioned such a character in the genus, it is expected to occur in other members of *Chrysymenia*.

Lomentaria LYNGBYE (1819)

The genus *Lomentaria* was erected by LYNGBYE (1819) on the basis of a single species, *L. articulata* (HUDSON) LYNGBYE (*Ulva articulata* HUDSON (1762)). He described the character of the genus as *articulato-constracta* thallus with *oppositis verticillatisque* ramification. On the other hand, the genus was interpreted as *Chondrothamnion* and *Chondrosiphon* by KÜTZING (1843) or *Hooperia* by J. AGARDH (1896) (cf. BLIDING 1928, KYLIN 1956).

The genus is characterized currently by branched cylindrical or slightly flattened thallus articulated by multi-rowed cellular septa at various intervals, consisting of cortical and medullary layers, bearing gland cells, tetrahedrally divided tetrasporangia occurring terminally in cortex with hollow superficial wall in sorus, and by hemispherically elevated cystocarps in which carposporangia are converted from almost all the cells of gonimoblast.

The genus was investigated taxonomically by HAUPTFLEISCH (1892), KYLIN (1923), BLIDING (1928), and SVEDELIUS (1937) on the structure of vegetative thallus or development of reproductive organs.

Lomentaria hakodatensis YENDO

(Text-figs. 45～52 : Plate V, A-C)

(1920) Nov. Alg. Japon., p. 6. OKAMURA (1927) p. 12 ; (1936) p. 684 ; YAMADA (1928) p. 518 ; INAGAKI (1933) p. 41, figs. 14～15 ; SEGAWA (1935) p. 84 ; TAKAMATSU (1939) p. 67, pl. 12, fig. 1 ; YAMADA & TANAKA

(1944) p. 72; DAWSON (1944) p. 308, pl. 75, fig. 2; (1950) p. 337; (1963) p. 466, pl. 86 (10), fig. 2; TOKIDA (1954) p. 195; KANG (1966) p. 87; FUNAHASHI (1966) p. 141; (1967) p. 31.

Lomentaria sinensis HOWE (1924) p. 139, pl. 1, fig. 1; TSENG & LI (1935) p. 221.

Hooperia baileyana J. AGARDH sensu SETCHELL et GARDNER (1930) p. 153.

Japanese Name: *Kosujifushitsunagi* (OKAMURA)

Type Locality : Hakodate, Japan

Materials

Shiribeshi District. Oshoro: June 4, 13; July 11; Aug. 10, 19; Sep. 11, 1966. Feb. 11; Mar. 11; May 27; June 3; July 7; Aug. 3, 17; Sep. 20, 1967. Jan. 24, 1968. *Iburi District*. Charatsunai, Muroran: July 1, 20; Aug. 1, 20; Sep. 13; Oct. 13; Dec. 26, 1966. Jan. 25; May 26, 1967. Tokkarisho, Muroran: May 27; June 23, 1967. *Kushiro District*. Aikappu, Akkeshi: Aug. 26, 1966. *Hidaka District*. Horoizumi: Aug. 30, 1966. Erimo: Sep. 28; Nov. 14, 1966. *Nemuro District*. Rausu: May 13~4, 1968.

Discription

Thallus intertangled, forming spherical to hemispherical masses in tuft, cylindrical, very gelatinous, flaccid, branching three to five times, articulated at intervals of 1.5~6 mm, monopodial in growth, estipitate, attaching to substratum by means of stoloniferous discoid holdfast, 6~9 cm high, 0.8~1.3 mm wide at the broadest part; holdfast erecting a few fronds; main axis slightly narrowed at base, slightly or scarcely constricted at septa, gradually attenuate upwards, tapering at apex, branches strictly opposite, verticillate or rarely alternate, spreading widely, issued at or just beneath septa, similarly broad throughout, ultimate branchlets slightly curved inwards, much constricted at septum; frond in section composed of cortical and medullary layers, 75~120 μm thick, central cavity with cellular septa, cortical layer single cell-rowed, cortical cells oblong to elliptical, sometimes cutting off small cells obliquely outwards, densely pigmented, arranged in palisade-like row, 17~24 μm high, 11.2~19.5 μm wide, medullary layer composed of four to six cell-rows, medullary cells round to elliptical, increasing in size inwards, elongated longitudinally inward, inner cells hyaline, 14.5~27.5 μm high, 20~32 μm wide, 70~150 μm long, transverse septa multi-cellular rowed, gland cells attaching to innermost cells, solitary or aggregated, unicellular hairs abundant in upper portion of branches or branchlets; tetrasporangia occurring in sori on inflated inter-septa of branches, with hollow superficial wall in sorus, sinking inwards, almost round, tetrahedrally divided, 90~110 μm in length, 95~125 μm in width, surrounded by filaments of modified medullary

cells; spermatangia developed in sori over whole thallus surface except for lower portion of main axis, developed terminally on mother cell, hemispherical to elliptical, 4.6 μm long, 2.9 μm wide; cystocarps scattered mostly on upper portion of frond, solitary or aggregated, elevated, mammiform, sessile, with pericarp of stellately modified cells, with carpostome, 860~1100 μm high, 750~980 μm wide, carpogonial branch three-celled, carposporangia polygonal to round, 90~110 μm in diam.; color brownish purple; specimens adhered to paper firmly in drying. Annual.

Habitat : Lower tidal zone on rocks or other algae.

Distribution : Middle to Northern Honshu and Hokkaido, Japan; Southern California, Gulf of California; Vladivostok; China; and Korea.

Phenological Observation

The investigations were carried out at Oshoro and Muroran from June, 1966 to May 1968. The plants were common in these areas on rocks or other algae such as *Rhodomela larix*, *Corallina pilurifera*, *Symphyocladia latiuscula*, and *Sargassum thunbergii*. In Oshoro Bay they inhabited in lower tidal zone at calm place of inner Bay, but in Charatsunai, Muroran at exposed place to direct wave action.

In Oshoro Bay in early June, 1966 erect plants were sparse from a prostrate cushion-like mass. They were mostly less than 2 cm high and 0.5 mm wide and had several primary branches only. Some of them about 4 cm high issued secondary branches with small protrusions of tertiary branches. The upper portion of branches or branchlets is very slender. In mid June, the plants increased in number and were intertangled, forming a rounded tuft. The fusion of fronds was rather frequent from early growth. Tetrasporangial and spermatangial plants bore the sori in early developmental stage. In July they became 6~7 cm high and 0.5~0.8 mm wide on an average. As mentioned by INAGAKI (1933), the plants growing at the inner Bay affected almost by no wave action were very slender. They formed a strictly spherical to hemispherical tuft in 10~18 cm diam. Such thalli were intricate so much that it was almost impossible to separate branches from each other. More than half of the thalli collected were tetrasporic with mature sori, while the others were spermatangial and young cystocarpic plants. In early August the female thalli had mostly mature cystocarps. After late August, the plants decreased in number rapidly. On the other hand, several germlings less than 2~3 cm high and 0.3 mm wide were among the mature thalli. Some were erect, but most of them were procumbent. In September, the mature tufts were rare, but the germlings were common. Some of the latter had spermatangial or tetrasporangial sori, and also cys-

tocarps. They were less than 1.5 cm high on an average. In February, 1967 procumbent thalli with a few to several erect fronds were found. However, they were not larger than the ones seen in September, though they had rather broad branches, about 1 mm on an average, constricted very much at upper one to two septa. Such procumbent thalli were found also in March, 1967 and January, 1968. On the other hand, the plants collected in May, 1967 had frequently erect fronds and abundant procumbent stolons, expanding on substratum rather broadly.

At Charatsunai, Muroran, the plants appeared in May to early June, and formed also intertangled tufts, but expanded on the substratum rather irregularly. The tufts decreased in number after late August and were rare in September. All fertile organs appeared almost at the same time as in Oshoro Bay. On the other hand, spores germinated occasionally after July. They bore tetrasporangia and spermatangia after early August and cystocarps after September. These germlings were found in October as intertangled thalli of about 5 cm high and 0.5 mm wide at the broadest part. In addition, the procumbent to decumbent thalli of a few centimeters height were not rare in September, October, December, January and May. Most of them were epiphytic on *Corallina pilurifera*, developing lots of stolons and rhizoids. The plants found in May, 1967 protruded erect fronds frequently 2～3 cm high. They extend rather broadly on the substratum. Besides, the plants encountered in July, 1967 at Tokkarisho, Muroran were characteristic especially in having many large branches. They were mostly more than 8～9 cm high and 1～1.3 mm wide at the broadest part, and form very intertangled tufts of 15～20 cm or more in diam. Tetrasporangial and spermatangial plants were common, but the cystocarpic plants occasional.

Considering the above investigations, this species both at Oshoro Bay and Muroran protrudes erect fronds in May and forms a tufty mass later. They become most luxuriant during July and August, and decrease in number rapidly, so that the mature thalli disappear after September to early October. However, during the luxuriant period, there appear new germlings derived from spores. Some of them remain as small procumbent to decumbent cushion-like mass during the winter season, and wait for next May to protrude the erect fronds. Both spermatangial and tetrasporangial sori appear from June, and cystocarps from late June to early July. The germlings developed during the luxuriant period form reproductive organs after August. They remain until the mature thalli disappear. Tetrasporangial plants occur most commonly and cystocarpic ones frequently, while spermatangial plants are not so frequent. The male plants were generally small in size.

Morphological Observation

External Appearance

The plant is cylindrical and grows monopodially. It appears at first as stoloniferous procumbent to decumbent thalli, producing only short primary branches and sometimes a few protrusions of secondary branches. These branches erect themselves later and become prosperous.

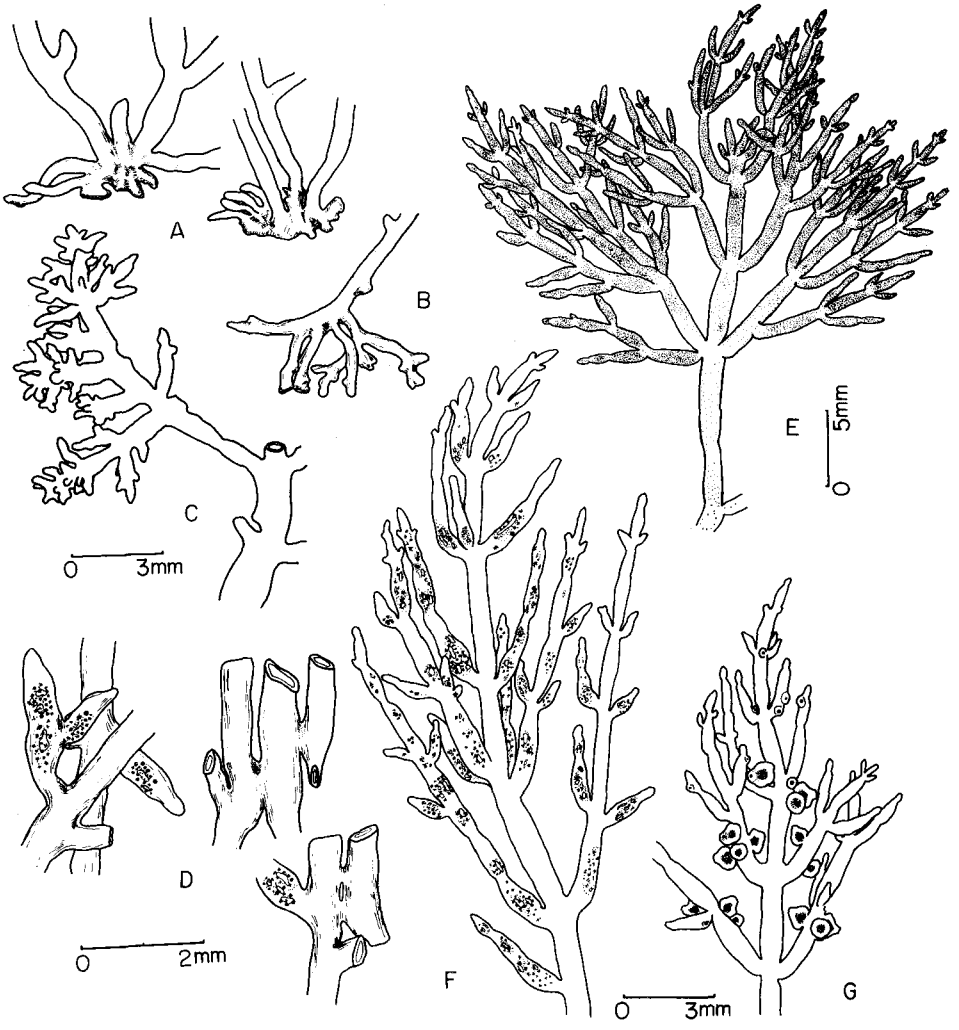

Fig. 45. *Lomentaria hakodatensis* YENDO

A, part of holdfasts; B, rhizoid formation from stolon; C, peculiar ramification; D, fusion of branches; E, part of male thallus bearing spermatangial sori; F, part of tetrasporic thallus; G, part of cystocarpic thallus.

The mode of ramification is similar in all the branches. They occur three to five times repeatedly in strictly opposite manner or sometimes in verticils of three to four branches and rarely alternate. The lower branches are longer than the upper, so that the mature thallus becomes mostly pyramidal to paniculate in outline. The branches are issued at or just beneath the septa with divergence of about 45°. The inter-septa are variable within 2～8 mm, or more than 10 mm long. Especially lower septa of mature thalli are much longer than the others.

The septum is indiscernible in outer appearance as the plant grows,

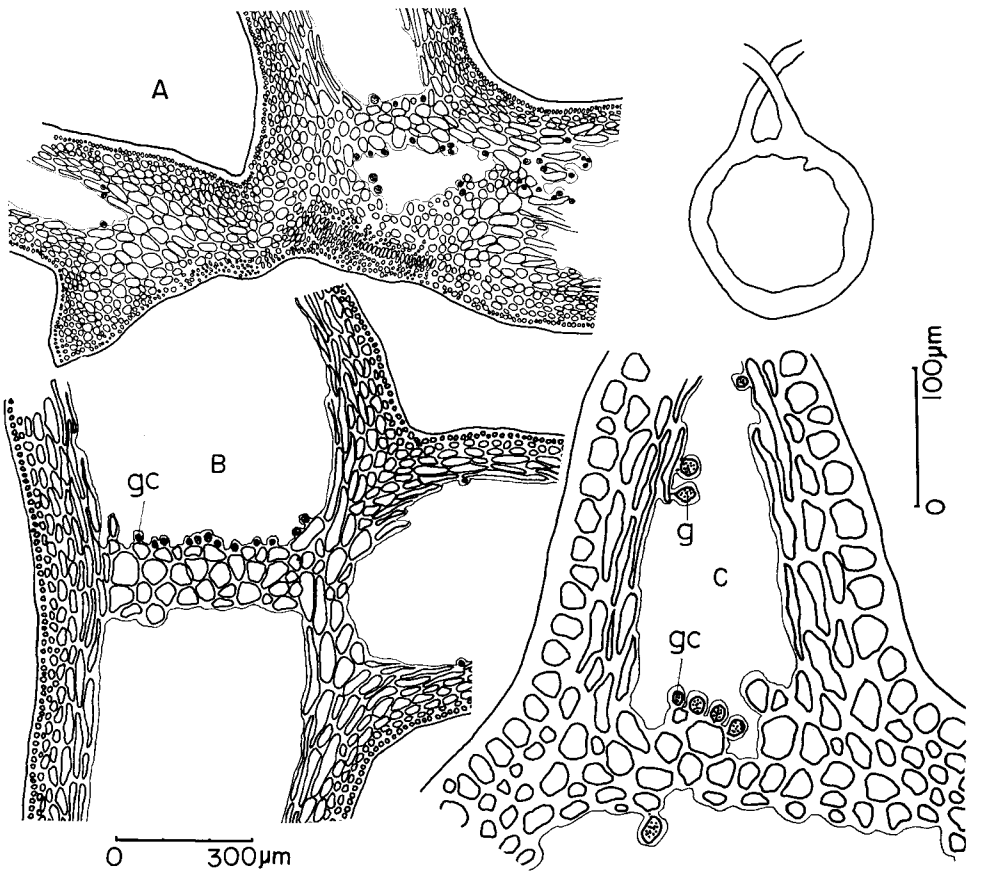

Fig. 46. *Lomentaria hakodatensis* YENDO

A, part of base in longitudinal view; B, a ramified portion in longitudinal view, showing multi-cellular septum and gland cells; C, the same in transverse view, the branch (upper part) being sectioned longitudinally.

g, gc: gland cell.

especially in the main axis and primary or secondary branches. However, it is distinct in branchlets or young branches by a remarkable constriction. In fertile branches bearing tetrasporangial or spermatangial sori, the septa are very distinct owing to the inflation of soral areas.

The discoid holdfast erects several fronds, and develops more frequently procumbent to decumbent stolons. The stolons protrude fronds at various intervals and develop rhizoids at random (Fig. 45 A–B). There occurs frequently the fusion of thalli, and the plant becomes much intertangled as it grows. It is very difficult to find the original base from such a mass of thalli.

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers (Fig. 47 F), which surround the central cavity interrupted by multi-rowed cellular septa at definite intervals. The cortical layer is single rowed with comparatively large and oblong to elliptical cells, which cut off sometimes small cells of one third to one fifth in size obliquely outwards. The cortical cells are arranged in a palisade-like row and contain plastids densely. Observed from surface they are polygonal to elliptical in middle to upper portion and longitudinally elongate about two to three times as long as wide in lower portion of the thallus.

The medullary layer is composed of four to six rows of cells. The medullary cells are round to periclinally elliptical and gradually larger inwards. Outer two to three cells are pigmented poorly, while the inners are hyaline. In longitudinal section outer cells are elongated to two to five times of transverse width, while inner cells about seven to ten times. The cells become narrow at both ends. In addition, there occur at random almost filamentous cells developed longitudinally on the inside of innermost medullary cells. They are smaller than the cortical cells in diameter, but elongate and nearly as long as the inner medullary cells. A gelatinous substance fills the cellular layer rather thickly (Fig. 47 E).

In young thallus, the cortical cells are slender and vertically oblong, while the medullary cells are few in number and arranged loosely (Fig. 47 D). The gland cells are developed inwards on the innermost medullary cell, or more frequently on filamentous cell. They are originally round to ovoid or polygonal and occur in solitude or aggregation (Fig. 47 C). As mentioned by INAGAKI (1933), they appear abundantly upon the septa. The large one is 17～21 μm in diam. (cf. INAGAKI 1934).

The base is composed of small cells outwards and large and longitudinally elliptical cells at the central portion (Fig. 46 A). The central cavity is developed soon in the stipe as somewhat rotund outline. The filamentous cells

are abundant at the base of the cavity. The transverse septum is composed of three to four irregularly arranged rows of cells (Fig. 46 B). The cells are hyaline, almost round to polygonal and thin walled. As mentioned previously, the gland cells are aggregated more abundantly upon the septum.

The fusion of thalli occurs with the modification of mutual cortical cells, which are elongated anticlinally three to seven times as long as wide, and interwoven with opposite elongate cells. The border of fusion disappears

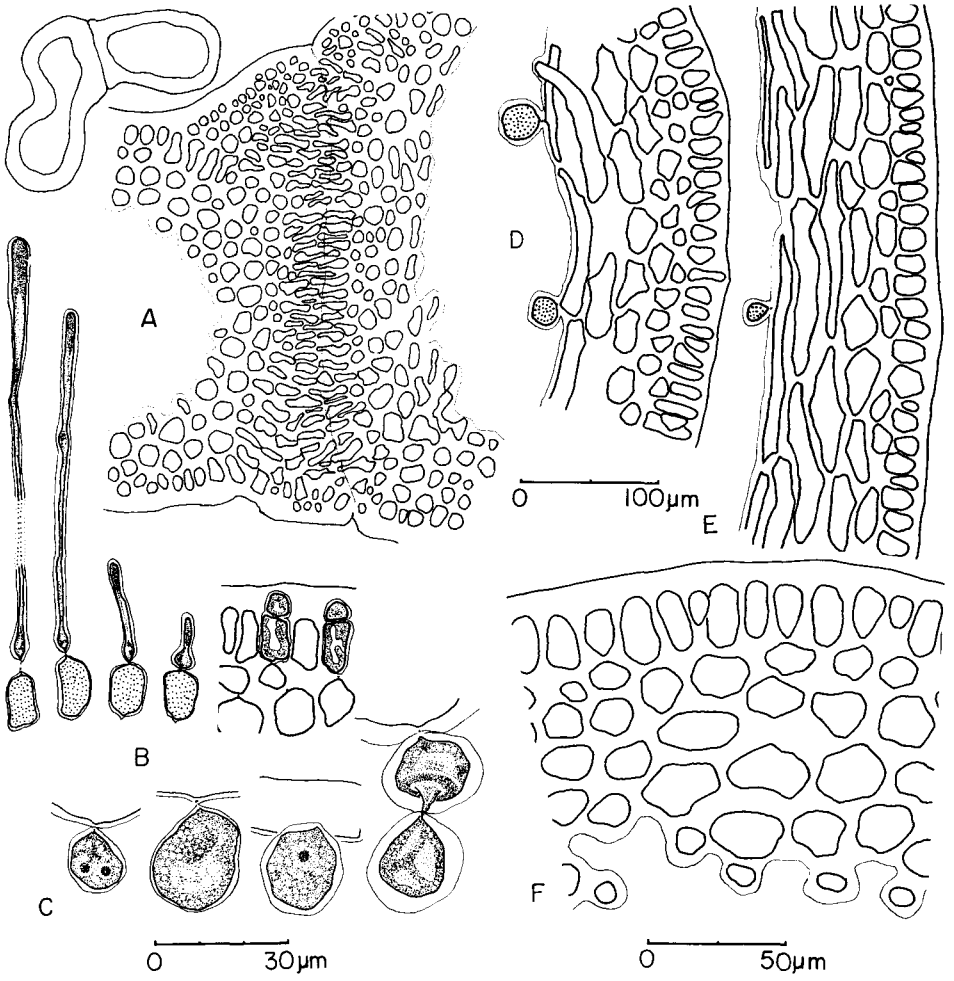

Fig. 47. *Lomentaria hakodatensis* YENDO

A, transverse section of thallus at fusing portion; B, development of hairs; C, gland cells; D–E, part of frond in longitudinal view, D being young; F, mature thallus in transverse view.

later. Protoplasmic connections are common (Fig. 47 A). Unicellular hairs are dispersed densely and uniformly over whole the thallus surface, especially on upper segments, but scarcely in lower portion of fronds. At the beginning the cortical cell cuts off a small semicircular cell outwards. It becomes pyriform before elongating as the hair (Fig. 47 B).

Reproductive Organs

Tetrasporangia : The tetrasporangial sori appear at first on secondary or tertiary branches issued at middle portion of the main axis (cf. YENDO 1920, HOWE 1924, YAMADA 1928, INAGAKI 1933). The sori are dispersed around inter-septa in round to elliptical form. When they are developed, the fertile inter-septum is inflated to one and a half to two times as broad as the sterile one. The soral portion is discerned by a dark purple color (Fig. 45 A).

As the tetrasporangial sorus is developed, the superficial gelatinous wall at the portion is ruptured forming an elliptical or round to oblong hollow at first, and becomes irregular as the sorus matures. It is generally 200～300 μm or more than 400 μm in diam. (cf. HOWE *l. c.*, DAWSON 1950). Observed from surface, there are lots of small cells developed in net-work. The sporangia in various stages of development are connected terminally with these cells (Fig. 48 A).

The tetrasporangium originates from cortical cells. At the beginning several cortical cells are divided laterally into small cells successively. As the divisions proceed, the cells become much smaller with irregular shape and denser cytoplasmic substances. The sporangium-initials are formed terminally on these small cells. They have a large nucleus and almost round shape distinguishable easily from the sterile cells (Fig. 48 D). As the young sporangium grows to about 60μm high, showing obovate form, the tetrahedral furrows occur centripetally from the surface. For a while the central portion remains undivided. The division planes are formed simultaneously (Fig. 48 I). The tetrasporangium becomes round again during the division. The mature sporangium is 90～110 μm long and 95～125 μm wide (Fig. 48 F).

The medullary cells in the soral area become irregular in shape when the tetrasporangium-initials appear. Then, they change into filamentous cells, which form a net-work but is not so conspicuous. The superficial wall in the sorus ruptures when the small cells begin to sink inwards.

Spermatangia : The male plants are comparatively small in size. When the spermatangial sori are mature fully, the thallus has a light color and very soft texture (Fig. 45 E). The spermatangial sori appear at first in middle to upper portion of branches and branchlets (cf. SETCHELL & GARDNER

1930). Later, they are fused with one another, extending over whole thallus surfaces except for the basal portion of main axis. The soral area is swollen slightly as mentioned by DAWSON (1950). Even in fully mature sori, the spermatangia appear not compactly, but somewhat in circle upon the original superficial cortical cell (Fig. 49 C).

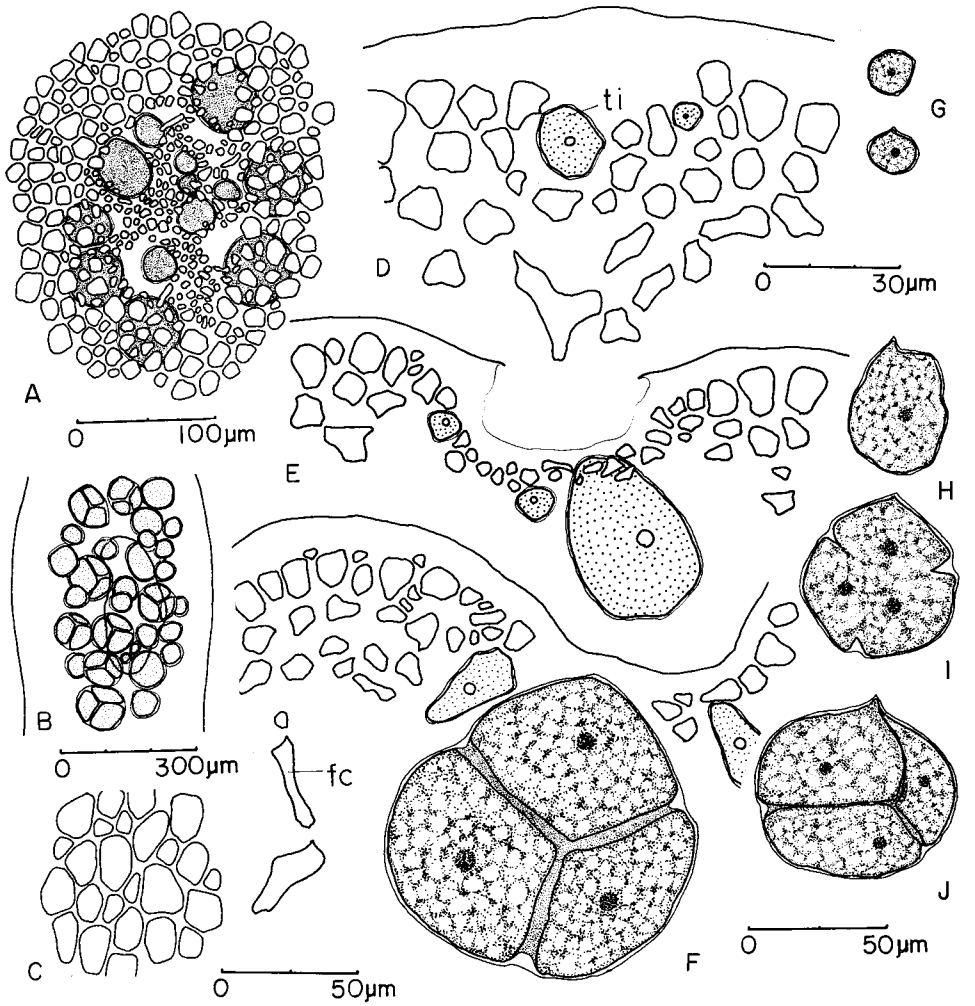

Fig. 48. *Lomentaria hakodatensis* YENDO

A–B, tetrasporangial sori in surface view; C, sterile cortex in surface view; D–F, development of tetrasporangia in transverse view, D cutting off small cells and inner cells modified filamentously; G–J, growth of tetrasporangia. ti: tetrasporangium-initial, fc: filamentous cell.

The spermatangia are developed terminally on the spermatangial mother cell. At the beginning the superficial cortical cell cuts off obliquely three to four mother cells around its upper corners and remains with a basal cell.

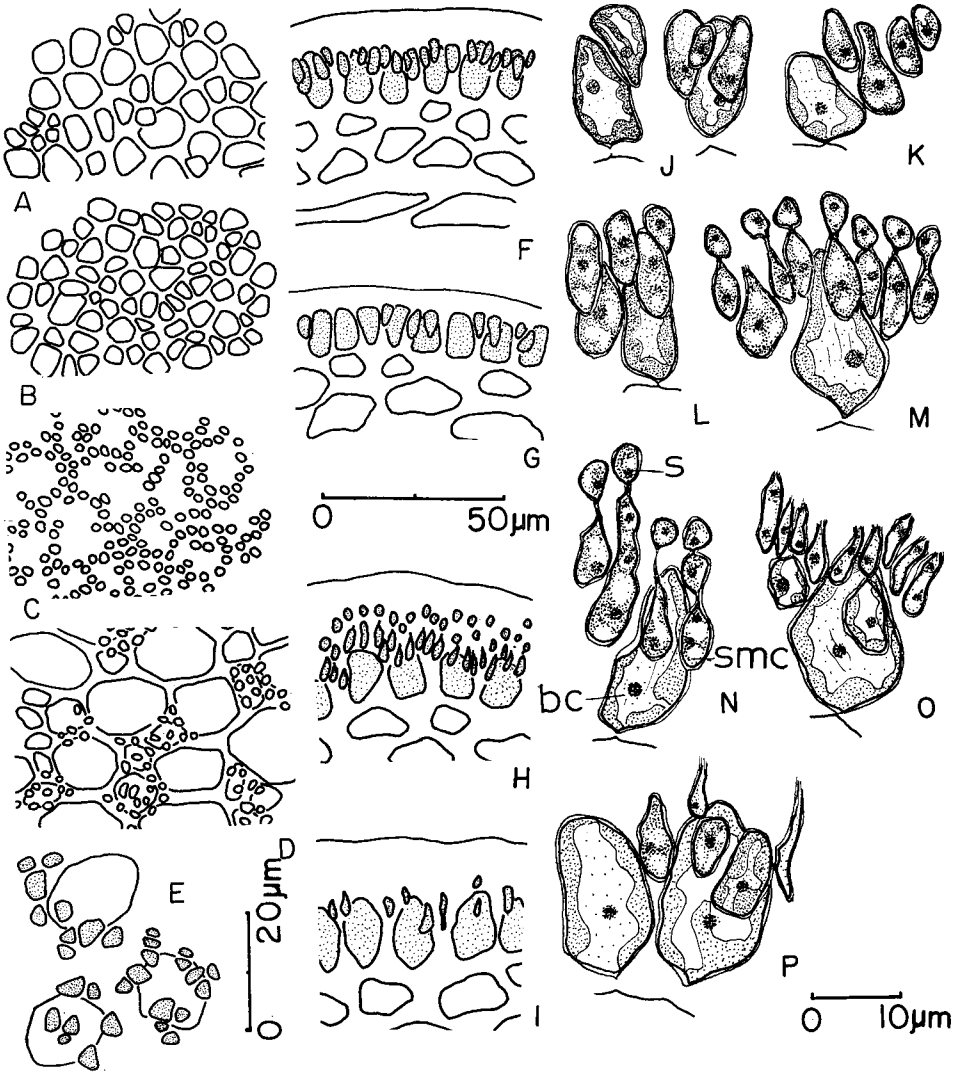

Fig. 49. *Lomentaria hakodatensis* YENDO

A–E, development of spermatangia in surface view, E being seriate mother cells; F–I, the same in transverse view; J–K, formation of mother cells; N–O, successive development of spermatangia; P, later stage of development.
s: spermatangium, smc: spermatangial mother cell, bc: basal cell.

These mother cells cut off again one or two secondary mother cells in a similar manner to the previous formation. Then, a single tertiary mother cell is cut off from the secondary. As a result, these mother cells originating from a single cortical cell are seriate in row around the cortical cell. The early formed mother cells are larger than the later ones, which are cut off convexly. Sometimes, after cutting off the primary mother cells, the cortical cell is divided into two transversely and the upper cell becomes also the mother cell and the lower remains as a basal cell.

Before or after later mother cells are formed, previous ones, about 10.3 μm high, become round at apex and cut off the spermatangium by a centripetal constriction (Fig. 49 M). The mature spermatamgium is hemispherical to elliptical, 4.6 μm high and 2.9 μm wide, while the mother cell is 6.8～9.7 μm high and 2.9～4.3 μm wide. The mother cells lose plastids before they cut off the spermatangia. The spermatangia and spermatia have no plastids. Often the hairs remain upon the mother cells in the early stages of spermatangium development. The superficial wall of the thallus remains always in the fertile area.

The mature spermatangium releases the pit-connection with the mother cell, and migrates through the outer gelatinous wall, where the spermatangial wall seems to be ruptured. The spermatium conveys all the contents of the spermatangium. After the liberation of primary spermatangium, the mother cell cuts off again a secondary spermatangium in a similar manner to the previous formation. Frequently the latter is formed while the previous one still remains within the outer wall, so that the two spermatangia are arranged anticlinally upon the mother cell (Fig. 49 N). The tertiary spermatangium is also not rare. As the spermatangium formation is continued successively, the mother cell becomes slenderer in form and poorer in contents, as seen in *Chrysymenia wrightii*. When the spermatangium formation is discontinued, most of the mother cells disappear and the remaining basal cells convert into ordinary cortical cells (Fig. 49 I, P).

Cystocarps: The cystocarps appear at first on the upper portion of lateral branches, and then numerously over whole branches except for the lower part of main axis. They appear in solitude or aggregation of two to four (Fig. 45 G). The cystocarp is sessile, elvated mammiform, 860～1100 μm high and 750～980 μm wide (cf. YENDO 1920, YAMADA 1928, INAGAKI 1933). The carpostome is about 90 μm in diam.

The carpogonial branch is three-celled, and curved more or less. It was abundant at the apical portion of branches and branchlets in early July at Charatsunai. The supporting cell is homologous to outer medullary cells.

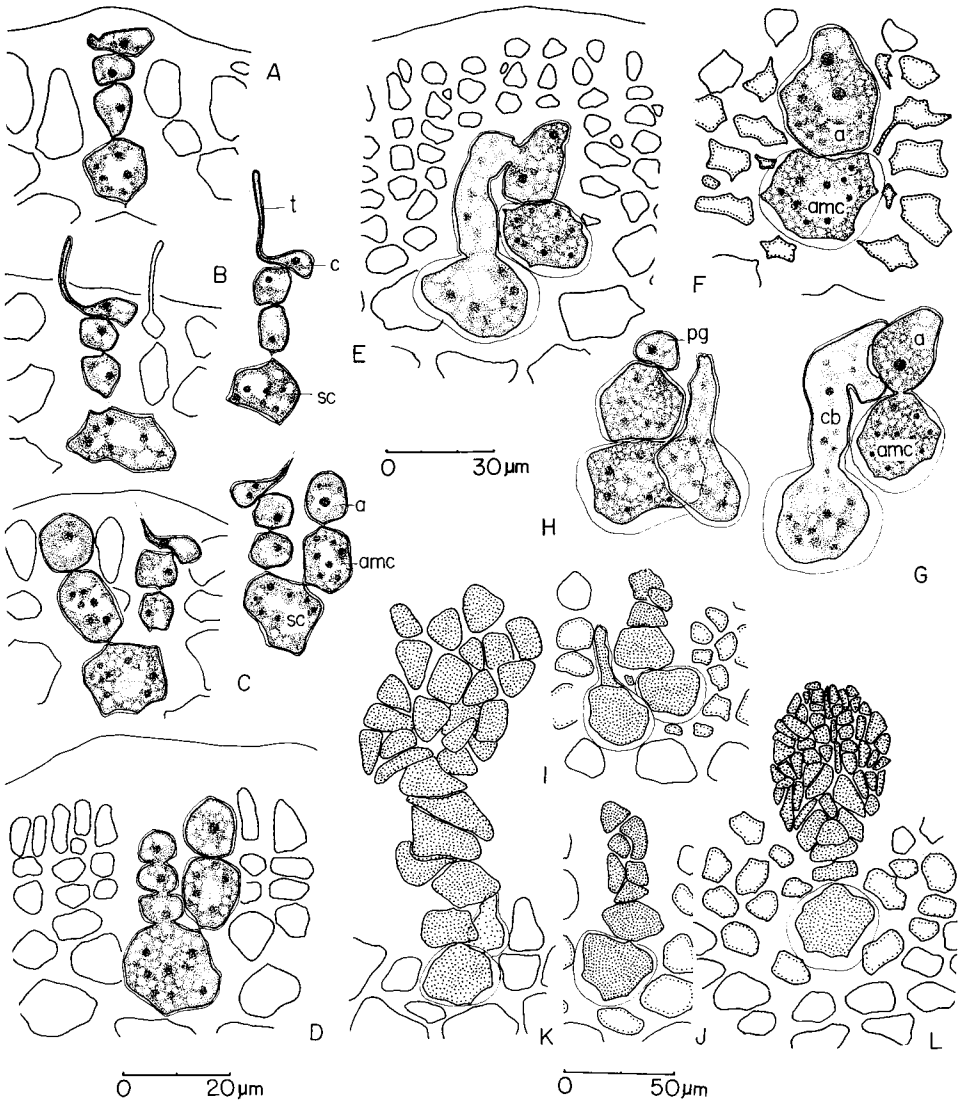

Fig. 50. *Lomentaria hakodatensis* YENDO

A, development of carpogonial branch; B, supporting cell and carpogonial branch; C, degeneration of trichogyne, showing auxiliary cell branch; D, enlargement of auxiliary cell branch before receiving fertilized nucleus; E, G, fusion between auxiliary cell and fusion cell of carpogonial branch; F, auxiliary mother cell and auxiliary cell; H, cutting off primary cell of gonimoblast; I-L, development of early gonimoblast cells.

t: trichogyne, c: carpogonium, sc: supporting cell, a; auxiliary cell, amc: auxiliary mother cell, pg: primary gonimoblast cell, cb: carpogonial branch.

It is slightly compressed polygonal in shape and somewhat larger than the adjacent sterile cells. The first cell of the carpogonial branch is tetragonal to obovate with a nucleus and homogeneously stained contents. Sometimes, large vacuoles are developed in it. The cell is 7.4 μm high and 6.3 μm wide. The hypogynous cell is almost similar in form and size to the first. The carpogonium is hemisperical. It is about a half the size of hypogynous cell and is placed obliquely on the latter. The filamentous trichogyne is protruded from its corner, showing almost the same diameter throughout and curves gently (Fig. 50 A-B).

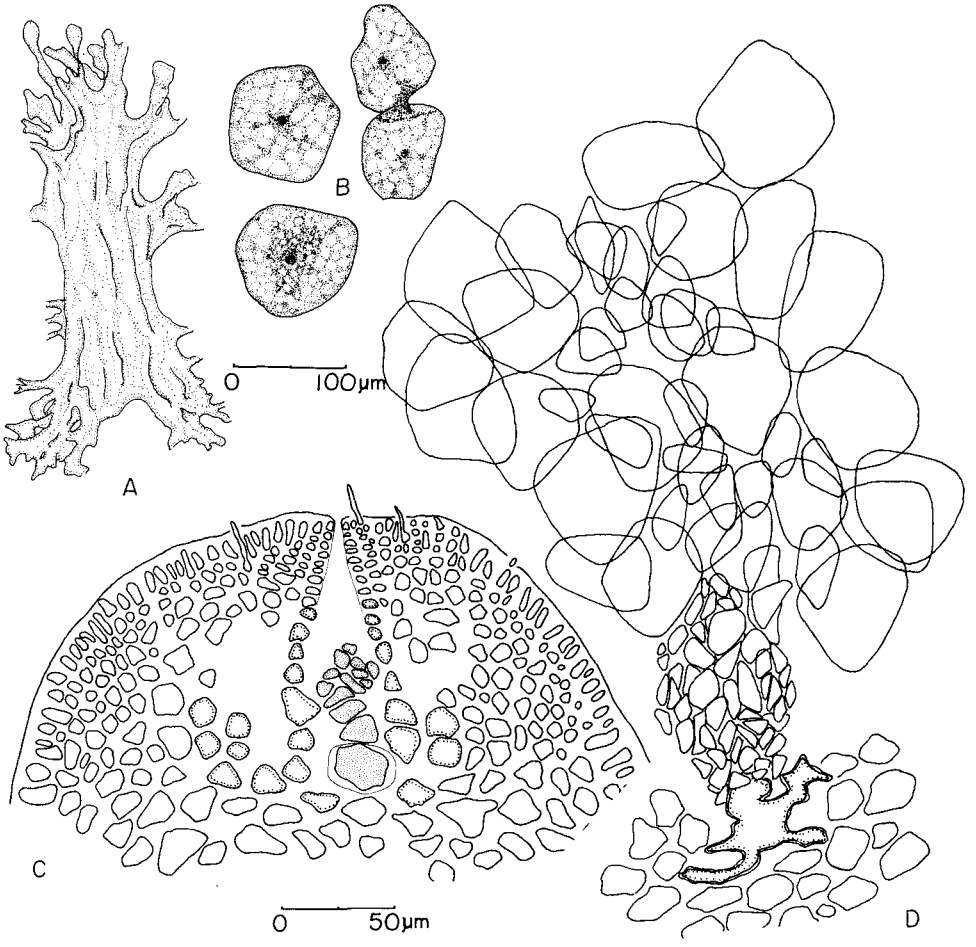

Fig. 51. *Lomentaria hakodatensis* YENDO

A, fusion cell of mature cystocarp; B, carposporangia; C, young cystocarp developing hairs on pericarp; D, young carposporophyte.

Two-celled auxiliary cell branch is distinguished when the trichogyne disappears. The auxiliary mother cell is connected with the supporting cell. It is oblong at first with many nuclei and vacuoles. The auxiliary cell is almost round and contains a single nucleus and homogeneously stained cytoplasm (Fig. 50 C). After the presumed fertilization, the auxiliary cell, auxiliary mother cell and supporting cell are enlarged rapidly during the trichogyne disappears. The pit-areas of the cells of carpogonial branch are widened. These cells form soon a column-like fusion cell, which curves extremely in its upper portion and coalesces with the auxiliary cell (Fig. 50 E). The presumed diploid nucleus seems to remove into the latter. In this arrangement, all these fertile cells continue the enlargement for a long while. Sometimes, the upper portion of the fusion cell surrounds one part of the auxiliary cell (Fig. 50 G, cf. BLIDING 1928, fig. 35 C). Later, the fusion cell loses its contents and is reduced gradually to a slender form, while the auxiliary cell and the auxiliary mother cell are enlarged more and rapidly.

The primary cell of the gonimoblast is cut off transversely from the distal end of auxiliary cell (Fig. 50 H). The two secondary cells of the gonimoblast are cut off obliquely from the upper corners of the primary (Fig. 50 I–J). The succeeding cells of the gonimoblast are also divided from the upper cells successively. The cells of the gonimoblast are variously shaped, aggregated densely and smaller outwards (Fig. 50 L). The protein body (cf. KYLIN 1930) is not observed in the present species. A young carposporophyte becomes elliptical to obovate in outline. Later, it grows rapidly from the upper portion (Fig. 51 D). The auxiliary mother cell is surrounded by a thick wall and forms many secondary pit-connections with adjacent sterile cells. The supporting cell is discernible no more.

As the carposporophyte grows, the auxiliary mother cell, auxiliary cell and early gonimoblast cells make a fusion cell of trunk-like column, and protrude numerous branches radially. The cells of the gonimoblast are connected with this fusion cell, being arranged in radial rows. The carposporangia are formed from the outer cells of the gonimoblast successively, so that almost all the cells of the gonimoblast are converted into carposporangia. However, in a fully mature carposporophyte, numerous small cells in various stages of development are observed around the fusion cell. They seem to form gonimolobes and carposporangia are produced gradually (Fig. 52 A). A mature carposporangium is almost round to polygonal and 90～110 μm in diam. (Fig. 51 B). It contains a nucleus and plastids.

The formation of pericarp begins when the fusion cell of the carpogonial branch coalesces with the auxiliary cell. Futher developmental processes are

similar to the ones seen in previous species. The inner cells surrounding the hollowed central cavity for development of the carposporophyte are arranged in straight rows to the apical pore, and the hairs are developed frequently on the surface of the pericarp (Fig. 51 C).

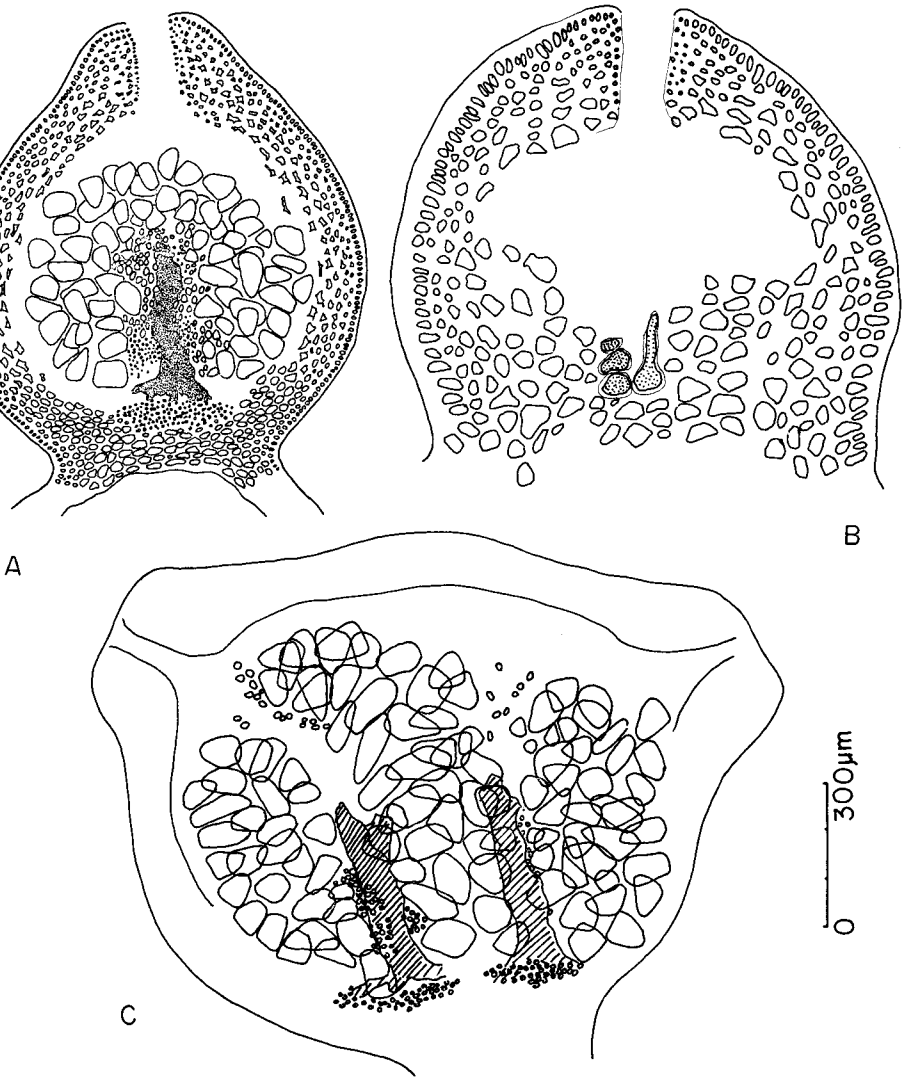

Fig. 52. *Lomentaria hakodatensis* YENDO

A, mature cystocarp; B, cystocarp containing aborted carposporophyte after cutting off primary gonimblast cell; C, cystocarp bearing two carposporophytes and two carpostomes.

The mature pericarp consists of two layers. The outer layer is similar to ordinary cortex, and the inner one is composed of four to six irregularly arranged rows of hyaline cells, which become large in size and stellate in form inwards. The pulvinus is developed rather considerably at the base of the cystocarp.

Two fully grown cystocarps within a single pericarp which has two carpostomes on its upper corners were observed (Fig. 52 C). Besides, there was an aborted cystocarp of which pericarp was fully developed, but the gonimoblast stopped the development at the early stage (Fig. 52 B), as reported by BLIDING (1928) in *Gastroclonium ovale* (HUDS.) KÜTZING.

Discussion

This plant was introduced by YENDO (1920) with the material from Hakodate and the other places in Japan. He mentioned that it was intermediate between *L. linearis* ZANARD. and *L. articulata* (HUDS.) LYNGBYE. Independently of this HOWE (1924) described a new species *L. sinensis* from China, and also mentioned alliance with *L. articulata* and *L. catenata* HARV. HOWE's plant was identified later with YENDO's (OKAMURA 1936).

YENDO described tetrasporic and cystocarpic characters briefly, while HOWE the tetrasporangia only. Judging from the latter description, HOWE's specimens seem to be small thalli, though tetrasporangial sori were present. On the other hand, DAWSON (1944, 1950) reported this species from Gulf of California and Mexico, noticing that the alga referred by SETCHELL & GARDNER to *Hooperia baileyana* J. AGARDH, collected from Guadalupe Isl., was also similar to his.

Spermatangia were described by SETCHELL & GARDNER (1930) under *Hooperia baileyana*, and by DAWSON (1950) referring only to the outer appearance observed from surface, while TAZAWA (1975) investigated them anatomically. The cystocarps are mentioned by YAMADA (1928), INAGAKI (1933) and OKAMURA (1936) only on the mature features. The column-like fusion cell of the carpogonial branch, a characteristic of the members of *Lomentaria* (cf. BLIDING 1928), is also seen in this species.

***Lomentaria catenata* HARVEY**

(Text-figs. 53～59 : Plate V, D–F)

(1856) in Gray's list dried plants coll. Jap., p. 33. J. AGARDH (1876) p. 635 ; De TONI (1895) p. 28, no. 60 ; (1900) p. 555 ; OKAMURA (1902) p. 75, pl. 26 ; (1916) p. 49 ; (1927) p. 12 ; (1930 b) p. 95 ; (1936) p. 683, fig. 326 ; YAMADA (1928) p. 508 ; INAGAKI (1933) p. 40 ; SEGAWA (1935) p. 83 ;

TAKAMATSU (1939) p. 66; DAWSON (1944) p. 331; (1963) p. 465, pl. 92 (16), figs. 1～10; INOH (1947) p. 181, figs. 175～6; KANG (1966) p. 86; FUNAHASHI (1967) p. 31.

Chylocladia catenata J. AGARDH (1876) p. 303.

Corallopsis excavata SETCHELL & GARDNER (1924) p. 756, pl. 23, figs. 24～25, pl. 44, b, pl. 48.

Japanese Name: *Fushitsunagi* (OKAMURA)

Type Locality : Simoda, Pacific Coast of Japan

Materials

Shiribeshi District. Oshoro: Oct. 7, 1966. Feb. 11; Mar. 11; Aug. 17; Sep. 20; Nov. 14; Dec. 18, 1967. Jan. 24; Mar. 28; Sep. 3, 1968.

Description

Thallus intertangled, forming a tufted mass, consisting of erect and creeping parts, cylindrical, cartilaginous, branching three to five times, monopodial in growth, articulated intervals of 2.5～7 mm, estipitate, attaching to substratum by means of discoid holdfast, 7～10 cm high, 1～1.5 mm wide at the broadest part; holdfast small, erect a few fronds, protruding lots of stolons radially, stolons procumbent, branching irregularly, issuing rhizoids with flat and discoid end; erect frond of main axis narrow at basal portion, slightly broad upward, obtuse at apex, branches opposite, verticillate, or sometimes alternate, issued mostly at inter-septa, patent, slightly or scarcely constricted at base, distinctly catenato-constricted at upper septa, ultimate branchlets slightly curved inwards, inflated at internode, 0.7～1.0 mm wide at the broadest part; frond in section composed of cortical and medullary layers and central cavity, 120～160 μm thick, cortical layer single rowed, cortical cells densely pigmented, oblong to tetragonal, arranged in palisade-like row, 12.5～19.5 μm high, 8.4～14.2 μm wide, medullary layer composed of four to six cell rows, medullary cells round to elliptical, gradually large and longitudinally elongate inwards, inner cells hyaline, 21～31 μm high and wide, 80～200 μm long, gland cells solitary or aggregated on innermost cells; tetrasporangial sori formed on inflated inter-septa of branches, round to irregular, with superficial wall hollow, sporangia round, tetrahedrally divided, terminal in cortex, sinking inwards to central cavity, surrounded by filamentously modified medullary cells forming net-work, 160～190 μm in length and width; spermatangial sori developed on bladder-like special ramuli, spermatangia terminal and subterminal on mother cell, elliptical, 4.6 μm long, 3.2 μm wide; cystocarps scattered uniformly on branches, elvated hemi-spherically, sessile, with pericarp composed of six to eight cell-rows, with carpostome, 760～

950 μm high and wide, carpogonial branch three-celled, carposporangia round to elliptical, 97~120 μm in diam.; color reddish purple; specimens adhered imperfectly to paper. Perennial.

Habitat : Lower tidal zone on rocks.

Distribution : Honshu and Hokkaido, Japan; Gulf of California; and Korea.

Phenological Observation

The plants were investigated at Oshoro Bay from October, 1966 to September, 1968. They occurred mostly on plain rocky substratum in lower tidal zone. One of locations studied was 10~20 m wide plain rock located at the inner Bay affected by no wave action. It ends in a steep cliff and is scarcely exposed to air even at spring low tide. The plants grow there along the margin.

In August, 1967 there were lots of filamentous germlings less than 0.1~0.8 mm wide and 4 cm high. They arose from sparsely developed procumbent stolons, which extended on the substratum forming net-works. The rhizoids were formed commonly from stolons at various intervals. Some thalli had secondary branches, while most of them only the primary. On the other hand lots of old thalli, the remainders of previous year, were also among the germlings. They protruded numerous olive green or blackish purple proliferations and had 0.5~1.0 mm broad branches (Fig. 53 E). Some of the old thalli bore already tetrasporangial sori on the proliferations. In September the young plants became about 7 cm high and developed commonly small tertiary branches intertangled frequently, though they were still slender as seen in August. The apical portion is specially inflated to 0.8~1.0 mm width. The spermatangial plants with a few small fertile ramuli and tetrasporangial plants with young sori were among these new plants. The old thalli had disappeared. In November the plants were rather abundant and grown fully, showing mostly 7~10 cm height and 1~1.5 mm width. They were much intertangled and extended to form a spherical and tufted mass. Most of them were tetrasporic, while the male plants with fully grown fertile ramuli and cystocarpic thalli were frequent. In December some of them were eroded or shed away at the upper portion of branches, and some others regenerated new branches from such eroded ends (Fig. 53 D). In January, 1968 they decreased in number rapidly. Most of them remained with lower fragments of the frond, bearing regenerated branches. They were about 8 cm high on an average. The tetrasporic thalli were still frequent and the spermatangial ones rare, but no cystocarpic ones. In March the plants were rare. All of them were eroded at the upper portion, remaining with 4~5 cm long fragments. There were no fertile organs on them.

In addition, the plants collected in October, 1966 were mostly 7 cm high and 1 mm wide on an average. Tetrasporic or spermatangial thalli were frequent and young cystocarpic often. On the other hand, the plants collected in February, 1967 were only the remainders of lower fragments except for some tetrasporic thalli.

Considering the above investigations, the plants at Oshoro Bay appear in August as a procumbent form from which the erect fronds appear soon. They become most luxuriant from October to December and decrease in number after January. Some of them however remain with lower fragments only and regenerate in next August when new erect fronds appear. Both tetrasporangia and spermatangia appear since September and cystocarps since October. The latter are found until December and the spermatangia until January, whereas the tetrasporangia remain until February. However, the tetrasporangia developed on the proliferations of old thalli are found in August. The cystocarpic plants are not common in number compared with those reported in other places of Japan.

Morphological Observation

External Appearance

The plant consists of erect fronds and procumbent stolons. At the beginning a single or a few fronds are erect from a discoid holdfast, which protrudes lots of procumbent stolons that are branched irregularly, forming a network and developing rhizoids at random, and also issue erect fronds (Fig. 53 A–B). The erect thalli are cylindrical, monopodially branched three to five times repeatedly and become round to pyramidal in outline. Sometimes, all the primary branches become almost similar in height, so that the thallus is somewhat reverse pyramidal in outline. However, in mature plants, by the numerous erect fronds developed from procumbent stolons they form generally a tufted mass extending broadly on the substratum (OKAMURA 1936, fig. 326 (1)).

The main axis is sometimes ramified dichotomously near the base. The branches are issued at the inter-septa in an opposite, verticillate or alternate manner, and become shorter outwards. As mentioned by OKAMURA (1902), all branches and branchlets are patent and horizontal especially the lower ones. The ultimate branchlets are commonly curved inwards slightly. The apex is obtuse. The frond is articulated at septa at various intervals. However, this *catenato-constrictis* (HARVEY 1856) is sometimes scarcely discernible in the lower portion, but comparatively distinct in the upper portion of branches and branchlets. The internode in the lower portion is generally long. Especially the inter-septa of fertile branches bearing tetrasporangial

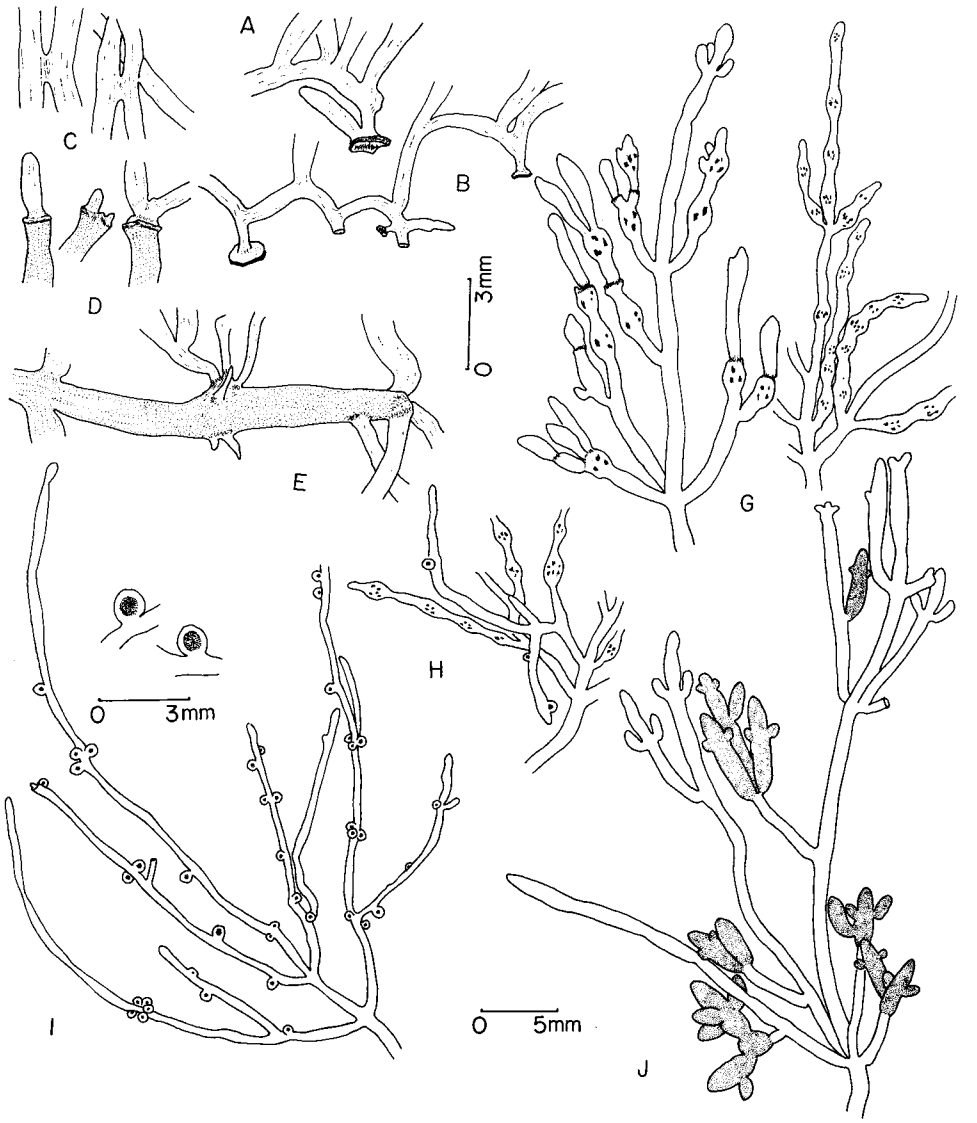

Fig. 53. *Lomentaria catenata* HARVEY

A, part of holdfast; B, part of rhizoids and procumbent stolons; C, fusion of branches; D, regeneration of branches; E, proliferation of new branches from old frond; part of tetrasporophyte bearing sori; G, regeneration of new branches from eroded end, developing tetrasporangial sori; H, part of tetrasporophyte bearing cystocarps as well; I, part of cystocarpic frond; J, part of male frond with fertile ramuli.

sori are inflated very much, and the terminal segment is frequently inflated obdeltoid in shape by protrusions of branchlets at the upper corners.

The proliferations occur radially at some intervals around the surface of old remaining fragments (Fig. 53 E). The regeneration of branches at the eroded end remains with distinct traces between new and old branches. The fertile branches bearing tetrasporangial or spermatangial sori also regenerate.

The plant is cartilaginous in texture. It is more or less firm after maturation. The central cavity is filled with transparent mucilage, which overflows out of the aperture of tetrasporangial sorus when the plants are fixed in formalin-seawater solution.

Structure of Thallus

The thallus is composed of outer cortical and inner medullary layers and central cavity (Fig. 55 B). The cavity is interrupted by multi-rowed cellular septa divided into compartments. The cortical layer is single rowed with densely pigmented cells, which are anticlinally oblong and arraanged compactly in palisade-like row. Sometimes, the cortical cell cuts off obliquely small cells outwards. In a young thallus the cortical cells are elongated three to five times as high as wide and develop no small cells.

The medullary layer consists of four to six rows of transversely round to elliptical cells, which become larger but loosely arranged inwards. Outer one or two rows of cells are pigmented poorly and more or less similar in size to cortical cells, while inner three to four rows of cells are hyaline. In longitudinal section, the medullary cells are elongated very much inwards, the innermost becoming filamentous, and some longer than 230 μm. They occur more abundantly than in *L. hakodatensis.*

The transverse septum is composed of four to five irregularly arranged rows of hyaline cells which are transversely round and longitudinally elliptical (Fig. 55 A). Gland cells are common on the septa and apical portion of the thallus, though OKAMURA (1902) mentioned they did not occur in this plant. On the septa they are connected with upper cells and protrudes into the cavity, while in the apical portion they are placed on the inner medullary cells. The gland cell contains vacuoles and homogeneously stained substances. They occur frequently in aggregation or sometimes in a branch system of two to three cells (Fig. 55 F). A large one is about 35 μm long and 28 μm wide.

The discoid holdfast consists of round to elliptical cells arranged rather irregularly (Fig. 54 F). In the central portion, the cells become longitudinally elongate upwards, where the central cavity of the erect frond is developed

rotundly in outline. The rhizoid is developed from cortical cells, which are elongated anticlinally and extend on the substratum by successive divisions. It becomes flat at end (Fig. 54 A). The fusion of thalli occurs by the modification of cortical cells at the contacting portion. It begins with elongation

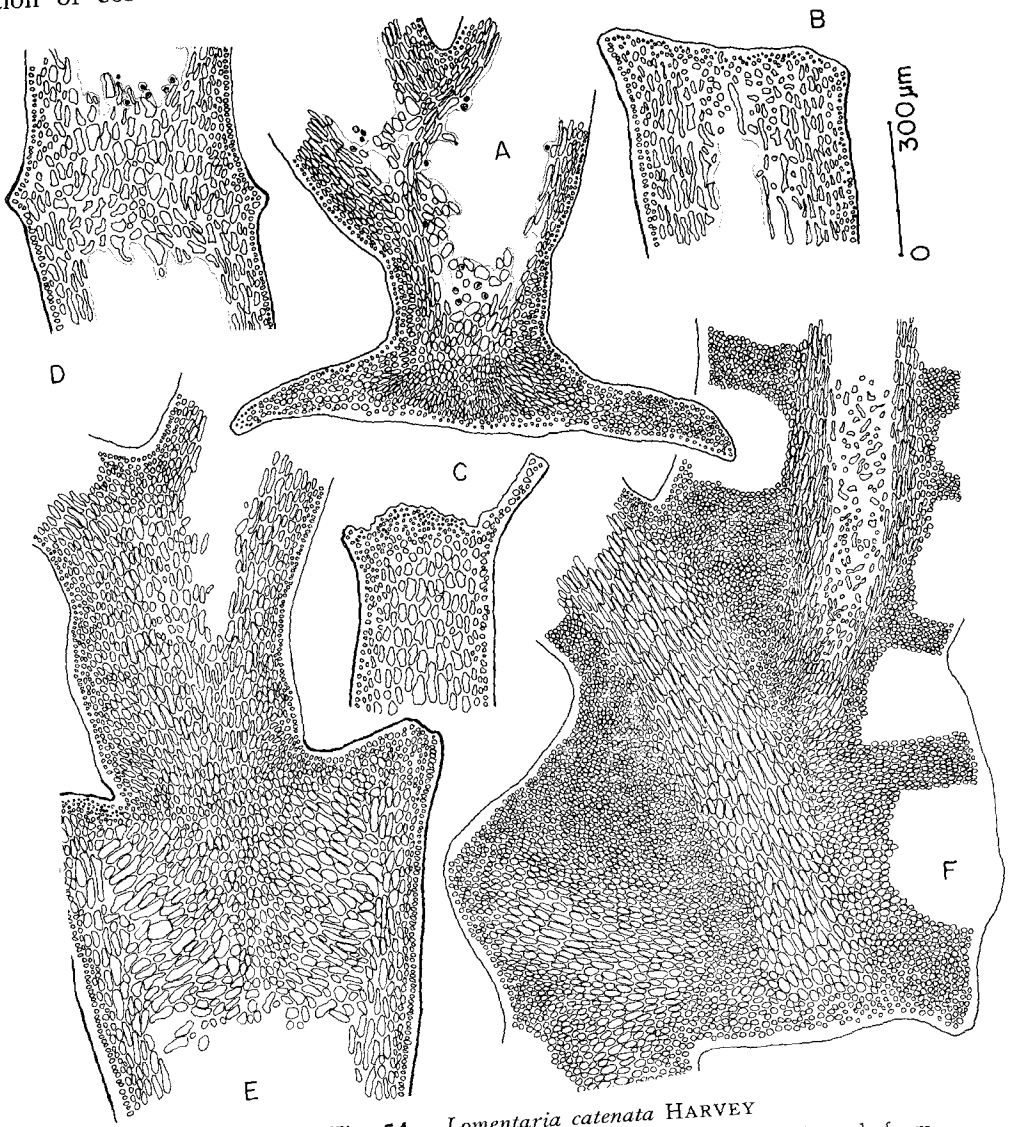

Fig. 54. *Lomentaria catenata* HARVEY
A, longitudinal section of rhizoid; B–E, regeneration of new branch from eroded margin of old plant in longitudinal view; F, longitudinal section of holdfast.

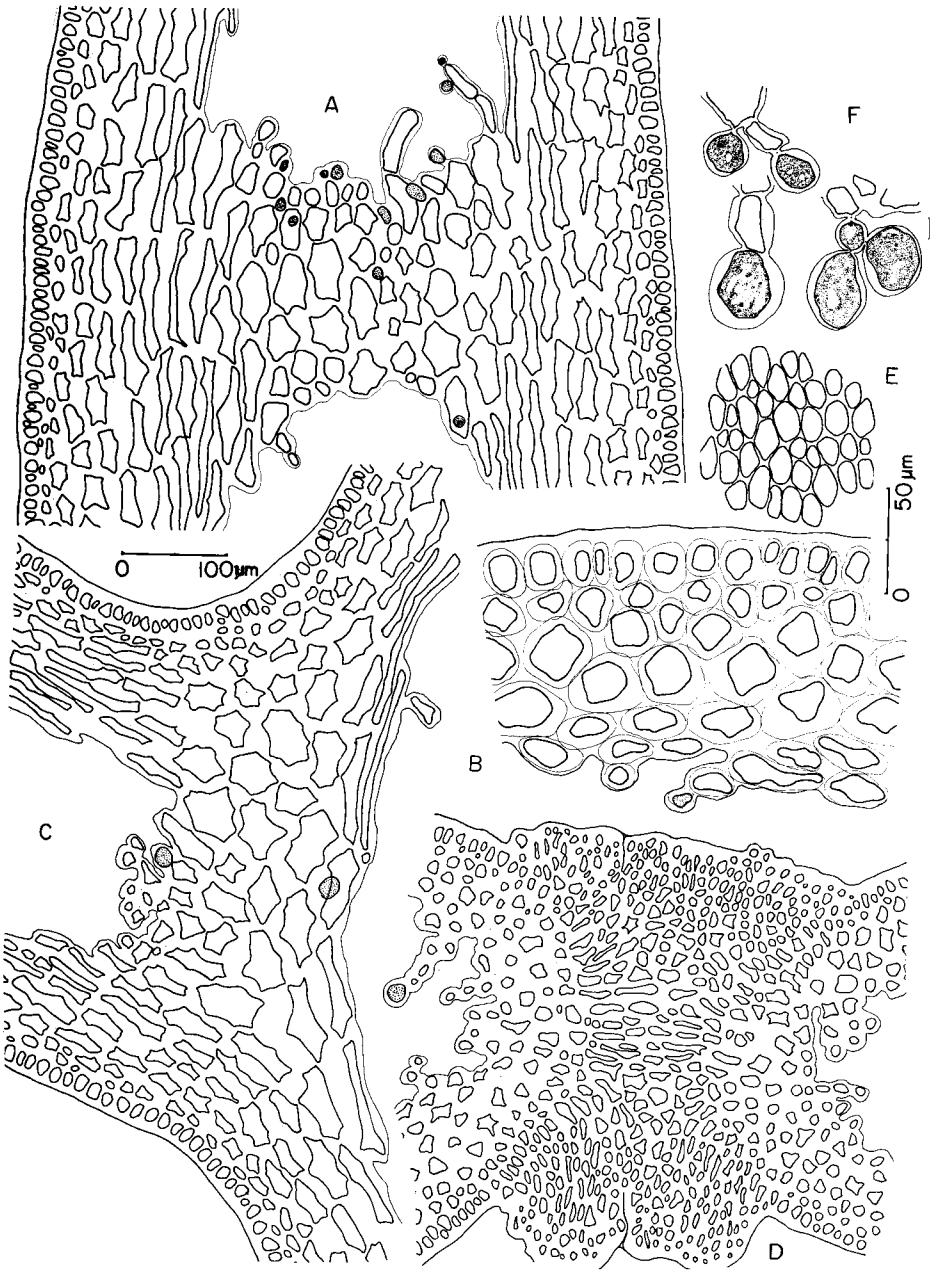

Fig. 55. *Lomentaria catenata* HARVEY

A, longitudinal section of mature frond at septum, showing aggregation of gland cells; B, the same in transverse view; C, a ramified portion in longitudinal view; D, fusion of thalli in transverse view; E, cortex in surface view; F, gland cells.

and divisions of cortical cells of both fronds contacted. The cells became interwoven mutually, bearing many secondary protoplasmic connections. No contacting border occurs at the fusion area (Fig. 55 D).

The regeneration of branches at the eroded or broken ends begins with successive divisions of the marginal cells at the area. Both cortical and medullary cells cut off numerous small and round cells, so that the area is filled completely with them. A regenerated branch is developed from there small cells. It is generally more narrow in diameter than the old branch at the beginning. Even after it becomes as broad as the old one, there remains still a trace like a ring around the margin (Fig. 54 B–E).

The proliferation of new fronds from old thalli shows also a similar modification of cortical cells by anticlinal elongation and division successively. A new frond is developed from these cells, as seen in the regeneration. Rarely small cells are cut off from the cortical cell outwards, as seen in early stage of the hair formation in *L. hakodatensis*, but this divided cell never develops into a hair.

Reproductive Organs

Tetrasporangia : Tetrasporangial sori appear at first in uppermost portion of primary or secondary branches which become slightly broader than the other sterile part. Later, they extend over almost all branches except for the main axis, leaving small intervals between two adjacent fertile areas. In mature thallus there are several hollows in the superficial wall owing to sorus formation even in a single segment. The sori are frequently fused later and become sometimes more than 1300 μm in diam.

The sporangium is formed quite in a similar manner as seen in *L. hakodatensis* (Fig. 56 A–B). The mature tetrasporangium is almost round and about 160$\sim$190 μm in width and length. The medullary cells in soral area are modified filamentously into a characteristic stellate form. Before the maturation of tetrasporangia, they form a beautiful frame of networks (cf. OKAMURA 1902), and surround the sporangia (Fig. 56 C–D). This modification is very conspicuous compared with that of *L. hakodatensis*.

Spermatangia : Most of male plants were not as large as the other fertile thalli. As mentioned by TAZAWA (1975), spermatangial sori appear on the specially developed ramuli. They become pinkish purple in color, showing a quite different shape from sterile ones. In early developmental stage the fertile ramuli are elongated cylindrical and constricted very much at base, while the apex is round to obtuse. Then, they branch in opposite or verticillate manner with much constricted septa. A fully grown ramulus

is about 1 cm high on an average, while its main segment is about 7 mm long and 1.2 mm wide (Fig. 53 J). When the ramuli are wounded or worn away at the upper portion, they regenerate frequently another fertile ramulus

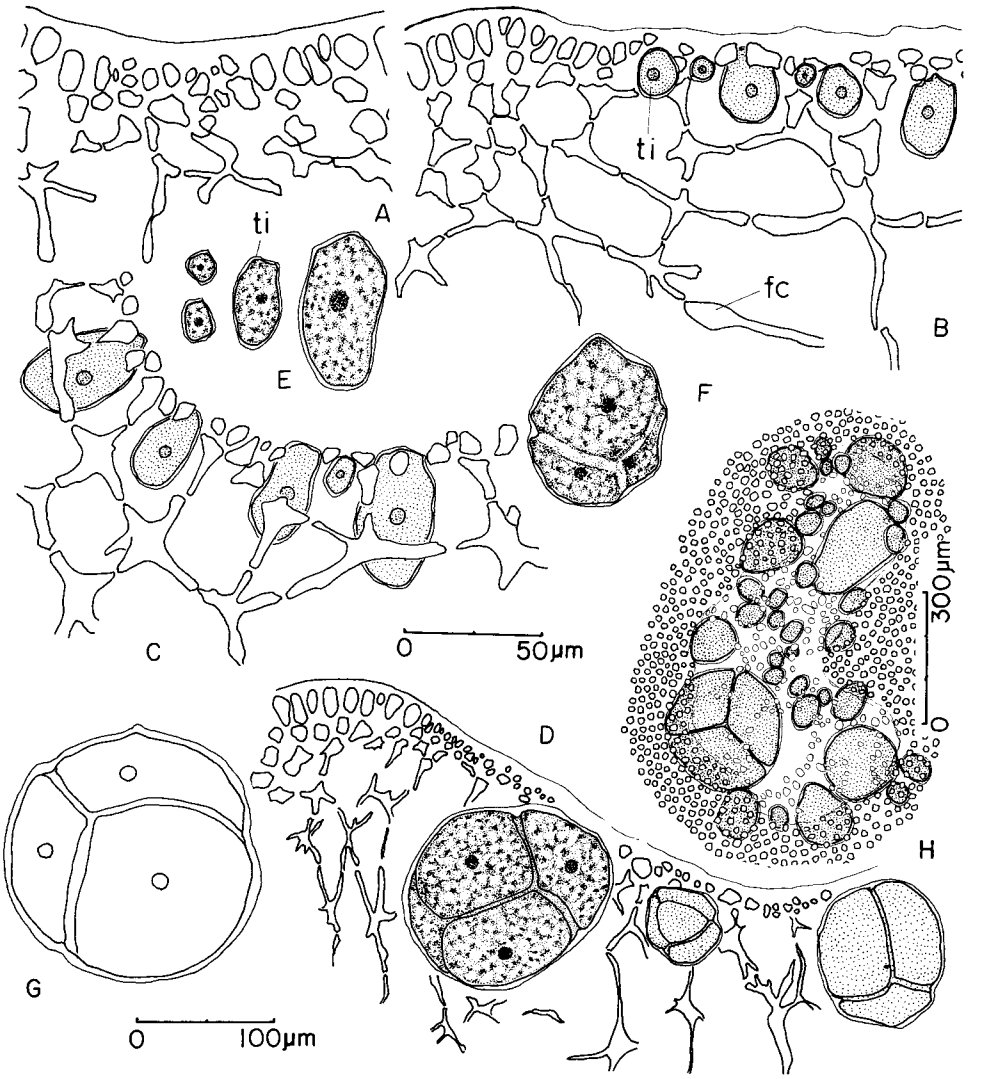

Fig. 56. *Lomentaria catenata* HARVEY

A–D, development of tetrasporangia terminally on small cells, inner cells forming fine filamentous net-works; E–F, growth of sporangia; G, mature tetrasporangium; H, surface view of tetrasporangial sori.

ti: tetrasporangium-initial.

newly from the margin. The spermatangial sori are formed from the top of fertile ramulus. They extend gradually toward the lower portion, and cover the whole surface completely.

Spermatangia are produced terminally or subterminally on a sperma-

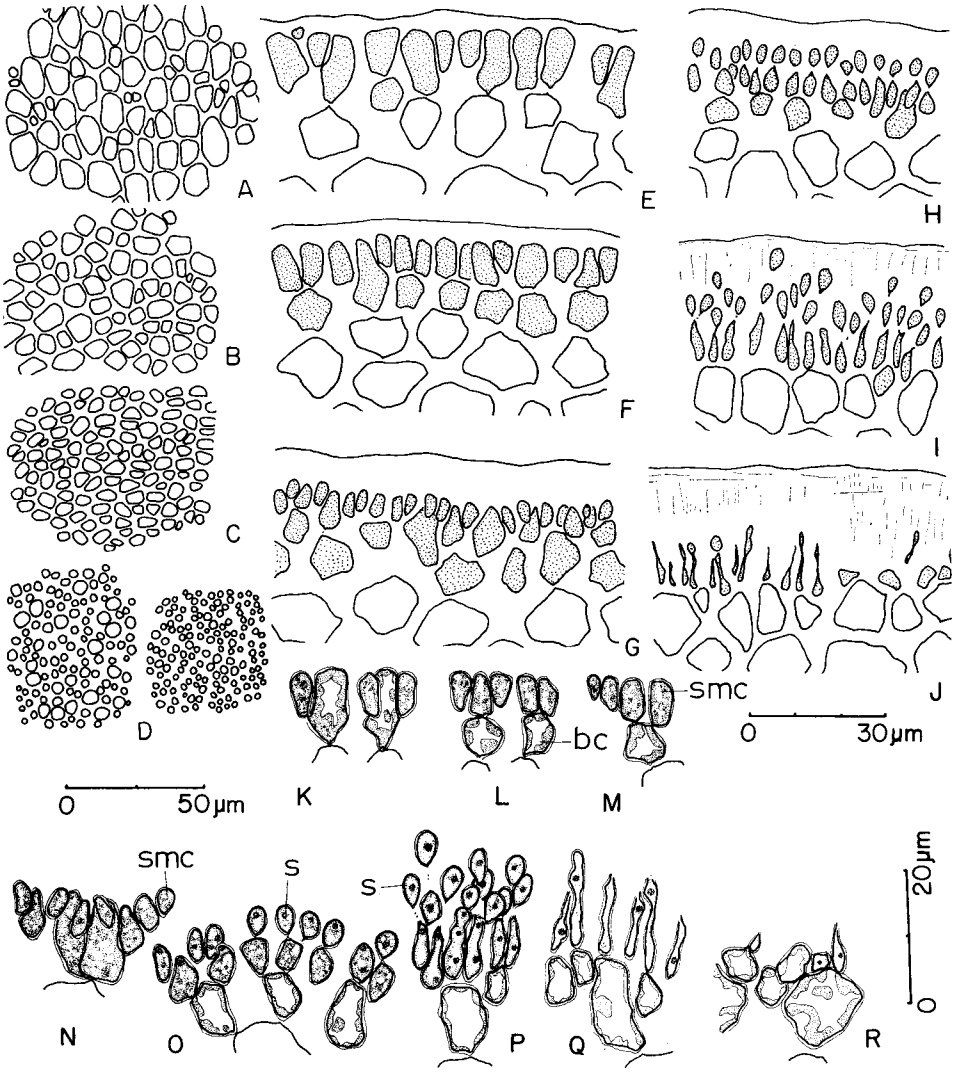

Fig. 57. *Lomentaria catenata* HARVEY

A–D, development of spermatangia in surface view, D left being early stage; E–J, the same in transverse view; K–N, formation of mother cells in seriate row; O, development of spermatangia terminally or subterminally on mother cell; P–Q, successive development of spermatangia; R, later stage of spermatangium formation.

s: spermatangium, smc: spermatangial mother cell, bc: basal cell.

tangial mother cell. They originate from a cortical cell, which is elongated and cuts off three to four mother cells obliquely from its upper corners. These mother cells cut off again two to three secondary mother cells in a similar manner to the previous formation. Then, the secondary mother cell cuts off also one or two tertiary mother cells, which cut off often a single fourth mother cell. As a result, these mother cells originating from a single cortical cell are seriate in radially arranged rows, showing a reverse pyramidal outline (Fig. 57 E-G, K-N). They become smaller outwards. The cortical cell after cutting off primary mother cells cuts off frequently a mother cell outwards and remains as the basal cell (Fig. 57 L-M). Such basal cells are formed also from primary mother cells, after cutting off the secondary (Fig. 57 P-Q).

The spermatangium is cut off transversely from the mother cell, bearing a pit-connection with it. The cells have no common wall. The second spermatangium is also formed on the same mother cell beside the first. So, the two spermatangia grow subterminally on a mother cell (Fig. 57 O). The mature spermatangium is elliptical and 4.6 μm long and 3.2 μm wide, while the mother cell is almost oblong and 4.6$\sim$6.9 μm high and 2.3$\sim$3.4 μm wide. The mother cells lose plastids when the secondary mother cells are formed. However, the sterile basal cells contain them always. The superficial wall in soral area is not shed.

After the liberation of primary spermatangium, the secondary spermatangium is formed commonly on the same mother cell. Sometimes, it is formed while the previous spermatangium still remains in the superficial wall of the thallus. Thus, the two spermatangia are arranged in a longitudinal row on the mother cell (Fig. 57 P). The tertiary spermatangium is not rare, as well. The mother cell becomes very slender, as it protrudes more spermatangia successively. The later spermatangia are connected with mother cell by a slender protoplasmic continuation. When the spermatangium formation is discontinued, the mother cells become almost filamentous in form and hyaline in contents except for the nucleus (Fig. 57 Q). Later, most of the mother cells disappear. There is no return of the mother cells to ordinary cortical cells (Fig. 57 R).

Cystocarps: The cystocarps occur at first on the upper portion of branches, and scattered later over almost all the branches. They are formed commonly around the septa or frequently on inter-septa in aggregation (Fig. 53 I). Sometimes, more than eight cystocarps are aggregated verticillately around one segment. The mature cystocarp is sessile, elevated spherically and about 760$\sim$950 μm high and wide. The carpostome is 100$\sim$120 μm

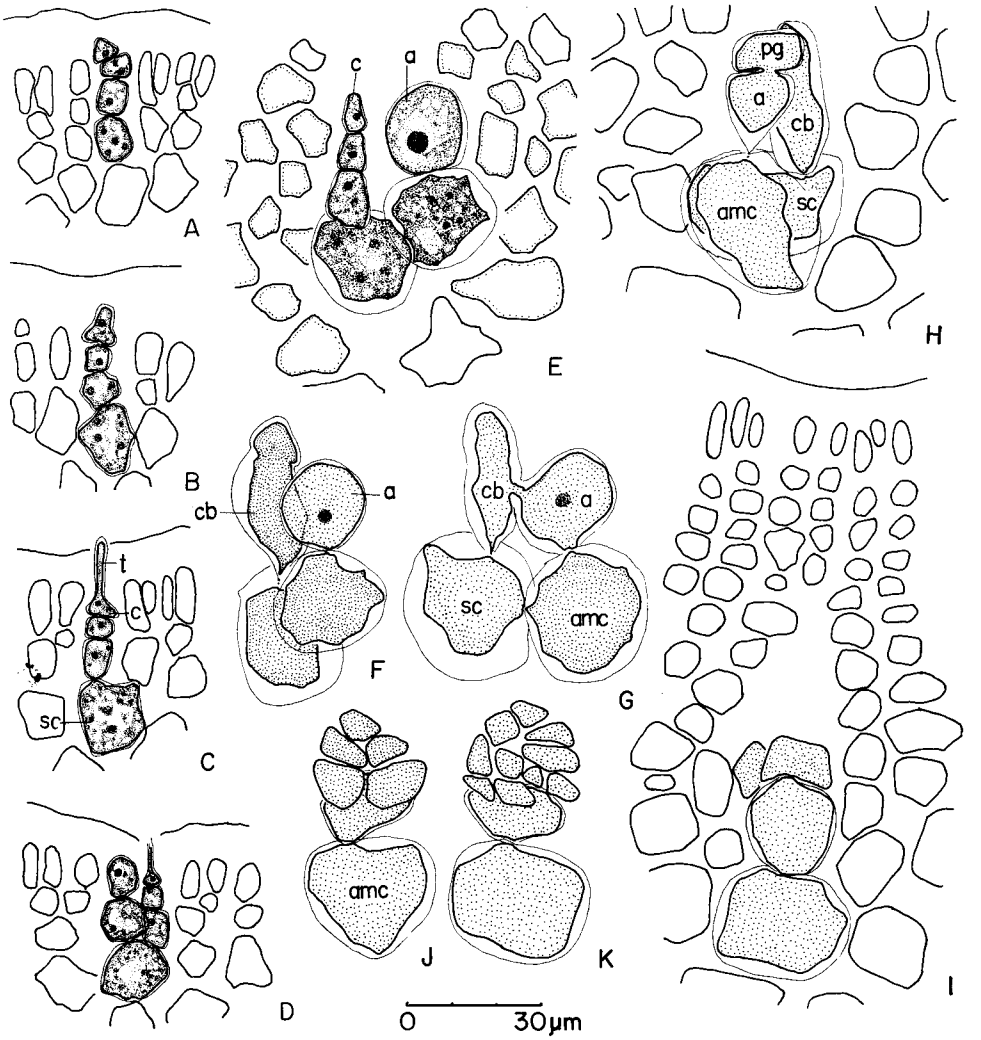

Fig. 58. *Lomentaria catenata* HARVEY

A-B, development of carpogonial branch; C, supporting cell and carpogonial branch; D, degeneration of trichogyne, showing auxiliary cell branch; E, enlargement of auxiliary cell branch; F, column-like fusion cell of carpogonial branch; G, fusion between carpogonial branch and auxiliary cell; H, cutting off primary gonimoblast cell; I, cutting off secondary gonimoblast cell; J-K, development of embryonic cells of gonimoblast.

c: carpogonium, t: trichogyne, sc: supporting cell,
a: auxiliary cell, amc: auxiliary morther cell,
cb: carpogonal branch, pg: primary gonimoblast cell.

in diam. A rostrum is not protruded.

The supporting cell is homologous to outer medullary cells. It is nearly elliptical and contains multi-nuclei and dense protoplasmic substances. The supporting cell is almost same in size to the adjacent sterile cells during the development of carpogonial branch. The carpogonial branch consists of three cells. The first is almost tetragonal and a half to two third the size of supporting cell. It contains two nuclei. The second, hypogynous cell, is also almost tetragonal and half the size of the first. A single nucleus is in it. The third, carpogonium, is deltoid before it protrudes a trichogyne. It is almost similar in size to the hypogynous cell and contains a single nucleus. The trichogyne is developed from the top of carpogonium in a slender cylindrical form. The carpogonial branch is generally straight (Fig. 58 C). Two-celled auxiliary cell branch is distinguished when the trichogyne disappears. The auxiliary mother cell is connected with supporting cell. It contains many nuclei and dense protoplasmic substances. The auxiliary cell is elliptical to oblong and half to two thirds the size of mother cell. It contains a single nucleus.

After the presumed fertilization, the carpogonium loses the trichogyne. The cells of carpogonial branch are enlarged slightly and fused rapidly by opening pit-areas. They make a large column-like fusion cell, as seen in *L. hakodatensis*. There is a slight constriction at the upper portion of this fusion cell (Fig. 58 F). The supporting cell does not coalesce with this fusion cell. The auxiliary mother cell and auxiliary cell are enlarged rapidly before the latter coalesces with the fusion cell of carpogonial branch, while the supporting cell is enlarged gradually. Thus, procarpic cells except for the fusion cell of carpogonial branch become almost same in size afterwards. The supporting cell and the auxiliary mother cell are surrounded by a thick wall.

The auxiliary cell laterally and the fusion cell of carpogonial branch in mid-portion coalesce long after the carpogonial branch is formed (Fig. 58 G). The presumed diploid nucleus seems to migrate down from the carpogonial unit into the auxiliary cell through this connection. After that, the fusion cell of carpogonial branch decreases gradually and disappears later.

The primary cell of the gonimoblast is cut off transversely from the distal end of auxiliary cell in almost equal size (Fig. 58 H). The large nucleus observed in the auxiliary cell remains in the upper cell. The two scondary cells of the gonimoblast are cut off obliquely from the primary. They are much smaller than the remaining cell of the primary gonimoblast cell. These three gonimoblast cells lie upon the auxiliary cell. Succeeding cells of the gonimoblast are formed from outer cells successively, and a young

carposporophyte is formed in a round to elliptical outline (Fig. 58 J-K). The auxiliary mother cell and auxiliary cell form a large fusion cell, which supports the gonimoblast, while the supporting cell becomes very small and disappears later.

The cells of the gonimoblast are surrounded by a common thick gelatinous wall (Fig. 59 C). The carposporangia are developed from the outer cells of the gonimoblast successively, so that almost all the cells of gomimoblast are converted into carposporangia. However, there remain numerous small cells in the central portion of the mature carposporophyte (Fig. 59 D). The

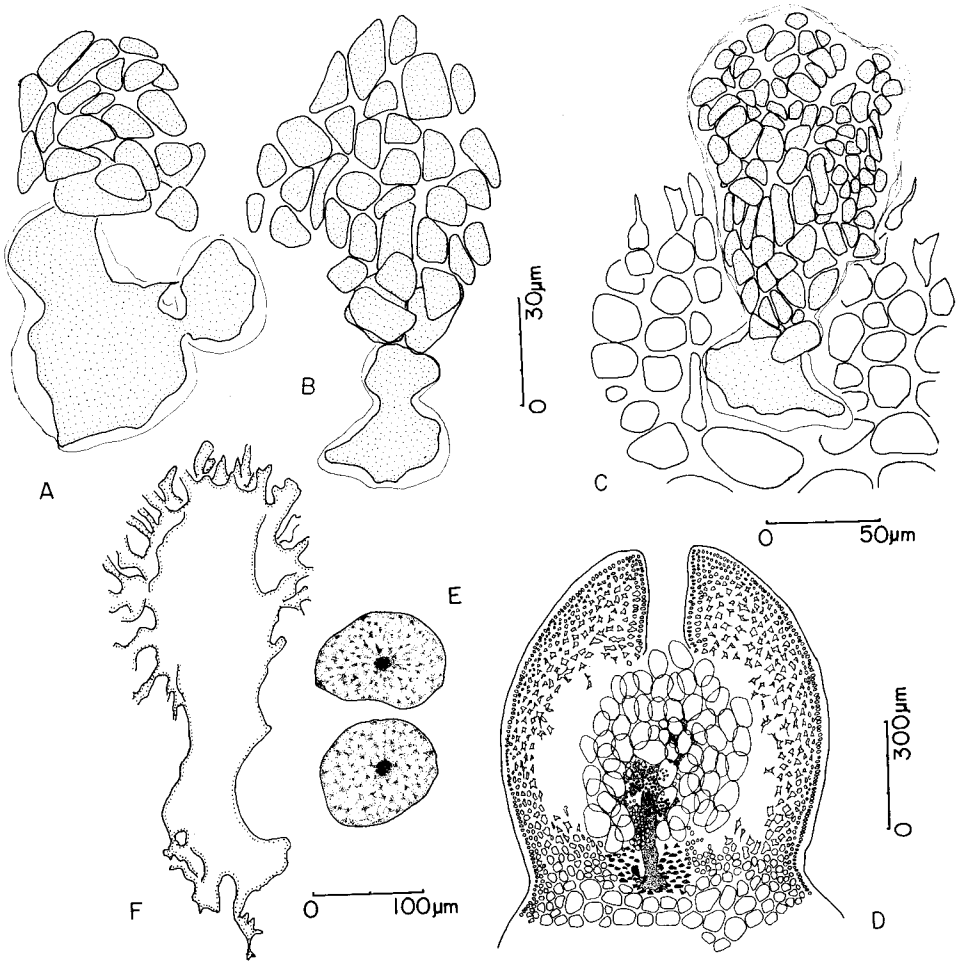

Fig. 59. *Lomentaria catenata* HARVEY

A-C, development of young carposporophyte, forming large fusion cell; D, a mature cystocarp; E, carposporangia; F, fusion cell of mature cystocarp.

carposporangium is almost round to elliptical and 97～120 μm in diam. The trunk-like fusion cell formed by auxiliary mother cell, auxiliary cell and initial cells of the gomimoblast is very large. It protrudes numerous complicated branches radially (Fig. 59 F). The pulvinus at the base of carposporophyte is rather considerable in development.

The pericarp is formed in a similar manner to the ones seen in the previous species. It begins to develop when the trichogyne disappears. A mature pericarp consists of a single rowed anticlinally elongate cells outwards and five to seven rowed round to irregular cells inwards. The inner cells are large, stellately modified and form a characteristic net-work later (OKAMURA 1902). The pericarp around the carpostome is thick layered.

It is interesting to find often the plants bearing both tetrasporangia and cystocarps in the same thallus (Fig. 53 H). As seen in *Champia parvula*, they are tetrasporic thalli, in which a definite branch only develops the cystocarps. These cystocarps were found on the proliferation of old plants.

Discussion

HARVEY (1856) described this alga with the materials collected from Japan by Williams and Morrow. He referred to it 'a remarkable species, having much the habit of a *Corallopsis*, but not the structure'. However, both J. AGARDH (1876) and De TONI (1900) treated it as an uncertain species of *Lomentaria*. J. AGARDH once removed it to *Chylocladia* without mentioning the reason. In 1902 OKAMURA gave a detailed description of the alga, and concluded beyond any doubt it was a distinct species related to *L. articulata* (HUDS.) LYNGB., the type species of the genus.

It is interesting to find the gland cells rather commonly, though OKAMURA (*l. c.*) noticed they were lacking in this species. All the plants investigated are rather slender compared with those occurring in Honshu, Japan and Korea. INOH (1947) observed the early developmental process of both tetraspore and carpospore, and mentioned that they showed a similar pattern of development in formation of no special apical cell at early germination.

In the cystocarp formation, it is characteristic that the cells of carpogonial branch form a column-like fusion cell before coalescing with auxiliary cell, as seen in *L. articulata* (BLIDING 1928) and *L. hakodatensis*, and also in *Binghamia californica* J. AGARDH (LEE & KUROGI 1973). Therefore, the character seems to be peculiar among these members of Lomentarioideae.

The development of fertile ramuli in spermatangium formation seems to be also an important character in this species.

The plant is distributed commonly along the coast of Honshu, Japan (TAKAMATSU 1939) and Korea (KANG 1966). It was also reported from Gulf

of California (DAWSON 1944, 1966). According to DAWSON, the plant introduced by SETCHELL & GARDNER (1924) as *Corallopsis excavata* was nothing but the present species.

Champia DESVEAUX (1808)

The genus *Champia* was proposed by DESVEAUX (1808) with a single species *C. lumbricalis*, known previously as *Mertensia lumbricalis* ROTH (1806). Later, LAMOUROUX (1813) described this genus precisely and mentioned it was different from the other related genera in the situation of fructification and the mode of ramification. He also pointed out that almost all parts of the thallus were compartmented by constrictions at various intervals. On the other hand, HARVEY (1853) placed this genus beside *Lomentaria*, whereas J. AGARDH (1876) put it beside *Chylocladia*. In establishing the family Champiaceae, BLIDING (1928) elected this genus as type of the family, where *Lomentaria* and *Chylocladia* were included, as well.

This genus is characterized currently by a cylindrical or sometimes slightly flattened branched thallus consisting of a single layer with filaments inwards, single rowed transverse septa, tetrahedrally divided tetrasporangia occurring intercalarily, and by hemispherically elevated cystocarps bearing the carposporangia converted from outer gonimoblast cells only.

Champia parvula (C. AGARDH) HARVEY

(Text-figs. 60~68 : Plate IV, D-F)

(1853) Nereis Bor.-Amer. II, p. 75. J. AGARDH (1876) p. 303 ; DAVIS (1892) p. 339, pl. 21 ; (1896) p. 109, pls. 7~8 ; HAUPTFLEISCH (1892) p. 321, 344 ; De TONI (1900) p. 558 ; OKAMURA (1910) p. 89, pl. 76 ; (1916) p. 49 ; (1936) p. 686 ; BØRGESEN (1920) p. 407 ; (1929) p. 92 ; GRUBB (1925) p. 191 ; WEBER van BOSSE (1928) p. 476 ; BLIDING (1928) p. 5 ; YAMADA (1928) p. 518 ; SETCHELL & GARDNER (1930) p. 5 ; KYLIN (1931) p. 28 ; INAGAKI (1933) p. 39 ; TSENG & LI (1935) p. 221 ; TAYLOR (1937) p. 289 ; TAKAMATSU (1939) p. 67 ; DAWSON (1944) p. 310 ; (1950) p. 341 ; (1963) p. 468, pl. 93 (17) ; KANG (1966) p. 88 ; FUNAHASHI (1966) p. 141.

Chondria parvula C. AGARDH (1824) p. 207.

Lomentaria parvula GAILLON (1828) p. 19 ; KÜTZING (1849) p. 864 ; (1865) pl. 87, figs. a-b ; J. AGARDH (1863) p. 729.

Gastridium parvulum GREVILLE (1830) p. 119.

Chylocladia parvula HOOKER (1833) p. 298 ; J. AGARDH (1842) p. 111 ; HARVEY (1847) p. 80 ; (1849) pl. 210.

Fuscus kaliformis var. *γ. nanus* TURNER (1808) p. 61.
Lomentaria brevis KÜTZING (1843) p. 441; (1849) p. 864; (1865) pl. 88, figs. d-e; J. AGARDH (1863) p. 729.
Champia disticha DAWSON (1944) p. 310, pl. 46, fig. 5.
Champia caespitosa DAWSON (1944) p. 311, pl. 46, figs. 3~4.
Japanese Name: *Watsunagiso* (OKAMURA)
Type Locality : Cadiz, Spain

Materials

Iburi District. Charatsunai, Muroran: July 1, 20; Aug. 1, 20; Sep. 14; Oct. 13, 1966. June 25; Aug. 19, 1967. Masuichi, Muroran: Sep. 13, 1966.

Description

Thallus forming spherically tufted intertangled mass, cylindrical, tender, gelationous, branching three to four times, monopodial in growth, estipitate, attaching to substratum by means of discoid flat holdfast, 5~7 cm high, 1.5~2.0 mm wide at the broadest part; holdfast erecting a few to several fronds, 1.0~2.0 mm in diam.; frond articulated in cask-like rows at 1~2 mm intervals, main axis much narrow at base, broad in middle portion, attenuate upwards, obtuse to round at apex, branches irregular, verticillate, sometimes alternate or opposite, wide or patent, occurring at septa or inter-septa with less than 1 cm intervals, ultimate branchlets much constricted at base, 0.5~1.0 mm wide; rhizoids developing from frond, compressed; frond in section single layered with central cavity interrupted by diaphragms, 55~65 μm thick, cells polygonally angled, 28~35 μm high, 35~42 μm wide, 45~83 μm long, cutting off small cells outwards, small cells round to polygonal, 20~28 μm high, 14~28 μm wide, cutting off frequently much smaller cells of 11~17 μm height and 5.5~8.3 μm width obliquely outwards, longitudinal filaments attaching to large cell, running through frond, diaphragm single or sometimes partially two cell-rowed, gland cells attaching to filament inwards, unicellular hairs abundant; tetrasporangia occurring in sori, intercalary among large or small cells, ovoid, bulging inward to cavity, divided tetrahedrally, 110~120 μm long, 83~92 μm wide; spermatangia occurring in sori, elliptical, subterminal on mother cell, 6.8 μm long, 4.3 μm wide, cystocarps abundant, solitary or aggregated, spherically elevated, sessile, with carpostome, 860~1100 μm high and wide, carpogonial branch four-celled, carposporangia round to polygonal, 49~55 μm in diam.; color dark purple to brownish red, sometimes greenish purple; specimens adhered to paper firmly. Annual.
Habitat : Lower tidal zone on other algae or rocks.
Distribution: Honshu and Hokkaido of Japan, Atlantic Ocean of Europe

and America, Mediterranean Sea, Australian Ocean, Pacific Coast of America and Mexico, East Indies, Malay Archipelago, China and Korea.

Phenological Observation

The plants were investigated at Charatsunai, Muroran from July, 1966 to August, 1967. They are mostly epiphytic on other algae such as *Rhodomela larix*, *Corallina pilurifera*, *Symphyocladia latiuscula*, and *Sargassum thunbergii*, or on plain rocky substratum in lower tidal zone exposed to the direct wave action. The plants appear commonly as an intertangled tufted mass.

In early July, 1966 there were several plants growing on rock sparsely. They were erect, branched and about 1 (~1.5) cm high and 1 (~7) mm wide at the broadest part. Large plants had primary and small secondary branches, showing about twelve septa in main axis. The primary branches were issued commonly as early as the plant became about 0.5 cm high. In late July they appeared abundantly on rocks and other algae. The primary and secondary branches spread radially and the plant showed a small spherical to hemispherical tufted mass intertangled by fusion of branches. It was very difficult to discern the original base from such a tufted mass. The large plants, about 2.5 cm high and 1.5 mm wide, bore commonly small protrusions of tertiary branches. Almost half of them investigated had spermatangia and about one third tetrasporangia in early developmental stages. In August they were about 6.5~7.0 (max. 8) cm high and 1.3~2.0 mm wide on an average, and became most luxuriant. A fully grown tufted mass was 10~15 cm in diam. The plants had commonly lots of tertiary branches and fourth branchlets, too. Spermatangial plants were not so many, but the tetrasporangial abundant. The cystocarpic plants appeared at this time. In September the plants decreased in number rapidly and in October they were rare and small. One of the small thalli was 1.2 cm high and 0.5 cm wide, bearing only a few primary branches with mature sporangial sori. Since November there were no plants in this area. In addition at the end of June, 1967 there were the germlings less than 1.5 cm high and 1 mm wide, bearing a few primary branches or not.

Considering the above investigations, the plants at Muroran appear in June and become most luxuriant during August. They decrease rather rapidly after September, but remain until October. Both spermatangial and tetrasporangial plants appear since late July, and the cystocarpic ones since early August. These fertile thalli remain until the plants disappear from the area.

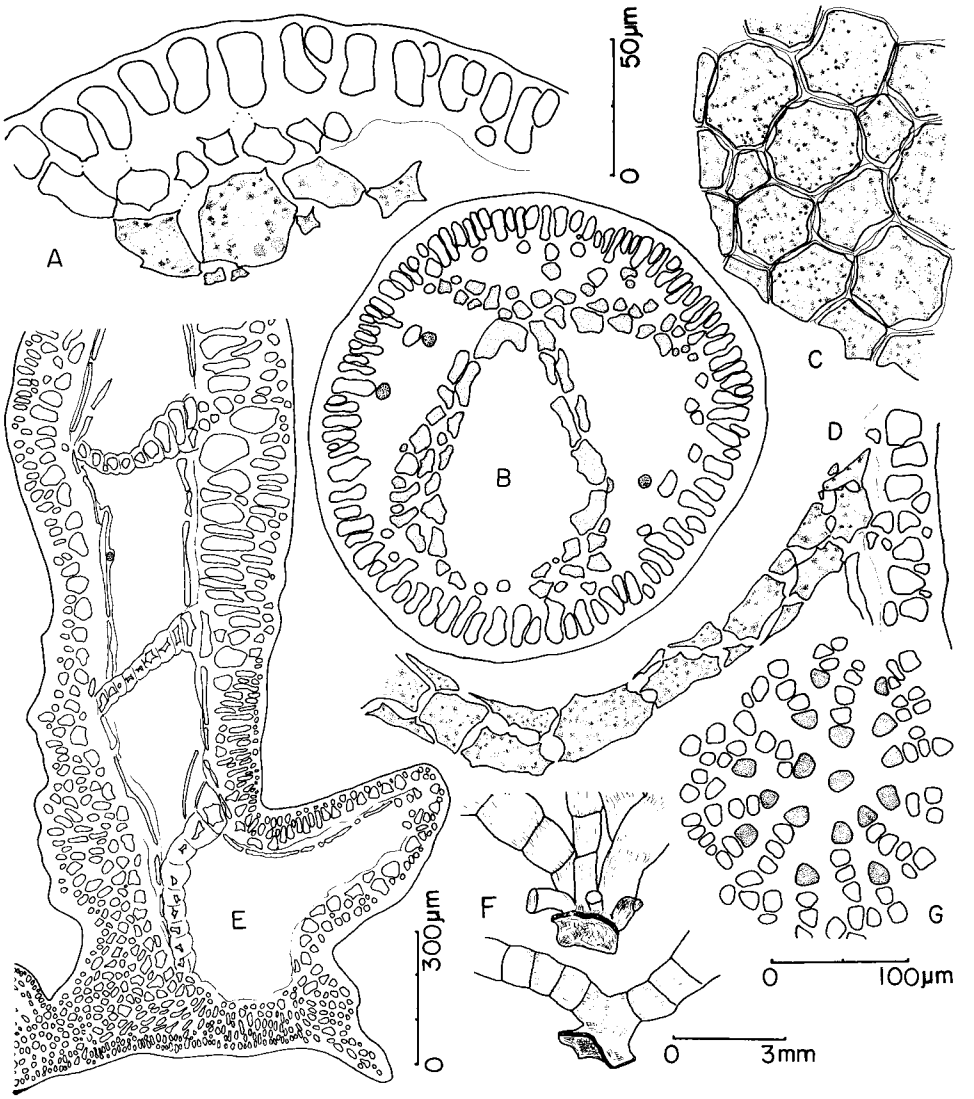

Fig. 60. *Champia parvula* (C. AGARDH) HARVEY

A–B, formation of diaphragm in transverse view; C, part of diaphragm; D, the same in longitudinal view, marginal cells connecting with cortex; E, part of holdfast in longitudinal view; F, the same in outer appearance; G, apex in surface view, showing 17 apical cells.

Morphological Observation

External Appearance

The plant is cylindrical, articulated and branching three to four times repeatedly. The primary branches appear soon after the thallus develops. A few to several fronds are erect commonly from a single holdfast. They are intertangled with one another, fuse with branches and develop rhizoids so much, that it becomes very difficult to separate a single plant from such a tufted mass.

The branches and branchlets are issued mostly at septa or inter-septa. At every one to three septum of the main axis one to a few branches are issued. The mode of ramification is irregular, verticillate, opposite and alternate. In verticillate ones two to three branches are issued at one place around the septum. Sometimes, the main axis is ramified dichotomously at the lower portion. In such a plant, the basal portion of main axis beneath the ramification becomes generally slender, something like a stipe.

All the branches spread widely or patently and become longer downward, so that the thallus is pyramidal to paniculate in outline. In this area the plant bearing such a forked apical portion as described by OKAMURA (1910, pl. 76) is not encountered. The young plant shows more distinct constriction at the septa and the main axis is more inflated at two third portion from the base, where the septum becomes about 1.5 mm high and 1.3 mm wide.

Frequently flat and discoid rhizoids are developed from the frond surface of contacting portion to the substratum (Fig. 61 G). They are similar in shape to the original holdfast. Besides, the fusion of thalli is common in this species. Sometimes, several branches fuse with one another at the same area.

Structure of Thallus

The thallus has a single layer of large cells bordering the central cavity (Fig. 61 B). In transverse section the large cells are polygonally round and similar in size to one another. They cut off obliquely small cells outwards, which are densely pigmented, round to polygonal and about a half to two third times the size of a large cell. In addition, the small cells cut off frequently much smaller cells obliquely outwards, which are oblong to elliptical and about one fifth to one eighth smaller than the penultimate cell. Observed from surface, the large cells are longitudinally elongate about two times as long as broad on an average (Fig. 61 A). The small cells are located among the intercellular spaces of large cells. In young thallus, however, there are only the large cells.

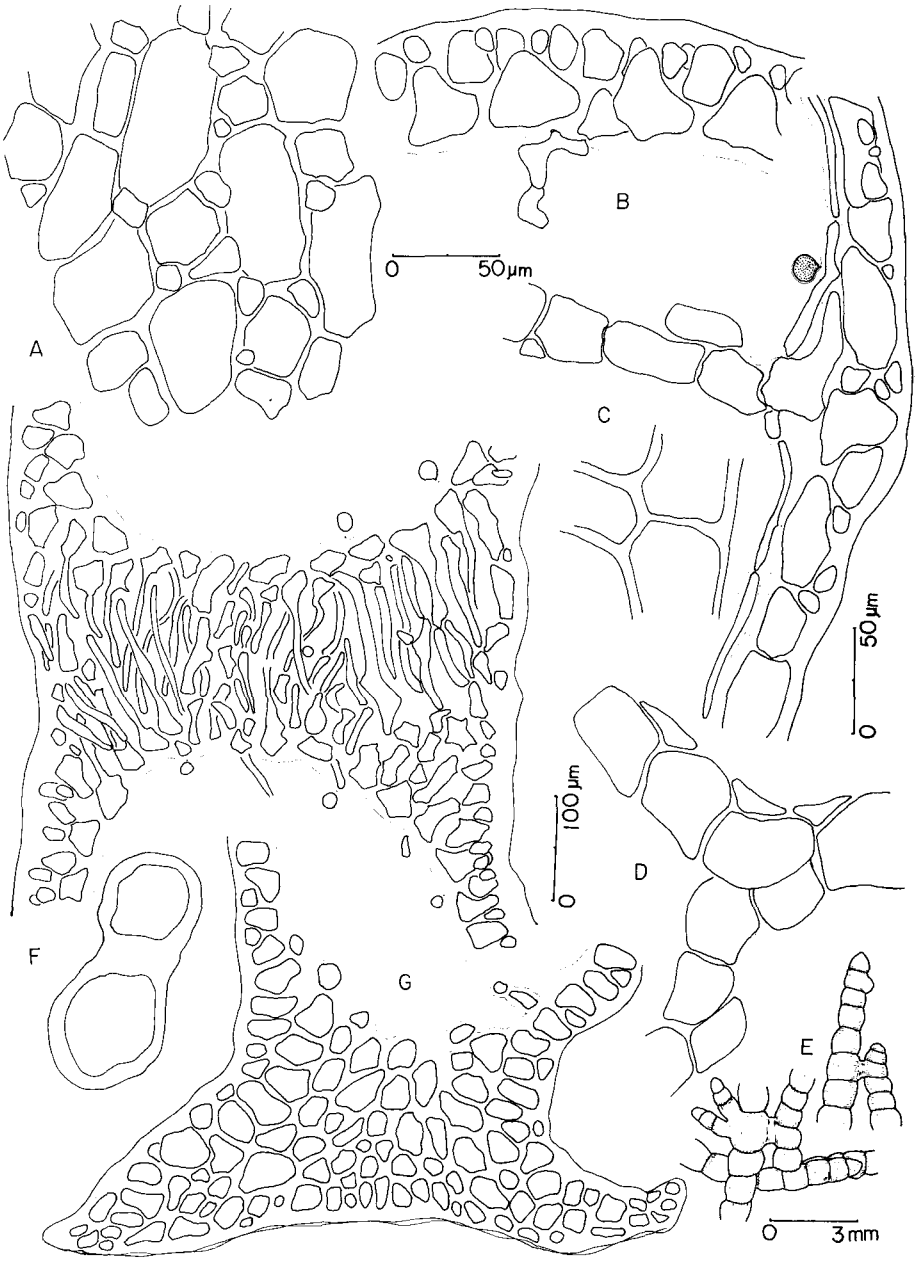

Fig. 61. *Champia parvula* (C. AGARDH) HARVEY

A, cortex in surface view; B, mature thallus in transverse view; C, the same in longitudinal view at septum; D, part of diaphragm at ramified portion, continued to diaphragm of C; E, fusion of branches; F, part of it in transverse view; G, rhizoid in longitudinal view.

The longitudinal filaments developed in central cavity of the thallus are attached to large cells and anchor at septa. In branch apex the filament-initials are cut off periclinally towards the cavity from the cells near the apical cells. They are elongated longitudinally into filaments later. A single filament is composed of three cells generally, which are connected by pits at first but are fused later, leaving articulations there. The filament is frequently branched dichotomously or connected with adjacent ones (Fig. 62 F). The cell of filaments becomes sometimes more than 750 μm long and 10 μm wide. There are about 30~40 filaments in a single segment of the thallus. They are discernible as stripes from the thallus surface even in the field.

The diaphragm at the septum is also single rowed with thin walled hyaline cells. It is connected to both large cells and filaments, and becomes even in upper and lower sides of frond, as if it were cut by knife. There are very small and triangular cells placed among the intercellular spaces, facing their tops inwards (Fig. 60 D). The central portion is slightly thicker than the margin. In transverse section of frond the cells of diaphragm are polygonally round except for those at the margin. Small granules are dispersed in group in the cell (Fig. 60 C).

The diaphragm originates from inner large cells near the apex. In longitudinal section at apical portion of the thallus, some of the cells located at the same distance from the apical cells cut off periclinally the diaphragm-initials inwards. It is very difficult to discern at the beginning, whether they are the initials of diaphragm or those of filament, because both are developed similarly from the large cells (Fig. 62 E, cf. BLIDING 1928, fig. 1 B-C). In transverse section, however, the initials of diaphragm are discerned easily from those of filament. They cut off the cells of diaphragm centripetally and successively toward the cavity (Fig. 60 A). In the early developmental stage a few to several belt-like cell planes are developed centripetally from a few several sites located at the same distance from apex. These plane cells fuse with one another so that they complete the diaphragm formation accordingly (Fig. 60 B).

The gland cells are developed solitarily on the filament inwards (cf. DAVIS 1892, BLIDING 1928, INAGAKI 1934). They appear more often in the upper portion of branches and are round to elliptical, bearing one to three nuclei (Fig. 62 H). A large one is about 15 μm in diam.

The apical cells are arranged characteristically as shown by BIGELOW (1887), DAVIS (1892) and BLIDING (1928). Seventeen were counted in this observation, which accords well with BLIDING's number. The apical cell is triangular of which upper angle is directed to the apical center (Fig. 60 G).

In longitudinal section these apical cells cut off the large cells perpendicularly to the surface, which become longitudinally elongate oblong later.

The branch is developed by periclinal divisions of a few large cells.

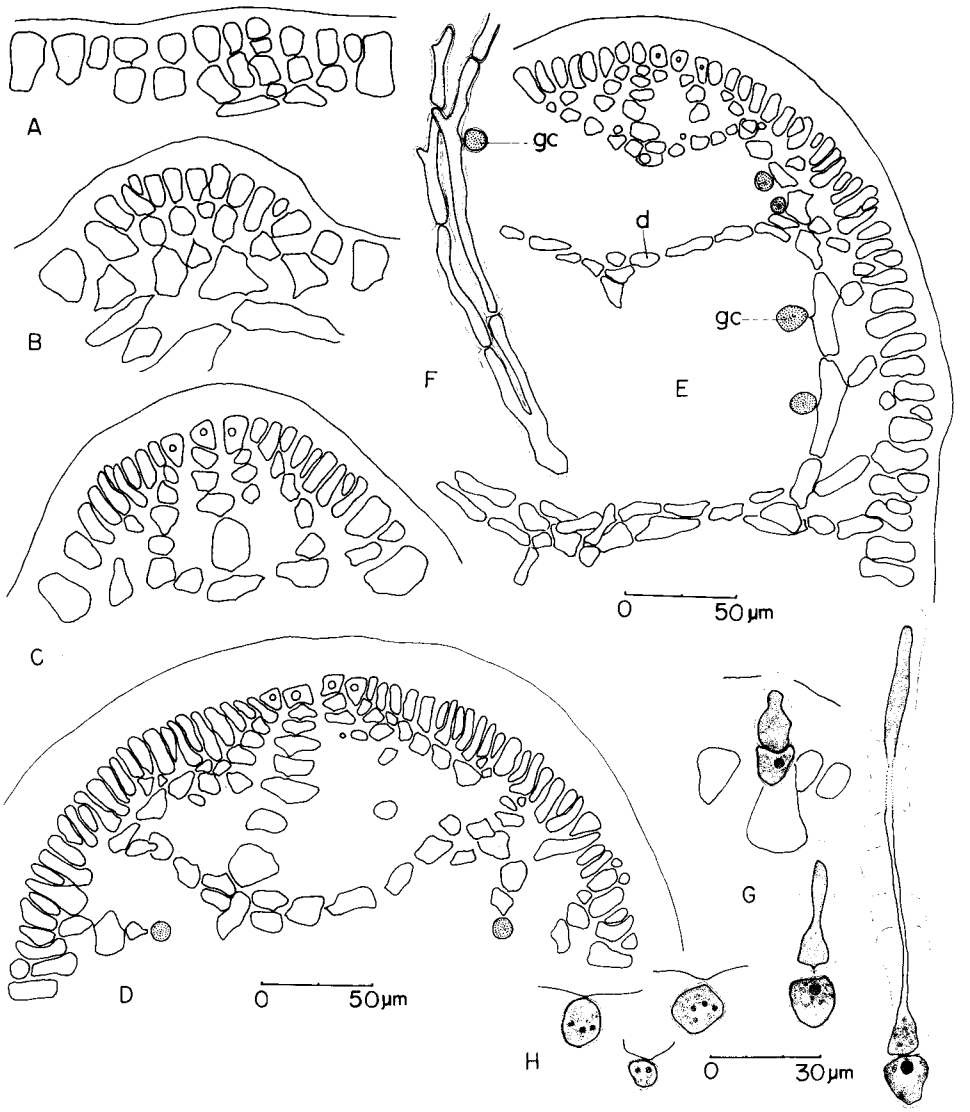

Fig. 62. *Champia parvula* (C. AGARDH) HARVEY

A–E, development of branch, D and E showing development of diaphragms, filaments and gland cells; F, branched filament with gland cell; G, development of hairs; H, gland cells.

Then, the divided superficial cells become apex of the new branch, while the divided inner cells remain as a basal septum after the branch is developed (Fig. 62 A-D).

The holdfast is composed of irregularly arranged small cells which are elongated longitudinally in the central portion. The central cavity is formed

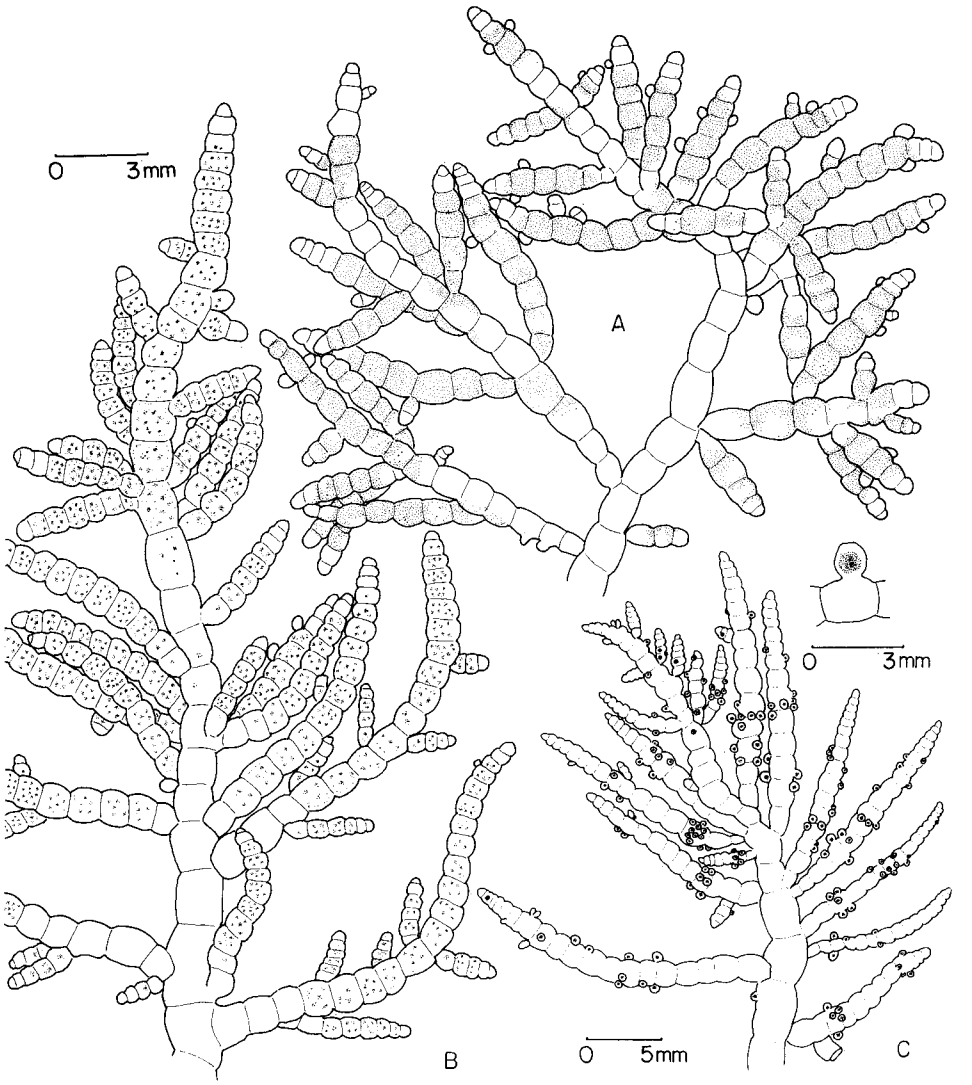

Fig. 63. *Champia parvula* (C. AGARDH) HARVEY

A, part of male thallus bearing spermatangial sori; B, part of tetrasporic plant; C, part of cystocarpic plant.

just above the base. The stipe is not discernible. Sometimes, in old thallus the lower part of the main axis becomes very thick by anticlinal elongation of large cells irregularly (Fig. 60 E). The rhizoids are formed by repeated divisions of inner large cells. One of them about 600 μm in diameter is composed of four to five irregularly arranged cell rows (Fig. 61 G).

The fusion of fronds occurs by the modification of the cells in contact with the opposite ones. These cells are elongate filamentously and interwoven mutually, without showing a fusion border. The protoplasmic connections occur between the opposite fusion cells (Fig. 61 E-F). The hairs are dispersed densely and uniformly over the frond surface. Especially they are abundant in upper portion of branches and branchlets. The large one is about 160 μm long and 15 μm wide (cf. BØRGESEN 1929). The hair is cut off from the outer small cells.

Reproductive Organs

Tetrasporangia: The tetrasporangial sori appear in the lower segment of primary and secondary branches at first, and extend to all branches later. They occur poorly in the upper portion of the main axis (Fig. 63 B). When the sori are developed, the segments become blackish purple and inflated very much, so that the articulations appear more conspicuously. Such a segment becomes almost round instead of common tetragonal form. The fertile branch issues branchlets poorly, compared with sterile ones.

The tetrasporangia occur intercalarily in connection with outer small cells as well as inner large cells (Fig. 64 C). From the early developmental stage the tetrasporangium-initial is discerned by a round shape, densely stained contents, and a large nucleus. The cell is elongate inwards in elliptical to ovoid form, and divided tetrahedrally by simultaneous centripetal planes. The mature sporangium is generally ovoid, 110～120 μm long and 83～92 μm wide. It sinks deeply into the central cavity (Fig. 64 E). Even after the spores are liberated, the gelatinous wall of the sporangium remains clearly. The sterile cells around the tetrasporangia cut off obliquely many small cells from the upper corners.

Spermatangia: The spermatangial plants are generally small compared with the other fertile thalli. The spermatangial sori after maturation become light purple and the thallus has much inflated fertile inter-septa. They appear at first on lateral branches and the upper portion of main axis, and extend later over the thallus surface, forming a girdle-shaped zone (Fig. 63 A, cf. GRUBB 1925, TAZAWA 1975).

In cross section three spermatangia are developed subterminally on the same mother cell. At the beginning of the development the small cell cuts

off obliquely three to four spermatangial mother cells at the upper corners and remains as a sterile basal cell. This mother cell is divided into two to three secondary mother cells obliquely, and the secondary cell is also divided into one or two tertiary mother cells, which cut off often a single fourth mother cell as well. As a result, these mother cells originating from a single

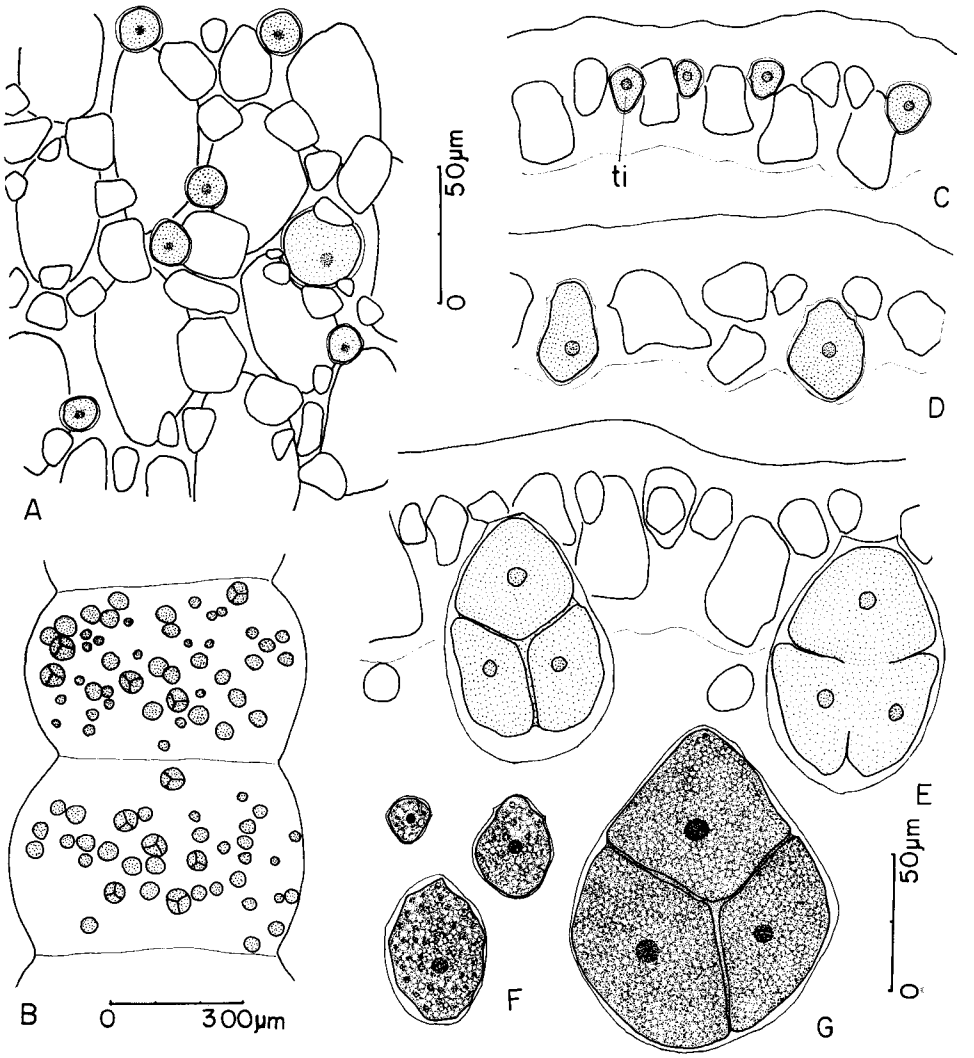

Fig. 64. *Champia parvula* (C. AGARDH) HARVEY

A–B, development of tetrasporangia in surface view; C–E, the same in transverse view; F, young tetrasporangia; G, mature tetrasporangia.
ti: tetrasporangium-initial.

cell are seriate in radial rows around the basal cell, so that they form a reverse pyramidal shape in outline. The mother cells become smaller outwards (Fig. 66 A–C).

When the later mother cells are formed, the early ones protrude a spermatangium from the top. The spermatangium is cut off transversely and has a pit-connection with the mother cell. There is no common wall between the spermatangium and the mother cell (Fig. 66 F). The mother cell cuts off additionally two spermatangia beside the first at almost same time (cf. GRUBB 1925). Thus, these three spermatangia are developed on the same mother cell subterminally.

The secondary spermatangium is also formed from the same mother cell after the primary spermatangia are released. They are developed quite in a similar manner to the previous ones. The tertiary ones were very difficult to confirm in this species.

During the spermatangium formation, the mother cells lose the plastids

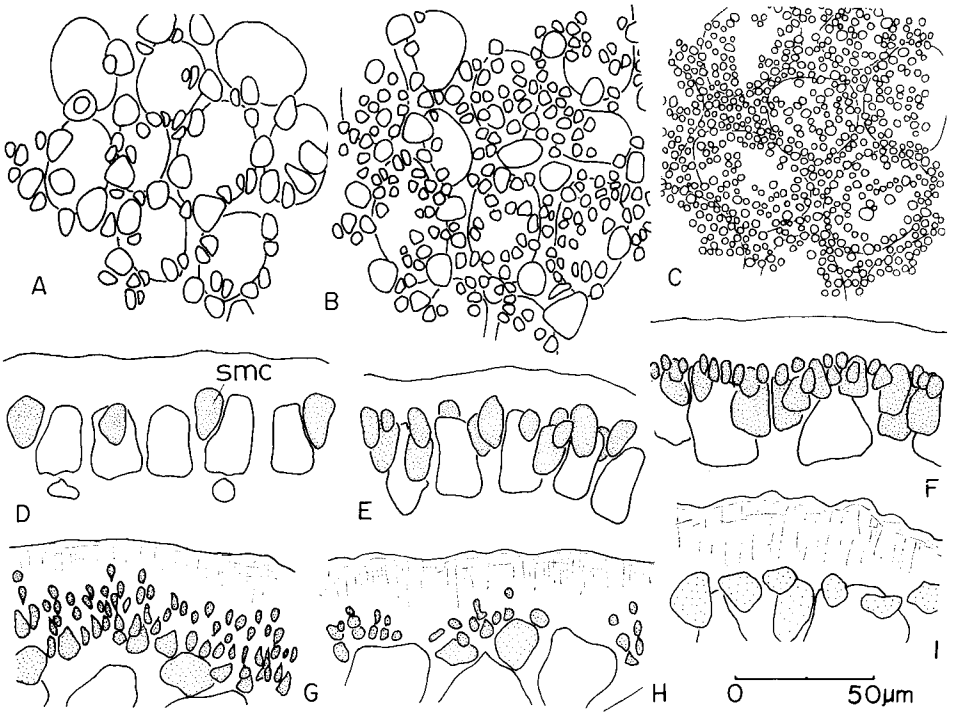

Fig. 65. *Champia parvula* (C. AGARDH) HARVEY
A–C, development of spermatangia in surface view; D–G, the same in transverse view; H–I, later stages of spermatangium formation.
smc: spermatangial mother cell.

before they cut off the primary spermatangia. Therefore, spermatangia and spermatia contain no plastids, while the basal cell of the mother cell contains them generally. The superficial wall of the thallus in soral area are not shed during the spermatangium formation. The mother cell becomes slenderer in form and poorer in contents in later stage of spermatangium formation. When the spermatangium formation is discontinued, all the mother cells disappear and the basal cells only remain. The trace of spermatangium liberation is seen for a while in the superficial wall in the soral area (Figs. 65 I, 66 H). Often the sterile cell bearing hair remains solitarily among the mother cells in fully mature sori.

Cystocarps: The mature cystocarpic thalli are similarly large as the tetrasporangial plants and issue many lateral branches. The cystocarps ap-

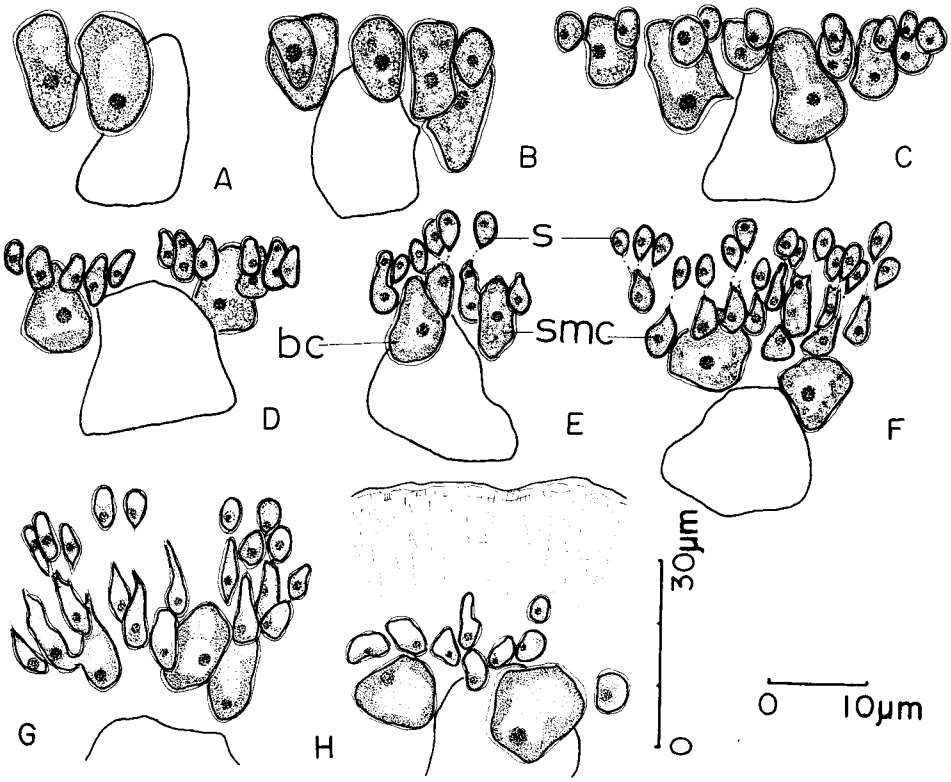

Fig. 66. *Champia parvula* (C. AGARDH) HARVEY

A–C, formation of mother cells seriately; D–F, development of primary spermatangia subterminally on mother cell; G, successive development of spermatangia; H, later stage of the development.

s: spermatangium, smc: spermatangial mother cell, bc: basal cell.

pear at first in the middle to upper portion of primary branches. Later, they are developed on all branches, branchlets and on upper portion of main axis. They appear in solitude or aggregation on septa and inter-septa (Fig. 63 C). Sometimes, more than ten mature cystocarps are aggregated on a single segment. The cystocarp is sessile, spherically elevated from the thallus surface. The rostrum around the carpostome is scarcely recognizable. A fully mature cystocarp is about 860～1100 μm high and wide, while the carpostome is about 75～100 μm in diam.

The carpogonial branch consists of four cells (Fig. 67 A-C, cf. BLIDING 1928, HAUPTFLEISCH 1892, DAVIS 1896). They are scattered sparsely and uniformly. The supporting cell is homologous to inner large cells. It is tetragonal to polygonal and almost similar in size to adjacent sterile cells, and contains many nuclei and densely stained cytoplasmic substances. The central portion of the cell is filled frequently with vacuoles. The first cell of carpogonial branch is transversely elliptical to oblong and about one third to fourth the size of supporting cell. It has homogeneously stained contents and one or two large nuclei. The pit-connection with supporting cell is located at the lower center. The second cell is transversely oblong with a single nucleus and about half to one third times larger in size of the first. The pit-connection with the first cell is also located at the lower center. The third, hypogynous cell, is quite similar in size and form to the second and is connected with the latter in a similar manner to the previous cell. The fourth, carpogonium, is almost similar in size to the first and has a single nucleus. The pit-connection is between the lower central potion of the carpogonium and the upper corner of the hypogynous cell. Before the protrusion of trichogyne, the carpogonium is almost trapeziform. The trichogyne is uniformly thick and straight. One of them was about 64 μm long and 3.5 μm wide. The carpogonium is located above the first cell, while the hypogynous cell is above the second.

The two-celled auxiliary cell branch is clearer after the presumed fertilization. In several instances, however, the auxiliary cell branch appears before the trichogyne is protruded out of the superfical wall. The two auxiliary cell branches reported by DAVIS (1896) were not found. The auxiliary mother cell is about two third times the size of the supporting cell and is a compressed globose form with many nuclei. The auxiliary cell is round, almost similar in size to the first cell of the carpogonial branch and has a single nucleus.

When the trichogyne disappears gradually after the presumed fertilization, the auxiliary mother cell and auxiliary cell increase in volume (Fig. 67 E).

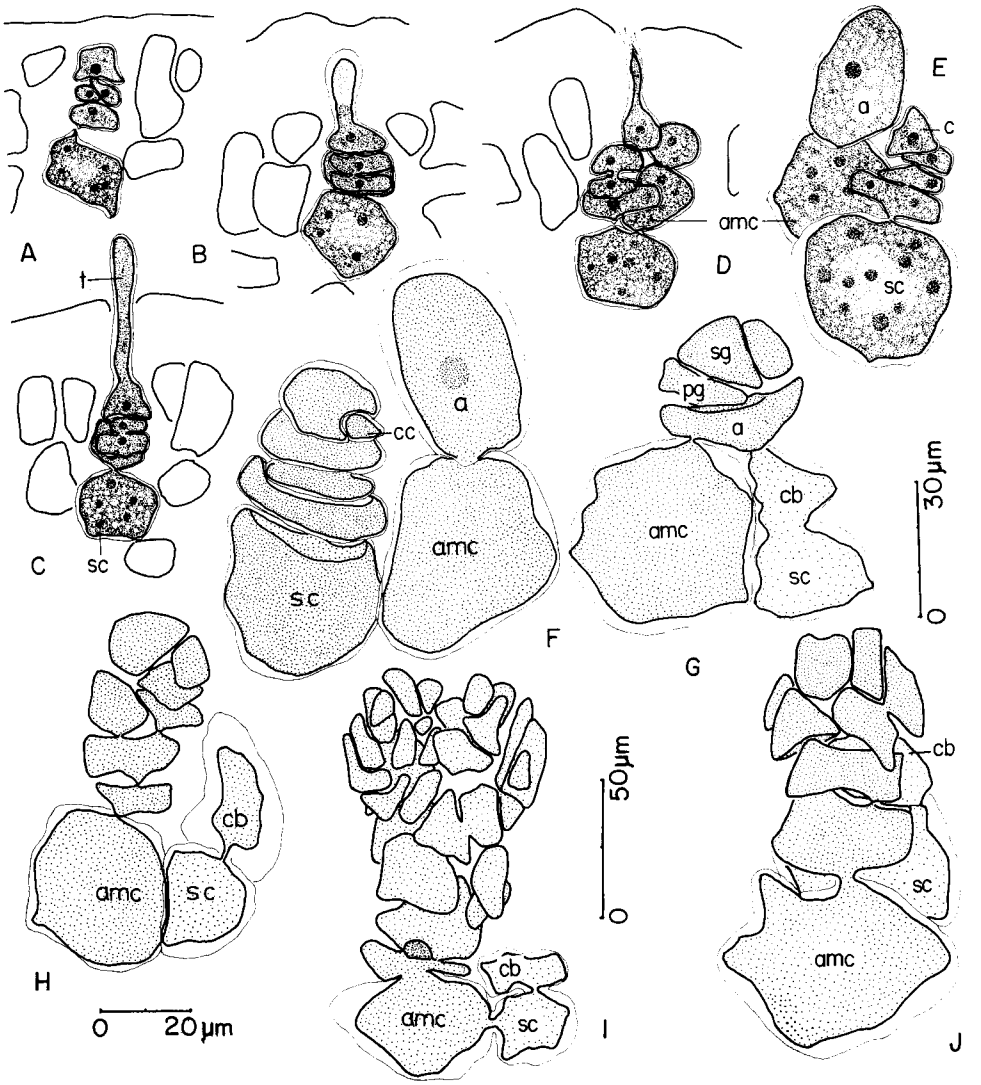

Fig. 67. *Champia parvula* (C. AGARDH) HARVEY

A–B, development of carpogonial branches; C, supporting cell and carpogonial branch; D, degeneration of trichogyne, showing auxiliary cell branch; E, enlargement of auxiliary cell branch; F, cutting off a connecting cell from carpogonium; G, cutting off a few gonimoblast cells, degenerating fused carpogonial branch and supporting cell; H–J, development of embryonic cells of gonimoblast.

t: trichogyne, sc: supporting cell, a: auxiliary cell, amc: auxiliary mother cell, cb: carpogonial branch, c: carpogonium, cc: connecting cell, pg: primary gonimoblast cell, sg: secondary gonimoblast cell.

The cells of carpogonial branch are enlarged slightly, opening the pit-areas. A connecting cell, mentioned by no previous investigators, is cut off from one corner of the carpogonium (Fig. 67 F). It is comparatively small until the cells of carpogonial branch form a fusion cell completely, and coalesces with the auxiliary cell (Fig. 68 A). Later, the fusion cell of the carpogonial branch becomes almost round and disappears gradually, losing the contents. On the other hand, the auxiliary mother cell and the supporting cell are enlarged exceedingly during the period and surrounded by a thick wall respectively. The auxiliary mother cell becomes larger than the supporting cell, and develops numerous secondary connection with surrounding sterile cells.

The primary cell of the gonimoblast is cut off transversely from the auxiliary cell. The secondary gonimoblast cell is cut off rather obliquely from the primary. The tertiary is cut off almost vertically from the secondary. The auxiliary cell and the primary cell of the gonimoblast become flattened acetabuliform (Fig. 67 G). The later cells of the gonimoblast are cut off from the outer cells successively. The young carposporophyte is oblong in outline (Fig. 67 H–J). The cells of the gonimoblast become smaller outwards. Frequently a new gonimoblast, so called 'verspäter Gonimolob' by BLIDING (1928, fig. 10 A–B), is developed in the young cystocarp (Fig. 68 C–D). Later, the auxiliary mother cell, auxiliary cell and early cells of the gonimoblast form a large fusion cell, while the later cells of the gonimoblast are elongate and connected to radial branches. Even in a mature carposporophyte, the carposporangia are developed only from the superficial row of cells of the gonimoblast (Fig. 68 E–F). They are wedge-shaped during the growth (cf. GREVILLE 1930). The mature carposporangium is almost round to polygonal and about 49～55 μm in daim. It has a nucleus and plastids.

The pericarp formation begins soon after the presumed fertilization. It develops similar in a manner to the ones seen in the previous species. In this formation, however, the cells of pericarp take on a conspicuous stellate form, issuing protoplasmic strands radially in order to connect with adjacent cells (Fig. 68 B). The fully mature pericarp is composed of a single row of large superficial cells and three to five irregular rows of cells forming a net-work so called 'tela arachnoidea' (J. AGARDH 1876). The pulvinus at the base of the cystocarp is developed considerably, consisting of densely stained stellate cells.

As seen in *Lomentaria catenata*, among the plants collected in August there were several tetrasporangial thalli bearing cystocarps on branches, where

no tetrasporangial sori were developed (cf. DAVIS 1896).

Discussion

C. AGARDH (1824) introduced this alga as *Chondria parvula*, from Cadiz, Spain. Several combinations were made before HARVEY (1853), combined it with *Champia* as *C. parvula*. Later, J. AGARDH (1876) gave the same name for this plant, which becomes accordingly a later homonym. In addition *Fucus kaliformis* TURNER (1808) var. γ *nanus* was also accepted as a synonym of this plant.

This plant was investigated many times. Among them, most important works were carried out by DAVIS (1892, 1896), HAUPTFLEISCH (1892) BØRGESEN (1920), and BLIDING (1928). DAVIS observed early development of the thallus from carpospores, and mentioned that this plant showed usually 'four cap-cells' at the top of the germling from which the apical growth of thallus began.

Concerning the filamemt of vegetative thallus, this investigation accords well with DAVIS' and BLIDING's results in that the filament is not developed directly from the apical cell, but is the secondary structure (DAVIS 1892). The initial cells are cut off periclinally from large cells near the apex and become filaments by longitudinal elongation (BLIDING 1928, fig. 1 B–C).

NÄGLI (1847) mentioned the occurrence of gland cell for the first time. It was noticed frequently by later workers under various names (DEBRAY 1890, HAUPTFLEISCH 1892, DAVIS 1892, BLIDING 1928, INAGAKI 1934). DEBRAY observed the gland cell as an undeveloped diaphragm. However, it is quite different from the diaphragm as mentioned above (cf. BLIDING 1928).

GRUBB (1925) reported that the branched basal cells of the spermatangial mother cell, from which the mother cells were cut off singly or in pairs. However, as pointed out by BLIDING (*l. c.*), there are no branched basal cells in this species. It is thought that she mis-understood the seriate nature of mother cells as basal cells. However, the formation of three primary spermatangia from a single mother cell, mentioned by GRUBB, accords well with this investigation.

In cystocarp development, there are not three-celled carpogonial branch (HAUPTFLEISCH 1892), nor two to three-celled ones (DAVIS 1896), but always four-celled one (BLIDING 1928). Moreover, there are no auxiliary cell branches as reported by DAVIS (1896, cf. OLTMANNS 1922) where he claimed that the supporting cell bears two auxiliary cell branches.

The occurrence of a connecting cell in the members of Champiaceae was reported by HAUPTFLEISCH (*l. c.*) and KYLIN (1923) in *Lomentaria clavellosa*. It is interesting that the connecting cell divided from the carpogonium

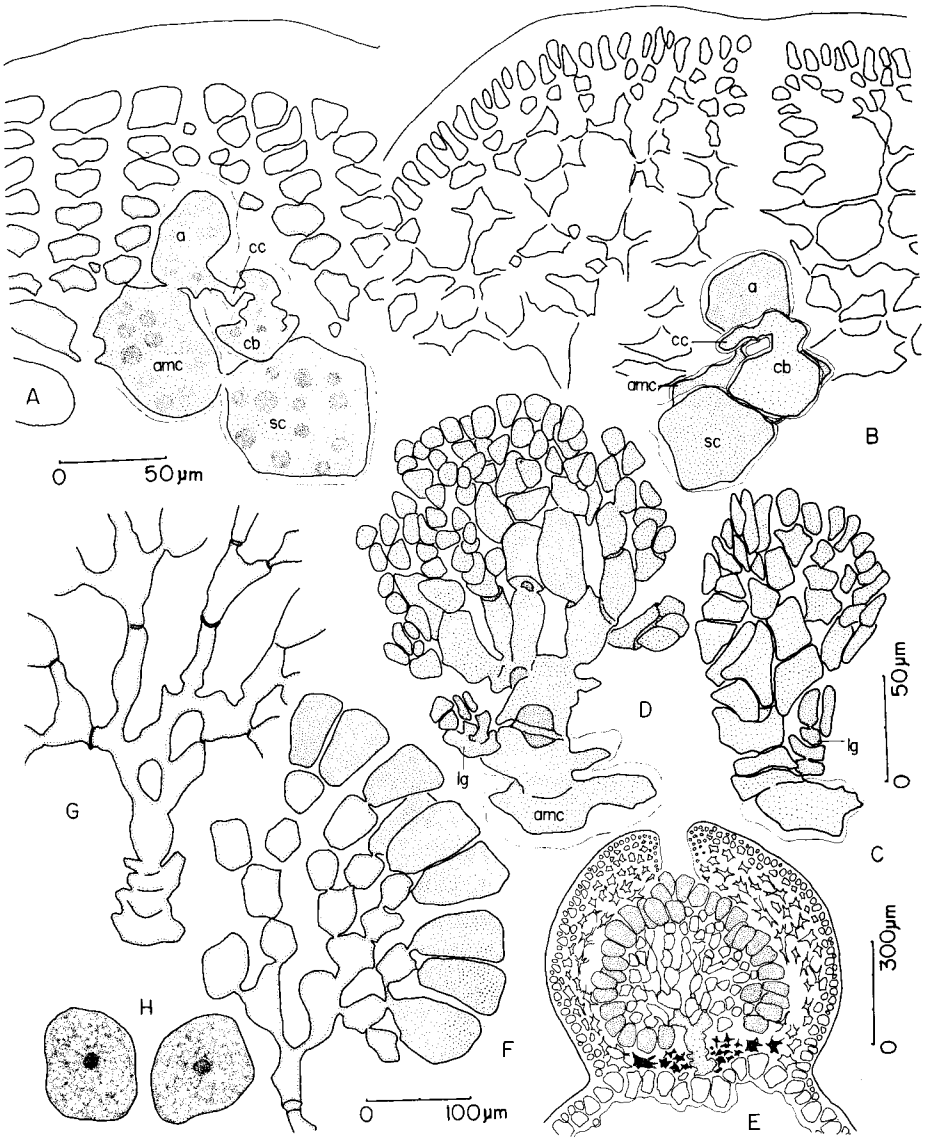

Fig. 68. *Champia parvula* (C. AGARDH) HARVEY

A, fusion between auxiliary cell and connecting cell, cells of carpogonial branch coalescing; B, development of pericarp, showing exceedingly modified inner cells; C–D, young carposporophytes, developing later gonimoblast cells; E, mature cystocarp; F, part of gonimoblast with carposporangia; G, fusion cell of mature cystocarp; H, carposporangia.

a: auxiliary cell, amc: auxiliary mother cell, cc: connecting cell, cb: carpogonial branch, sc: supporting cell, lg: later goniomblast.

was found in this species after the presumed fertilization. The other characters of the cystocarp development accord well with the BLIDING's observation in general.

General Account

A key to taxa of Rhodymeniales investigated in Hokkaido is shown here. The phenological and morphological features as well as the developmental anatomy of reporductive organs are comprehensively compared with one another.

Key to Taxa of Rhodymeniales in Hokkaido

A. Tetrasporangium cruciately divided
  I. Thallus saccate — *Halosaccion*
    1. Thallus composed of 3～5 cell rows, with large medullary cells — *H. yendoi* sp. nov.
    2. Thallus composed of 9～13 cell rows, without large medullary cells — *H. firmum*
  II. Thallus flat
    1. Tetrasporangia with stalk cell — *Palmaria*
      a) Cortex specially thick at margin — *P. marginicrassa* sp. nov.
      b) Cortex not thick at margin — *P. palmata*
    2. Tetrasporangia without stalk cell — *Rhodymenia*
      a) Thallus with perforated obovate to elliptical frond — *R. pertusa*
      b) Thallus with flabellate frond — *R. intricata*
  III. Thallus cylindrical, without articulation — *Chrysymenia wrightii*

B. Tetrasporangium tetrahedrally divided
  I. Thallus with multi-rowed cellular septa — *Lomentaria*
    a) Sterile cells in sporangial sori forming net-work — *L. catenata*
    b) Sterile cells not forming net-work — *L. hakodatensis*
  II. Thallus with uni-rowed cellular septa — *Champia parvula*

Phenology (Fig. 69)

The summerized results on the phenological observation of these species were reported by LEE & KUROGI (1972).

The present members inhabit mostly in lower tidal zone, except for *R. pertusa* which is in subtidal zone as well. The habitats are sheltered more or less from violent wave action, and sometimes exposed to air at lower tide. Especially *R. intricata* and *C. wrightii* are found at rather calmer places,

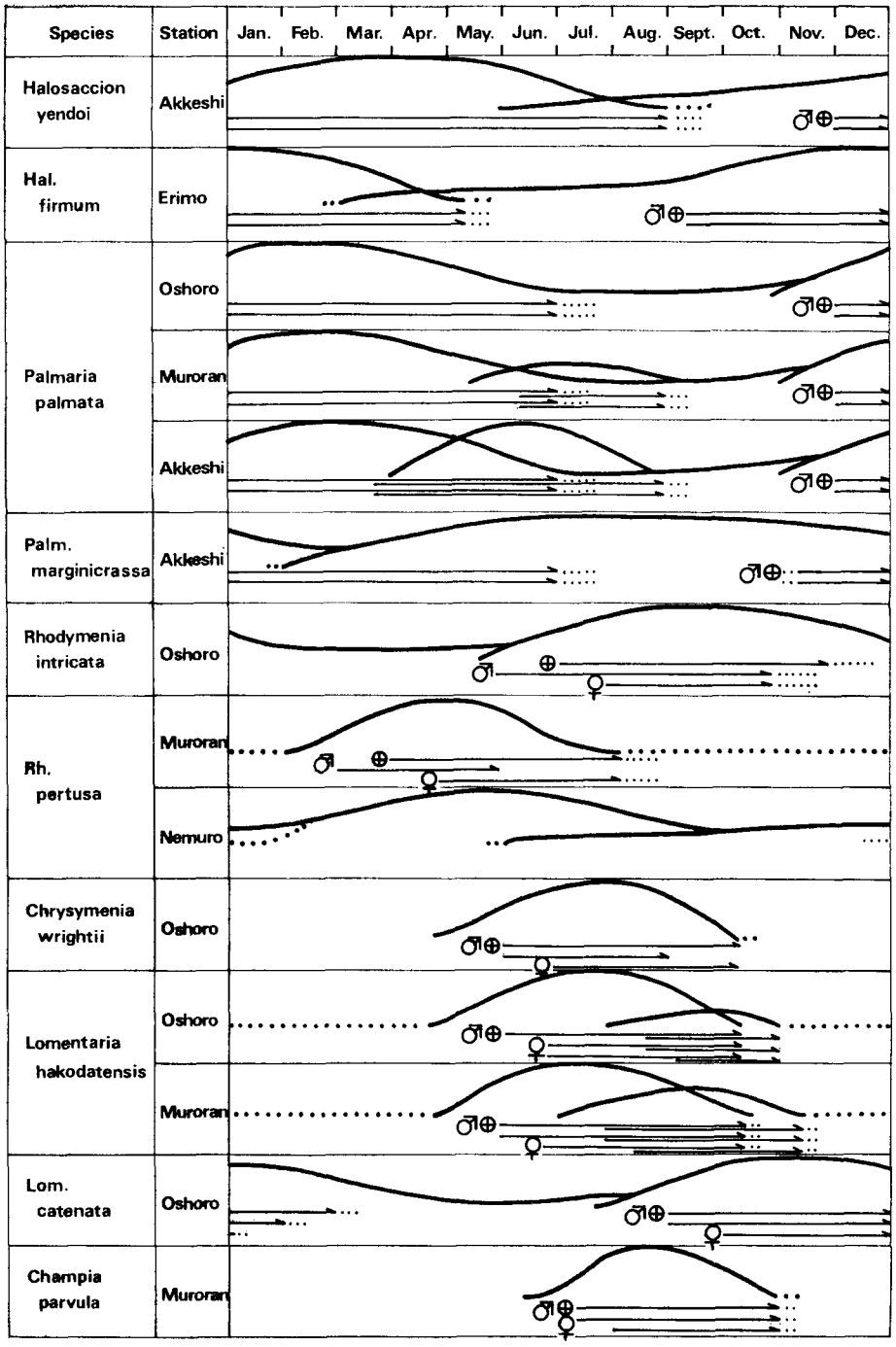

Fig. 69. Phenology of the members of Rhodymeniales in Hokkaido (LEE and KUROGI 1972).

whereas *H. firmum* and *C. parvula* are found at places exposed to the open sea. *H. yendoi*, *H. firmum*, *L. hakodatensis* and *C. parvula* are epiphytic on other algae or growing on rocks, whereas *P. palmata*, *P. marginicrassa*, *R. intricata*, *R. pertusa*, *C. wrightii* and *L. catenata* grow on rocks generally. *R. pertusa* and *C. wrightii* occur rather sparsely, and *P. palmata* very densely. *H. firmum* occurs in such a compact aggregation of the thalli, that there remains almost no space in the habitat. *L. hakodatensis* and *C. parvula* form spherical tuffed masses at a calm place and an expanded mass at an exposed place.

There are annual and perennial species. The perennial ones remain frequently with the lower portion of thalli from which new fronds are developed in the next year. Among the perennial species, *H. firmum*, *P. palmata*, and *P. marginicrassa* are encountered rather commonly through the year, whereas *R. pertusa*, *R. intricata* and *L. catenata* are found in small members or scarcely after the luxuriant period. *H. yendoi*, *L. hakodatensis*, *C. wrightii*, and *C. parvula* are annual. *H. yendoi* is encountered through the year, while *L. hakodatensis* is found rarely as a small procumbent thalli after the growth period.

The first germlings of *H. firmum*, *C. wrightii*, and *L. hakodatensis* appear in spring; *R. intricata* in late spring to early summer; *H. yendoi*, *L. catenata*, and *C. parvula* in summer; *P. palmata* in autumn; and *P. marginicrassa* and *R. pertusa* in winter. On the other hand, *H. yendoi* and *R. pertusa* are most luxuriant in spring; *P. marginicrassa*, *C. wrightii*, *L. hakodatensis* and *C. parvula* in summer; *R. intricata* in summer to early autumn; *H. firmum* and *L. catenata* in autumn to winter; and *P. palmata* in winter to early spring. As a result, the most luxuriant period of growth appears generally two to five months after their appearance, except for the two members of *Halosaccion*, which become luxuriant about nine to ten months later. This luxuriant period is continued for two to three months except for one month in *C. parvula*.

In addition, *P. palmata*, *R. pertusa* and *L. hakodatensis* develop new germlings again during or after their luxuriant periods. In *P. palmata* these new thalli grow to maturation and disappear about four months later, frequently remaining with the lower fragments of thalli. So called var. *sarniensis* (MERT.) GREVILLE and f. *ochotensis* NAGAI of *R. palmata* (syn. of *P. palmata*) are found among these newly germinating thalli. Forma *prolifera* KJELLMAN consists of nothing but the old remaining thalli bearing lots of proliferations. In *R. pertusa*, especially in Nemuro area, new germlings appear in May to June when mature thalli become luxuriant, while in Muroran area

they are not found. Some of the perennial plants grow slowly in young stage, but the annual ones, except for *H. yendoi*, grow more or less rapidly and become luxuriant sooner.

Except for *P. marginicrassa* and the two members of *Halosaccion*, spermatangia, tetrasporangia and cystocarps begin to appear about one or two months later from the appearance of thalli. In *Halosaccion*, however, the fertile organs appear about seven months later. It is interesting to note that the fertile organs of *P. marginicrassa* appear after the period when the thalli are most luxuriant both in size and number.

Among the reproductive organs of a single species, tetrasporangia and spermatangia appear almost at the same time, while cystocarps one month later. However, in *R. intricata* and *R. pertusa* the spermatangia appear earlier in time than tetrasporangia. It is a noticeable fact that the species developing no cystocarps, such as the members of *Halosaccion* and *Palmaria*, produce tetrasporangia for longer periods in about eight to nine months, while the ones developing cystocarps produce them for about a half or more of the former period, about four to six months. The latter species produce cystocarps for three to five months.

Morphology

External Appearance (Table 2)

The members investigated are saccate, flat or cylindrical. The saccate members, *Halosaccion yendoi* and *H. firmum*, are simple and oblong to ovate or linear-lanceolate to lanceolate, while the flat members, *Palmaria* and *Rhodymenia*, are ramified once to five times dichotomously to palmately. *Rhodymenia pertusa* has clefts or laciniations of the frond. In cylindrical members, *Chrysymenia wrightii* is not articulated, while *Champia parvula* is very distinctly articulated and two members of *Lomentaria* are more or less distinctly articulated. These members are ramified three to five times in various manners. Except for *C. wrightii*, the cylindrical members are intertangled more or less.

The mature thalli are less than 10～20 cm high generally, except for *P. palmata* and *R. pertusa*, which become up to 50～100 cm high. *R. intricata* is less than 4 cm high in the present area investigated, though it becomes larger in the other places (OKAMURA 1930). All the plants have a discoid holdfast and more or less distinct stipe, or no stipe at all. *R. intricata*, *L. hakodatensis* and *L. catenata* develop stolons, while those and *C. parvula* form rhizoids and show the fusion of thalli. There are proliferations of frond from old thalli remaining in *P. palmata*, *P. marginicrassa*, *R. intricata*, *R. pertusa* and *L. catenata*, whereas the regenerations of frond

occur at the wounded margin of old thalli in *H. yendoi*, *H. firmum*, and *L. catenata*.

The members show dark purple to blackish purple color in dried specimens. Some of them become dark red to brownish red, too. The saccate or flat members are mostly tender in substance and membranaceous in texture, except for *P. marginicrassa* and *H. firmum* which are firm and submembranaceous to coriaceous. *P. palmata* is membranaceous in young thalli and coriaceous in old. The cylindrical members contain generally abundant gelatinous substances and more or less flaccid. So, they adhere to paper

TABLE 2 The external

Species	Shape	Size		Ramification
		Height (cm)	Width (mm)	
Halosaccion yendoi	saccate oblong to ovate	10~15	40~50	none
H. firmum	saccate linear-lanceolate to lanceolate	8~15	20~30	none
Palmaria palmata	flat palmate to subpalmate	20~50	20~80	1~5 times palmate to dichotomous (with clefts)
P. marginicrassa	flat oblanceolate to spatulate	10~20	15~25	once dichotomous
Rhodymenia intricata	flat flabellate	2.5~ 4	2~6	3~5 times dichotomous to subpalmate
R. pertusa	flat obovate to elliptical	15~40 (−100)	70~200 (−500)	once dichotomous (with laciniations)
Chrysymenia wrightii	non-articulated cylindrical tree-like	15~18	2~3	3~4 times alternate, opposite and irregular
Lomentaria hakodatensis	articulated cylindrical tree-like	6~ 9	0.8~1.3	3~5 times opposite, verticillate and irregular
L. catenata	articulated cylindrical tree-like	7~10	1~1.5	3~5 times opposite, verticillate alternate and irregular
Champia parvula	articulated cylindrical tree-like	5~ 7	1.5~2	3~4 times irregular, verticillate alternate and opposite

(+) only within the same thallus

firmly in drying the materials. *L. catenata,* however, is somewhat cartilaginous and adheres to paper incompletely.

Structure of Thallus, (Table 3)

The thallus is composed of cortical and medullary layers. Except for the members of *Rhodymenia* and *Palmaria,* the central portion is provided with a cavity. The cortical layer is composed of small and densely pigmented cells. The superficial cortical cells are tetragonal and arranged in more or less compact palisade in *H. yendoi, P. palmata, P. marginicrassa* and the members of *Lomentaria* and *Champia.* In *R. intricata, R. pertusa* and *C.*

characters of the thalli

Color (dried specimen)	Texture or Substance	Hold-fast	Stipe	Stolon	Rhizoid	Fusion of Thalli	Duration of Growth
light to dark purple	membranaceous	discoid	+	−	−	(+)	annual
blackish purple	coriaceous	"	+	−	−	−	perennial
dark purple	membranaceous to coriaceous	"	±	−	−	−	"
blackish purple	submembranaceous to coriaceous	"	±	−	−	−	"
dark red	membranaceous	"	+	+	+	+	"
dark purple	membranaceous	"	+	−	−	−	"
dark red	gelatinous	"	±	−	−	−	annual
dark purple	gelatinous	"	−	+	+	+	"
dark purple	cartilaginous	"	−	+	+	+	perennial
dark purple	gelatinous	"	−	−	+	+	annual

wrightii, the superficial cortical cells are somewhat oblong anticlinally and arranged irregularly. In *H. firmum* the superficial cortical cells are oblong and compactly arranged but uneven. The cortical cells of the members of Rhodymeniaceae are generally smaller than those of Champiaceae.

The medullary layer is hyaline. It is composed of polygonally round cells, which become larger inwards. In *R. intricata, C. wrightii, L. catenata,* the medullary cells are more or less longitudinally elongate inwards. The innermost cells of the latter three members are slender and filamentous, while some members such as *H. yendoi, P. palmata, P. marginicrassa, R.*

TABLE 3 The anatomical

Species	Cortex (cell-row)	Medulla (cell-row)	Thickness (μm)	Central Cavity	Septum
Halosaccion yendoi	1~2	2~3	100~160	+	−
H. firmum	3~5	6~8	220~350	+	−
Palmaria palmata	3~4	3~5	300~500	−	
P. marginicrassa	3~4	3~5	350~510	−	
Rhodymenia intricata	1~3	4~8	120~150	−	
R. pertusa	1~2	3~5	200~230	−	
Chrysymenia wrightii	1~3	3~5	120~180	+	(+) (only at branch base)
Lomentaria hakodatensis	1	4~6	75~120	+	+ (multi-rowed)
L. catenata	1	4~6	120~160	+	+ (multi-rowed)
Champia parvula	1	0	55~ 65	+	+ (uni-rowed)

pertusa and *C. wrightii* show the outer medullary cells much smaller than the inner. There is no medullary layer in *C. parvula*.

The thickness of the thalli is different according to species. Members of *Rhodymenia* and *Palmaria* are generally one to three times thicker than saccate or cylindrical ones. Especially in *Palmaria* the thickness increases by repeated divisions of the superficial cortical cells as the thallus becomes old. In members of *Palmaria* and *Rhodymenia* there are annual ring-like thickenings of cortical layer in old stipe. Among the cylindrical members, *Lomentatia* develops transverse septa in the central cavity, which are com-

characters of the thalli

Innermost Medullary Cell	Filament	Gland Cell	Hair	Superficial Cortical Cell (μm) (height × width)	Inner Medullary Cell (μm) (height × width)
broad	−	−	+ (grouping)	6.9~8.4 × 8.4~9.2	55~70 × 80~100
"	−	−	−	8.3~15.2 × 3.5~4.0	48~55 × 48~55
"	−	−	+ (grouping)	5~10 × 6~12	180~300 × 250~450
"	−	−	−	8.3~11.2 × 5.6~9.7	120~280 × 120~280
elongate	−	−	−	4.2~5.6 × 2.8~4.2	28~30 × 35~42 (wide) 70~90 (long)
broad	−	−	−	5.6~8.3 × 5.6~8.3	70~100 × 50~140
linear	+ (hyphae-like)	+	+ (dispersed)	5.5~7.0 × 3.5~4.2	45~70 × 35~83 (wide) 73~680 (long)
"	−	+	+ (dispersed)	17~24 × 11.2~19.5	14.5~27.5 × 20~32 (wide) 70~150 (long)
"	−	+	−	12.5~19.5 × 8.4~14.2	21~31 × 21~31 (wide) 80~200 (long)
	+	+	+ (dispersed)	28~35 × 35~42 (wide) 45~83 (long)	

posed of three to five cell-rows, while *C. parvula* develops a single rowed diaphragm. *C. wrightii*, however, develops the septum only at the base of branches.

C. parvula is characterized by multi-cellular filaments developed in the central cavity, whereas *C. wrightii* by multi-cellular hyphae-like filaments issued from innermost medullary cells. The gland cells are developed only in cylindrical members. In *C. parvula* they are attached to the filament inwards, while in members of *Lomentaria* and *Chrysymenia* they appear rather abundantly upon the transverse septa or basal septa of branches. The fusion of thalli occurs with the modification of cortical cells in *R. intricata*, *L. hakodatensis*, *L. catenata*, and *C. parvula*. There remain no borderline later between the two, but develop protoplasmic connections between the opposite cells. *R. intricata* develops no protoplasmic connection.

TABLE 4 The characters

Species	Sorus Situation	Development in Cortex	Division
Halosaccion yendoi	whole surface	terminal	cruciate
H. firmum	"	"	"
Palmaria palmata	"	"	"
P. marginicrassa	whole surface (hieroglyphic)	"	"
Rhodymenia intricata	apical portion	intercalary (frequently)	"
R. pertusa	whole surface	"	"
Chrysymenia wrightii	branches	"	"
Lomentaria hakodatensis	"	terminal	tetrahedral
L. catenata	"	"	"
*Binghamia californica**	whole surface	"	"
Champia parvula	branches	intercalary	"

(* According to LEE & KUROGI (1973))

The rhizoid is formed by the modification of superficial cortical cells, likewise seen in the fusion of thalli. The unicellular hairs originate from superficial cortical cells and are found in *H. yendoi*, *P. palmata*, *C. wrightii*, *L. hakodatensis*, and *C. parvula*. They are abundant in young thalli or upper portion of the fronds. In *H. yendoi* and *P. palmata* they appear in group, while in cylindrical members they are dispersed over the surface rather uniformly.

In members of *Halosaccion*, *Palmaria* and *Rhodymenia* the thallus grows upwards by means of transverse and oblique divisions of the marginal meristems, as mentioned by SJÖSTEDT (1926, fig. 19 B) in *Rhodymenia pertusa*. In cylindrical members, however, there are apical initials, which are especially distinct in *C. parvula*. In the latter members the thickening of the fronds is initiated in addition with the divisions of superficial cortical cells.

of tetrasporangia

Shape	Size (μm) (length × width)	Stalk Cell	Secondary Fo mation	Modification of Sterile Cortical Cells in Sorus
elliptical	32~40 × 22~30	+	+	2~3 celled branch
elongated elliptical	40~48 × 20~28	+	+	elongation
elliptical	60~75 × 52~65	+	+	3~4 celled branch
oblong	49~53 × 21~27	+	+	4~5 celled paraphysis
elliptical to oblong	34~39 × 15~18	−	−	elongation
elliptical to ovate	63~77 × 42~49	−	−	none
round to elliptical	48~53 × 38~42	−	−	elongation
round	90~110 × 95~125	−	−	small cells formation
〃	160~190 × 160~190	−	−	〃
〃	90 × 97	−	−	〃
〃	110~120 × 83~92	−	−	none

Reproductive Organs

i) Tetrasporangia (Table 4): The tetrasporangia are developed in sori over the whole surface, except for *R. intricata* in which they are confined only to the apical portion of branches. Especially in members of *Rhodymenia*, *Palmaria* and *Halosaccion* the mature sori cover almost all the thallus surfaces, except for the basal and apical portions of thalli. In *P. marginicrassa* the sori develop into a characteristic hieroglyphic elevation from thallus surface dominantly. In members of *Lomentaria* there appears a hollow in the superficial wall in the sorus.

The tetrasporangia are developed from the cortical cells terminally or intercalarily. It is one of the noticeable characters that some members of Rhodymenioideae, *Rhodymenia* and *Chrysymenia*, develop the sporangia from inner cortical cells, so that the sporangia bear frequently obliquely divided

TABLE 5 The characters

Species	Sorus Situation	Mother
		Number & Development from Cortical Cell
*Halosaccion yendoi**	whole surface	6~8, separate
*H. firmum**	"	2, separate
Palmaria palmata	"	6~8, separate
P. marginicrassa	whole surface hieroglyphic	2~4, separate
*Rhodymenia intricata***	apical portion	2~6, seriate
R. pertusa	whole surface	3~4, seriate
Chrysymenia wrightii	branches	5-or more, seriate
Lomentaria hakodatensis	"	5-or more, seriate
L. catenata	bladder-like fertile ramuli	7-or more, seriate
*Binghamia californica****	whole surface	5-or more, seriate
Champia parvula	branches	7-or more, seriate

(According to LEE & KUROGI (1968 a)*, (1968 b)**, and (1973)***).

outer cortical cells and become intercalary in occurrence. Such a character has not been reported in the members of this subfamily. On the other hand, the members of *Halosaccion* and *Palmaria* develop terminally formed tetrasporangia which have a stalk cell. They develop secondary sporangium from the stalk cell, after the liberation of previous sporangium.

The members of Rhodymeniaceae have cruciately divided tetraspoangia, whereas those of Champiaceae tetrahedrally divided ones. In the Rhodymeniaceae the first division occurs periclinally to the thallus surface and the second anticlinally. In *C. wrightii* the first division is not always periclinal, but somewhat oblique. However, the second division is anticlinal to the first. In the Champiaceae the tetrahedrally divided tetrasporangia are formed simultaneously by centripetal divisions. They are somewhat larger than the cruciately divided ones. The cylindrical members bear generally round spo-

of male organs

Cell	Spermatangium			Superficial Wall in Sorus
Size (μm) (height × width)	Number	Cell Wall	Size (μm) (length × width)	
6.0~7.8 × 3.0~3.8	two	common to mother cell	8.5 × 5.5	shed
12.0~12.8 × 3.4~4.3	"	"	15.8 × 3.7	"
5.7~8.6 × 3.4~4.6	two to three	"	9.2 × 3.4	"
6.8 × 2.8	two	"	8.6 × 3.4	"
5.2 × 2.3	one to two	independent of mother cell	3.1 × 2.3	remaining
8.9 × 4.3	"	"	5.1 × 3.4	"
4.5~5.7 × 2.8~3.1	one	"	4.0 × 2.9	"
6.8~9.7 × 2.9~4.3	"	"	4.6 × 2.9	"
4.6~6.9 × 2.3~3.4	one to two	"	4.6 × 3.2	"
4.6~8.6 × 2.8~4.6	one	"	4.0 × 3.0	"
7.7 × 3.5	three	"	6.8 × 4.3	"

rangia, whereas the others elliptical to oblong ones.

The modification of sterile cortical cells in the sorus is variable according to species. In members of *Lomentaria* numerous small cells are cut off from superficial cortical cells, which produce tetrasporangia terminally, while the medullary cells in the sori are modified filamentously and surround the

TABLE 6 The cystocarpic characters

Species	Situation	Carpogonial Branch	Auxiliary cell Branch	Connecting Cell	Gonimoblast	
					Primary Division	Secondary Division
Halosaccion yendoi	unknown					
H. firmum	unknown					
Palmaria palmata	unknown					
P. marginicrassa	unknown					
Fauchea laciniata	scatter	3-celled	1, two-celled	+	transverse	oblique
Gloioderma saccatum	margin	〃	〃	+	〃	〃
Chrysymenia wrightii	scatter	4-celled	〃	−	〃	〃
C. ventricosa		3-celled	〃	−	〃	
Botryocladia pseudodichotoma		〃	〃	−	〃	oblique
Rhodymenia intricata	margin	2-celled	〃	(+)*	〃	〃
R. pertusa	scatter	4-celled	〃	−	〃	oblique or transverse
R. pseudopalmata		〃	〃	+	〃	oblique
Epymenia obtusa	fertile proliferation	〃	1, three-celled	−	〃	
Lomentaria hakodatensis	scatter	3-celled	1, two-celled	−	〃	oblique
L. catenata	〃	〃	〃	−	〃	〃
L. articulata		〃	〃	−	〃	〃
Binghamia californica	scatter	〃	〃	−	〃	〃
Champia parvula	〃	4-celled	〃	+	〃	〃
Chylocladia kaliformis		〃	2, two-celled	−	〃	radial
Gastroclonium ovale		〃	〃	−	〃	〃
Coeloseira parva	scatter	〃	〃	−	〃	〃

(* Two cells cut off from carpogonium and hypogynons cell, respectively).

sporangia, forming more or less distinct net-work, which is specially remarkable in *L. catenata*. Some other members, *H. firmum*, *R. intricata* and *C. wrightii* show only the elongation of cortical cells, whereas *R. pertusa* and *C. parvula* do scarcely the modification. In *H. yendoi*, *P. palmata* and *P. marginicrassa* these sterile cells are divided into two to four celled

of members of Rhodymeniales

Cystocarp		Pericarpic Cells	Carpostome	Carposporangium		Reference
Shape	Size (μm) (height × width)		(μm in diam.)	Conversion from Gonimoblast Cells	Size (μm)	
elevated, round to coronate		filamentous (net-work)		all		SPARLING (1957)
elevated, coronate		"		"		"
elevated, peachy-shaped	750~850 × 850~950	stellate	86~100	"	32~ 38	LEE (this paper)
		cellular		"		BLIDING (1928)
sink		"		"		"
elevated mammiform	680~770 × 600~690	"	60~100	"	19~ 23	LEE (this paper)
elevated, peachy-shaped	1200~1350 × 1400~1670	"	70~ 85	"	48~ 58	"
elevated		"		"		SPARLING (1957)
elevated		"		"		"
elevated, mammiform	860~1100 × 750~980	stellate	90	"	90~110	LEE (this paper)
elevated, spherical	760~950 × 760~950	"	100~120	"	97~120	"
elevated		"		"		BLIDING (1928)
elevated, peachy-shaped	900 × 1200	cellular	100	"	55~ 70	LEE and KUROGI (1973)
elevated, spherical	860~1100 × 860~1100	filamentous (net-work)	75~100	terminal only	49~ 55	LEE (this paper)
"		cellular	lacking	"		KYLIN (1923)
"		"	"	"		BLIDING (1928)
"	280~360 × 280~360	"	"	"	50~80 × 20~25	HOLLENBERG (1940)

sterile branches. In *P. marginicrassa* these sterile branches develop into paraphyses later.

ii) Spermatangia (Table 5): The spermatangium formation of the members of Rhodymeniales were reported by LEE (1969).

The spermatangial sori are generally similar in shape to the tetrasporangial sori, except for *L. catenata* which develops special fertile ramuli. The spermatangium originates from the superficial cortical cell, which cuts off spermatangial mother cells directly or indirectly. The spermatangial mother cells originated from the same superficial cortical cell are separate or seriate. In members of *Halosaccion* and *Palmaria* these mother cells have no pit-connection directly between each other, but are connected with the basal cell only and are thus separate. In the members of *Rhodymenia, Chrysymenia, Lomentaria* and *Champia* these mother cells are connected with pits directly to one another. Thus, they are seritate side by side. Among the former members, in *H. firmum* and *P. marginicrassa* two to four spermatangial mother cells are cut off from a single cortical cell, whereas in *H. yendoi* and *P. palmata* the cortical cell cuts off a few cells primarily from which several mother cells are cut off secondarily. Among the latter members, however, in *R. intricata* and *R. pertusa* the cortical cell cuts off a few mother cells which cut off secondary mother cells, whereas in *C. wrightii* and *L. hakodatensis* such secondary mother cells cut off the tertiary, and in *L. catenata* and *C. parvula* the tertiary mother cells cut off often the fourth in addition. In latter members the mother cells become smaller in size outwards.

The spermatangial mother cell produces a single spermatangium terminally or two to three subterminally. In *C. wrightii* and *L. hakodatensis* a single spermatangium is developed, whereas in *R. intricata, R. pertusa* and *L. catenata* a single or two spermatangia are developed. *H. yendoi, H. firmum* and *P. marginicrassa* develop two spermatangia from a mother cell, whereas *C. parvula* develops three. In *P. palmata* two or three spermatangia are developed from a single mother cell.

A single spermatium is formed within each spermatangium. It conveys all the contents of the spermatangium. After liberation, the same mother cell develops a secondary spermatangium in all members investigated, while a tertiary spermatangium is confirmed also in several species. It is very difficult to count the number of spermatangia developed from a single mother cell repeatedly. However, the mother cell becomes slenderer in form and poorer in contents as it produces more spermatangia.

The mature spermatangia are elliptical to oblong. They are especially

large in the members of *Halosaccion* and *Palmaria*. Moreover, the spermatangia and mother cell have a common wall, and the superficial wall in the sorus is shed when the spermatangia are developed. On the other hand, in the members of *Rhodymenia*, *Chrysymenia*, *Lomentaria* and *Champia*, the spermatangia are comparatively small, and have no common wall with the mother cell but a pit-connection only. The superficial wall in the sorus is not shed during the spermatangium formation.

iii) Cystocarps (Table 6): The members of *Halosaccion* and *Palmaria* develop no cystocarps in the geographic areas investigated nor in other regions (GUIRY 1975). In the other members the cystocarps are developed on the frond surfaces uniformly, except for *R. intricata* which develops them on the upper margins of the frond.

The procarps are found generally in young branches or in the upper portion of the branches of the female thallus. In *R. intricata* they are aggregated at slightly concave marginal areas, while in the other members they are dispersed uniformly. The supporting cell is homologous to inner cortical cells, or outer medullary cells. The fertile cells are easily distinguished from sterile ones by their dense contents. The cells of the carpogonial branch are stained homogenously and more intensely with cotton blue solution. The carpogonial branch is composed of three to four cells, except for *R. intricata* which has a two-celled one before fertilization, four following.

The auxiliary cell branch is composed of two cells and occurs singly. KYLIN (1923) and BLIDING (1928) reported the auxiliary cell branch to be produced before the fertilization. However, since fertilization was not observed, it is difficult to understand this statement. In this paper a fertilization is assumed when the trichogyne disappears and the cells of auxiliary cell branch enlarge at this time. In *C. parvula* the auxiliary cell branch is distinguishable sometimes before the trichogyne is protruded out of the thallus surface. The auxiliary mother cell is almost round, and connected with the supporting cell. The two cells are multi-nucleate, while the cells of carpogonial branch contain one or two nuclei. The carpogonium and the auxiliary cell bear generally a single nucleus at the beginning.

After the presumed fertilization, the cells of carpogonial branch enlarge pit-areas, and form a fusion cell sooner or later. In the members of *Lomentaria* this fusion cell is formed before the carpogonium coalesces with the auxiliary cell, and becomes a conspicuous column. In the other members, however, after fertilization, the auxiliary cell and the carpogonium coalesce soon and the cells of carpogonial branch make a fusion cell later. The

formation of a connecting cell from the carpogonium, reported by HAUPTFLEISCH (1892), KYLIN (1923), and SPARLING (1957) is observed in *C. parvula*. In *R. intricata*, however, the carpogonium and hypogynous cell are each divided into two cells after fertilization. Then, the upper most cell, a daughter cell of the carpogonium coalesces with the auxiliary cell.

The primary cell of the gonimoblast is cut off transversely from the auxiliary cell. The protein body (KYLIN 1930), observed in the auxiliary cell of *R. intricata* and *L. hakodatensis*, remains always in this primary cell of the gonimoblast. One or a few secondary cells of the gonimoblast are cut off obliquely from the primary cell. In *R. pertusa* the secondary cells are divided sometimes transversely as well. The further cells of the gonimoblast are divided from the outer cells successively. Almost all the cells of the gonimoblast are converted into the carposporangia sooner or later, except for *C. parvula* in which the carposporangia are formed only from the terminal gonimoblast cells. The auxiliary mother cell, auxiliary cell and the early gonimoblast cells make a fusion cell resembling more or less a column-like trunk.

The cystocarp is elevated from the thallus surface and has a carpostome of about 100 μm in diameter. The mature cystocarp is mammiform, peach-shaped or spherical. The carposporangium is round to elliptical. It is very small in *R. intricata*, and comparatively large in *Lomentaria*.

The pericarp formation begins after the trichohyne disappears. It is initiated with the transverse division of the sterile cortical cells surrounding the fertile cells. During the development of the pericarp, nutritive cells staining densely are formed around the fertile cells additionally, connecting directly or indirectly with the auxiliary mother cell. They are observed also at the base of a mature cystocarp. When a dome-shaped pericarp is formed, the inner pericarpic cells are modified in shape more or less. In *C. parvula* they form a filamentous net-work, so called *tela arachnoidea*, whereas in *C. wrightii* and the members of *Lomentaria* they become stellate in form. However, in the members of *Rhodymenia* they are modified scarcely at all.

Taxonomical Discussion

Some taxonomic characters of the members investigated are summarized in Table 7.

Among the Rhodymeniales, the manner of division of the tetrasporangium has been used to distinguish the families, Rhodymeniaceae and Champiaceae (BLIDING 1928, KYLIN 1956), but since this appears to be a variable character in these families, in which, for example, tetrahedrally divided tetrasporangia in *Hymenocladia* (KYLIN 1931) are reported for a

family Rhodymeniaceae that is otherwise characterized as showing cruciate divisions. Furthermore, among the Rhodymeniaceae, the intercalary or terminal occurrence of tetrasporangia in the cortical layer seems also to be a variable criterion upon which to distinguish the subfamilies Fauchioideae, Rhodymenioideae and Hymenocladioideae, though KYLIN (1931) adopted it as an important character for the Rhodymenioideae. Intercalary tetrasporangia as well as terminal ones are shown in species of *Rhodymenia* and *Chrysymenia*. However, the stalk cell formation of the sporangia in the members of Palmariaceae seems to be a noticeable character to distinguish it from the others, as mentioned by GUIRY (1974).

The classifications of spermatangia by GRUBB (1925) or TAZAWA (1975) seem not to clarify the taxonomical relations, but the development of mother cells from the cortical cell seems to be a character with more important taxonomical role in the Rhodymeniales, as reported previously (LEE 1969). The spermatangium formation of the Rhodymeniales can be divided into two types; the Separate Type and the Seriate Type. The Separate Type, seen in *Halosaccion* and *Palmaria*, is typified by 1) spermatangial mother cells originating from a single superficial cortical cell are not connected directly one another; 2) the spermatangia and the mother cell are surround by a common wall so that the spermatangial wall remains after the spermatium is released; 3) the spermatangia are comparatively large; and 4) the superficial wall of thallus in the sorus is shed when the spermatangia are developed. However, the Seriate Type, seen in *Rhodymenia*, *Chrysymenia*, Champiaceae as well as *Binghamia* (LEE & KUROGI 1972), is typified by 1) the spermatangial mother cells originating from a single cortical cell are connected directly by pits with one another; 2) the spermatangium and the mother cell have no common wall; 3) the spermatangium is comparatively small; and 4) the superficial walls of the sorus remain intact during the spermatangium formation.

In female reproductive structure the number of cells of the carpogonial branch, thought to be an important character to distinguish the families Rhodymeniaceae and Champiaceae by BLIDING (1928) and KYLIN (1931), is variable from two to four in the Rhodymeniaceae. However, it is well defined in the Champiaceae by that the members of Lomentarioideae have three-celled ones and those of Champioideae four-celled ones. On the other hand, in the species investigated in this study, there are not two auxiliary cell branches as seen in *Chylocladia* (KYLIN 1923, BLIDING 1928), *Gastroclonium* (BLIDING 1928), *Coeloseira* (HOLLENBERG 1940), and often in *Lomentaria* (HAUPTFLEISCH 1892, KYLIN 1923, SVEDELIUS 1937), nor the three-

celled auxiliary cell branch as seen in *Epymenia obtusa* (SPARLING 1957). The two auxiliary cell branches seem to be a general character of the Champioideae except for *Champia*, whereas the three-celled branch seems to be a special occurrence among the members of the order.

As seen in *Lomentaria* (HAUPTFLEISCH 1892, KYLIN 1923), *Rhodymenia* (SPARLING 1957) and *Champia*, the formation of a connecting cell seems to

TABLE 7. Comparision of some taxonomic

Species		*Halosaccion yendoi*	*H. firmum*	*Palmaria palmata*	*P. marginicrassa*
Ecological Feature	Luxuriant period	Mar.-May	Nov.-Feb.	Jan.-Mar.	Jun.-Aug.
	Duration	annual	perennial	perennial	perennial
Habit	Shape (branching)	saccate (none)	saccate (none)	flat (1~5 times)	flat (once)
Structure of Thallus	Hair	+ (grouping)	−	+ (grouping)	−
	Inner medullary cell	broad	broad	broad	broad
	Central cavity	+	+	−	−
	Septum in cavity	−	−		
	Gland cell	−	−	−	−
	Filament or hyphae-like filament	−	−	−	−
Tetrasporangium	Development	terminal	terminal	terminal	terminal
	Division	cruciate	cruciate	cruciate	cruciate
	Stalk cells	+	+	+	+
	Secondary formation	+	+	+	+
	Modification of sterile cells in sori	branch of 2~3 cells	elongation	branch of 3~4 cells	paraphysis of 4~5 cells
Spermatangium	Developmental type of mother cells	separate type	separate type	separate type	separate type
	Number of spermatangia from a mother cell	two	two	two to three	two
Cystocarp	carpogonial branch				
	Auxiliary-cell branch				
	Connecting cell				
	Pericarpic cells				
	Carpospoangium formation from gonimoblast cells				

(* According to LEE & KUROGI (1973)).

be not so rare in this order. However, the division of the carpogonium and the hypogynous cell into two respectively, as seen in *R. intricata*, seems to be a special character of this species, since no such cell formation is reported elsewhere previously.

During the development of the carposporophyte, the modification of the carpogonial branch to a column-like fusion cell is one of the interesting char-

characters among the members of Rhodymeniales

Rhodymenia intricata	*R. pertusa*	*Chrysymenia wrightii*	*Lomentaria hakodatensis*	*L. catenata*	*Binghamia californica**	*Champia parvula*
Jul.–Sept.	Apr.–May	Jul.–Aug.	Jul.–Aug.	Oct.–Dec.		Aug.
perennial	perennial	annual	annual	perennial		annual
flat (3~5 times)	flat (once)	cylindrical (3~4 times)	cylindrical (3~5 times)	cylindrical (3~5 times)	flat (5~7 times)	cylindrical (3~4 times)
–	–	+ (dispersed)	+ (dispersed)	–	+ (dispersed)	+ (dispersed)
elongate	broad	linear	linear	linear	elongate	
–	–	+	+	+	+	+
		(+) (branch at base)	+ (multi-rowed)	+ (multi-rowed)	+ (multi-rowed)	+ (uni-rowed)
–	–	+	+	+	+	+
–	–	+ (hyphae-like)	–	–	–	+ (filament)
intercalary	intercalary	intercalary	terminal	terminal	terminal	intercalary
cruciate	cruciate	cruciate	tetrahedral	tetrahedral	tetrahedral	tetrahedral
–	–	–	–	–	–	–
–	–	–	–	–	–	–
elongation	none	elongation	formation of small cells	formation of small cells	formation of small cells	none
seriate type	seriate type	seriate type	seriate type	seriate type	seriate type	seriate type
one to two	one to two	one	one	one to two	one	three
2-celled	4-celled	4-celled	3-celled	3-celled	3-celled	4-celled
one, 2-celled	one, 2-celled	one, 2-celled	one, 2-celled	one, 2-celled	one, 2-celled	one, 2-celled
(+)	–	–	–	–	–	+
cellular	cellular	stellate	stellate	stellate	cellular	filamentous
all cells	all cells	all cells	all cells	all cells	all cells	terminal cells

acters of the members of Lomentarioideae, as mentioned by LEE & KUROGI (1972) in *Binghamia californica.*

The primary cell of the gonimoblast is divided transversely from the auxiliary cell, while the secondary ones are cut off obliquely from the primary cell, except for *Chylocladia, Gastroclonium* and *Coeloseira* where they are divided radially. In the members of Champioideae the carposporangia are formed only from the superficial cells of the gonimoblast, while in the members of the Rhodymeniaceae and Lomentarioideae they are formed from almost all cells of the gonimoblast. The cystocarps sinking inwards in the thallus are characteristic of *Botryocladia,* while the ones without carpostome are *Chylocladia, Gastroclonium* and *Coeloseira.* According to species, pericarpic cells form a filamentous net-work so called *tela arachnoidea,* a stellate form, or a scarcely modified form. The stellate form seen in *Chrysymenia* and *Lomentaria* seems to be an intermediate modification between the other two.

Establishing the two families, Rhodymeniaceae and Champiaceae, BLIDING (1928) summarized their characters as follows. Rhodymeniaceae are characterized by the absence of longitudinal filaments in the inner portion of the thallus, the three-celled carpogonial branch, the conversion of almost all the cells of the gonimoblast into carposporangia, and the cruciately divided tetrasporangia, whereas Champiaceae by the presence of longitudinal filaments the four- or three-celled carpogonial branches, the conversion of almost all or only the superficial cells of the gonimoblast into carposporangia and the tetrahedrally divided tetrasporangia. He pointed out further that the discernible characters of the two groups were the differences of gonimoblast formation, and the shape of carposporangia.

Variations are shown by the following studies; *Lomentaria* of Champiaceae lacks longitudinal filaments (this paper), the carpogonial branch of the Rhodymeniaceae varies from two to four cell units (this paper), *Hymenocladia* of Rhodymeniaceae has tetrahedrally divided tetrasporangia (KYLIN 1931, SPARLING 1957), and *Coeloseira* of Champiaceae bears polysporangia (HOLLENBERG 1940). In spite of such exceptions, many species in both families appear to be related well among themselves (KYLIN 1956).

On the other hand, GUIRY (1974) in erecting the Palmariaceae separated it from the Rhodymeniaceae by the characters of the tetrasporangium possessing a stalk cell, of the superficial wall of the spermatangial sori shed during spermatangium formation, and of the lack of female plants in the life history. According to my studies, it appears that this family seems to be confined more safely, not only by the above mentioned characters, but

by the development of the spermatangium in that the mother cells are formed exclusively by the separate type, while other members of Rhodymeniales are of the seriate type. The cystocarp is quite missing in all the known members of the family.

Dividing the Rhodymeniaceae into three subfamilies, KYLIN (1931) distinguished the Fauchioideae by a *tela arachnoidea* in the cystocarp, the Hymenocladioideae possessed tetrahedrally divided tetrasporangia occurring intercalarily in the cortex, and the Rhodymenioideae lacked both of these. On the other hand, dividing the Champiaceae into two subfamilies, he recognized the differences shown by the Lomentarioideae in the multi-rowed cellular septa, three-celled carpogonial branch, the carposporangia converted from almost all cells of the gonimoblast, and the tetrasporangia appearing in spherical and small sori, whereas the Champioideae showed uni-rowed cellular septa, four-celled carpogonial branch, the carposporangia converted from only the terminal gonimoblast cells, and the tetrasporangia dispersed over the thallus surface. However, SPARLING (1957) recognized only two subfamilies in Rhodymeniaceae, and rejected KYLIN's Fauchioideae because she believed that the formation of a *tela arachnoidea* in the cystocarp was related to the degree of stretching of the cells of pericarp. Furthermore, some species showed only a slight *tela arachnoidea* in cystocarp formation. She thought that the character did not seem to be so significant as to distinguish a subfamily.

According to the present investigation, so far as the Rhodymeniaceae, SPARLING's hypothesis seems to be reasonable. In fact, *C. wrightii* shows such an intermediate modification of the pericarpic cells becoming stellate in form, less modified than a *tela arachnoidea.* Moreover, since some members of Rhodymenioideae such as *Rhodymenia* and *Chrysymenia* develop intercalary tetrasporangia frequently as mentioned above, the only criterion to separate Hymenocladioideae from Rhodymenioideae is the formation of tetrahedrally divided tetrasporangium in the former. The character, however, seems not to be so important as to divide a subfamily. Thus, the Hymenocladioideae may well be rejected in the Rhodymeniaceae.

On the other hand, the two subfamilies of Champiaceae defined well, not only in vegetative structure but in the reproductive organs. The important taxonomical characters of the two subfamilies are summarized as below :

Lomentarioideae (*Lomentaria* — *Binghamia*)

Thallus cylindrical or flat, medullary layer developed, central cavity septated by multi-rowed cellular wall.

Tetrasporangia forming aggregated sori, terminal in cortical layer, tetrahedrally divided, superficial wall of sorus ruptured, sterile medullary cells in sorus modified more or less filamentously.

Spermatangia terminal or subterminal on mother cell, spermatangial mother cells seriate type in formation.

Cystocarps elevated, with three-celled carpogonial branch forming column-like fusion cell soon after fertilization, auxiliary cell branch one or rarely two, carposporangia converted from almost all gonimoblast cells, carpostome opened.

Champioideae (*Champia* — *Chylocladia* — *Gastroclonium* — *Coeloseira*)

Thallus cylindrical, medullary layer not developed, central cavity septated by single rowed cellular wall.

Tetrasporangia forming dispersed sori, intercalary in cortical layer, tetrahedrally divided, superficial wall of sorus not ruptured, sterile cells in sorus scarcely modified.

Spermatangia subterminal on mother cell, spermatangial mother cells seriate type in formation.

Cystocarps elevated or sunk, with four-celled carpogonial branch not forming column-like fusion cell, auxiliary cell branch one or two, carposporangia converted only from terminal gonimoblast cells, with or without carpostome.

Considering the above characters, both subfamilies are fundamentally different in the anatomical characters of vegetative structure such as the formation of medullary layer and the cellular arrangement of the septum. Moreover, the sorus formation and the development of tetrasporangia as well as some significant taxonomical characters in the cystocarp development such as column-like fusion cell formation of the carpogonial branch and carposporangium formation are also well separated in the two subfamilies. Therefore, it would seem to be advisable to propose the elevation of the two subfamilies to family rank.

The family names Lomentariaceae and Champiaceae were proposed previously by NÄGELI (1847) and BLIDING (1928; KÜTZING 1843, orth. mut.), respectively. BLIDING adopted the Champiaceae to include both families. However, both family names would be available for these new families by the emendation of the diagnostic characters.

The genus *Halosaccion* seems to approximate *Palmaria* more in systematic position by the stalk cell formation of tetrasporangia and the separate type of spermarangial mother cells, and the genus *Palmaria* shows other characters in addition to those of GUIRY (1974) by the superficial cortical

cells being almost tetragonal in palisade-like row, the tetrasporangium developed from this superficial cortical cell terminally, and the spermatangial mother cells formed by the separate type.

The occurrence of intercalary tetrasporangia in the cortical layer may be added as an important character to distinguish the genus *Rhodymenia*, since such a character is also confirmed in *R. pseudopalmata*, the type of the genus (LEE & KUROGI, unpublished data). Moreover, this character is related to the seriate mother cells in spermatangium formation and also to the superficial cortical cells not arranged in a palisade-like row. As a result, J. AGARDH (1852) and DAWSON's (1941) criteria of the sections of *Rhodymenia* may be revised, considering the separation of the genus *Palmaria*.

Even though the genus *Cryptarachne* was separated from *Chrysymenia* by KYLIN (1931) with the presence of 'Rhizoiden' (=Hyphae-like filaments) and so on, such filaments are also seen in the *Chrysymenia* rather frequently, as seen in this investigation and by OKAMURA (1936). Thus, the only remaining criterion to distinguish the two genera is whether they are sack-like as in *Chrysymenia* or somewhat flat as in *Cryptarachne*. The difference, however, is not thought to be so important to separate the genera, since some members of *Chrysymenia* become somewhat flat in shape (cf. KYLIN 1956). The intercalary occurrence of the tetrasporangia may be added as a new character to discern *Chrysymenia* from the others related.

KYLIN (1931) arranged the genera of Rhodymeniales on several phylogenetic lines. He based the line mainly on the anatomical characters of the vegetative structure. In the arrangement, he noticed *Bindera* to be the most primitive one of the Faucheoideae, and *Chrysymenia* the most primitive one of the Rhodymenioideae. According to my studies, however, *Chrysymenia* approximates *Lomentaria* by having filamentous cells in the medullary layer, developing stellate pericarpic cells and showing a cylindrical feature.

According to the KYLIN's opinion that the saccate one is not advanced, *Halosaccion* will be placed below *Palmaria* on the generic line, and the *Binghamia* on more advanced position than *Lomentaria*.

Diagnosis of the families:

Lomentariaceae NÄGELI (1847) emend. I. K. LEE

Syn. Lomentarioideae KYLIN (1931)

Thallus cylindricus vel planus, ramosus, ex stratis corticalibus et medullosis et cavitatibus centralibus partitis ab pariete cellularum multi-seriatarum composita; tetrasporangia soros aggregatos formantia, ex cellula corticali terminale evoluta, tetrahedrale divisa, pariete superficiali in soro rumpenti,

cellulis medullosis sterilibus in soro filamentose mutatis; spermatangia terminalia vel subterminalia in cellula matris, cellulis matricalibus spermatangii seriatis; ramus carpogonialis tricellularis, post fecundatione cellula conjunctionem similem columnae formans, carposporangiis ex cellulis gonimoblastis fere omnibus evolutis, cystocarpiis elevatis, cum carpostomatibus.

Typus genus: *Lomentaria* LYNGBYE (1819)

Thallus cylindrical or flat, branched, composed of cortical and medullary layers and central cavity septated by multi-rowed cellular wall; tetrasporangia forming aggregated sori, developed from cortical cell terminally, tetrahedrally divided, superficial wall in sorus ruptured, sterile medullary cells in sorus modified filamentously; spermatangia terminal or subterminal on mother cell, spermatangial mother cells seriate side by side; carpogonial branch three-celled, forming column-like fusion cell after fertilization, carposporangia converted from almost all gonimoblast cells, cystocarps elevated, with carpostome.

Type genus: *Lomentaria* LYNGBYE (1819)

Champiaceae KÜTZING (1843) orth. mut. BLIDING (1928) emend. I. K. LEE

Syn. Champioideae KYLIN (1931)

Thallus cylindricus vel compressus, ramosus, ex stratis corticalibus et cavitatibus centralibus partitis ab pariete cellularum uni-seriatarum compositus; tetrasporangia soros dispersos formantia, ex cellula corticali intercalare evoluta, tetrahedrale divisa, cellulis sterilibus in soro vix mutatis; spermatangia subterminalia in cellula matris, cellulis matricalibus spermatangii seriatis; ramus carpogonialis tetracellularis, carposporangiis tantum ex cellulis gonimoblasti superficialibus evolutis, cystocarpiis elevatis vel depressis, cum vel sine carpostomatibus.

Typus genus: *Champia* DESVEAUX (1808)

Thallus cylindrical or compressed, branched, composed of cortical layer and central cavity septated by single rowed cellular wall; tetrasporangia forming dispersed sori, developed from cortical cells intercalarily, tetrahedrally divided, sterile cells in sorus scarcely modified; spermatangia subterminal on mother cell, spermatangial mother cells seriate side by side; carpogonial branch four-celled, carposporangia converted only from superficial gonimoblast cells, cystocarps elevated or sunken, with or without carpostome.

Type genus: *Champia* DESVEAUX (1808)

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Summary

The taxonomical study of the members of Rhodymeniales in Hokkaido, Japan was carried out morphologically and phenologically. The members investigated are *Halosaccion yendoi*, *H. firmum*, *Palmaria palmata*, and *P. marginicrassa* of Palmariaceae, *Rhodymenia intricata*, *R. pertusa* and *Chrysymenia wrightii* of Rhodymeniaceae, and *Lomentaria hakodatensis*, *L. catenata* and *Champia parvula* of Champiaceae (*sensu* in BLIDING 1928). *H. yendoi* and *P. marginicrassa* are new species described in this study.

The materials investigated were collected during 1966～1968. The phenological investigations of the members were performed seasonally in Oshoro Bay of Japan Sea Coast and Muroran, Hidaka and Akkeshi areas of the Pacific Coast.

The members are saccate, flat, or cylindrical, simple or branched, and erect or creeping. Some of them are provided with prostrate stolons or rhizoids. There are annual and perennial plants. *H. yendoi*, *L. hakodatensis*, *C. wrightii*, and *C. parvula* are annual. *H. firmum*, *P. palmata*, *P. marginicrassa*, *R. pertusa*, *R. intricata* and *L. catenata* are perennial. *H. yendoi* and *R. pertusa* are luxuriant in spring, *P. marginicrassa*, *C. wrightii*, *L. hakodatensis* and *C. parvula* in summer, *H. firmum* and *L. catenata* in

autumn to winter, *R. intricata* from summer to early autumn, and *P. palmata* from winter to early spring. The most luxuriant period of the thalli appears generally two to five months later from the appearance of their germlings, except for the members of *Halosaccion*, which become luxuriant about nine to ten months later. The reproductive organs begin to appear before the luxuriant period, except for *P. marginicrassa* in which they appear after the period. The spermatangia and tetrasporangia are developed almost at the same time except for *R. intricata* and *R. pertusa*, which develop spermatangia earlier than tetrasporangia. The cystocarps appear about one month later than the former two. Especially it is a noticeable fact that the members lacking of the female organs, *H. yendoi*, *H. firmum*, *P. palmata* and *P. marginicrassa*, have a longer period of the tetrasporangium for mation compared with the other members.

Some perennial members, *P. palmata*, *P. marginicrassa*, *R. pertusa*, *R. intricata*, and *L. catenata* proliferate new fronds from the remaining old thalli, whereas *L. catenata* and the two members of *Halosaccion* regenerate new fronds at the broken or eroded margin. *C. wrightii* and the two members of *Lomentaria* show fusion of adjoining thalli and rhizoid formation, while *C. parvula* fusion only.

The thallus is composed of outer cortical and inner medullary layers. *C. parvula* is provided with no medullary cells but multi-cellular filaments. The cortical cells are densely pigmented, while the medullary ones hyaline. The cells increase in size inwards. In *R. intricata*, *C. wrightii* and the two members of *Lomentaria* inner medullary cells are elongated more or less. Especially in the latter three members, the innermost cells become almost linear. Among the cylindrical members, *C. parvula* has cellular septa of a single row and the members of *Lomentaria* of multi-rows. *C. wrightii* has the septum only at the base of branch. Gland cells appear in the cylindrical members. Unicellular hairs appear in groups in *H. yendoi* and *P. palmata*, while they are dispersed in *C. wrightii*, *L. hakodatensis* and *C. parvula*. There is no hair in *H. firmum*, *P. marginicrassa*, *R. intricata*, *R. pertusa* and *L. catenata*. *C. wrightii* has multi-celled hyphae-like filaments.

Tetrasporangia occur in sori at the apical portion of thallus in *R. intricata*, or over whole surface in the other species. They are developed terminally or intercalary in the cortex. *P. palmata*, *P. marginicrassa*, *H. yendoi*, *H. firmum* and two members of *Lomentaria* have terminal ones, *R. intricata*, *R. pertusa* and *C. wrightii* terminal or intercalary ones. The intercalary occurrence of tetrasporangia in Rhodymenioideae is not reported

previously. *C. parvula* has an intercalary tetrasporangium. The members of Palmariaceae provide a stalk cell of the tetrasporangium and regenerate secondary sporangia.

The tetrasporangia of Rhodymeniaceae are divided cruciately, and those of Champiaceae tetrahedrally. The former is generally smaller than the latter. The modification of the sterile cells in the sorus varies from species to species. However, those of *Lomentaria* are characterized by the formation of small cells in cortex and by more or less filamentously modified medullary cells. *P. marginicrassa* is characteristic in the paraphysis formation.

The spermatangial sori appear in a similar form to the tetrasporangial sori, except for *L. catenata* which develops special spermatangial ramuli. The spermatangium originates from the superficial cortical cell. The spermatangium formation in the Rhodymeniales is divided into two types; the Separate Type and the Seriate Type. The Separate Type, seen in *H. yendoi, H. firmum, P. palmata* and *P. marginicrassa* of Palmariaceae, is characterized by that the spermatangial mother cells originating from a single cortical cell and separate from one another, bearing no pit-connection directly, the spermatangium and the mother cell have a common wall, the spermatia are comparatively large, and the superficial wall of the sorus is shed during the spermatangium formation. On the other hand, the Seriate Type, seen in *R. intricata, R. pertusa* and *C. wrightii* of Rhodymeniaceae and *L. hakodatensis, L. catenata* and *C. parvula* of Champiaceae, is characterized by that the seriate spermatangial mother cells originating from a cortical cell, bearing the pit-connections directly, the spermatangium and the mother cell do not have a common wall, the spermatia are comparatively small, and the superficial wall of the sorus remains always during the spermatangium formation.

The mother cell protrudes a single spermatangium terminally in *C. wrightii* and *L. hakodatensis*, one and two in *R. intricata, R. pertusa* and *L. catenata*, two subterminally in *H. yendoi, H. firmum* and *P. marginicrassa*, two to three in *P. palmata* and three in *C. parvula*. In all members the spermatangium formation is repeated a few times from the same mother cell.

The cystocarps are confined only to the upper margin of the thallus in *R. intricata* or scattered over the whole surface in the other species. The supporting cell is homologous to the inner cortical or outer medullary cells. The carpogonial branch is two to four celled in Rhodymeniaceae and three to four in Champiaceae. Two-celled one, seen in *R. intricata*, is not reported yet in this order. The two celled auxiliary cell branch is developed

from the supporting cell. It appears generally after the presumed fertilization. A connecting cell is cut off from the carpogonium in *C. parvula*, while in *R. intricata* the carpogonium and hypogynous cell are divided respectively after the fertilization. On the other hand, the members of *Lomentaria* form a characteristic column-like cell of carpogonial branch soon after the fertilization, and it coalesces with the auxiliary cell.

The primary cell of the gonimoblast is divided transversely from the auxiliary cell and the secondary ones are generally cut off obliquely from the primary gonimoblast cell. Later, most of the gonimoblast cells are converted into carposporangia in the mature cystocarps, except for *C. parvula* where the carposporangia are developed only from the terminal cells of the gonimoblast.

BLIDING (1928) divided Rhodymeniales into two families, Rhodymeniaceae and Champiaceae, based on the presence or absence of longitudinal filaments, the cell number in the carpogonial branch, the carposporangium formation and the development of tetrasporangium. However, no constant characters to distinguish the two families are available. On the other hand, GUIRY (1974) erected a new family Palmariaceae with the members of Rhodymeniaceae including *Palmaria* and *Halosaccion*, and mentioned their characters as the tetrasporangium had a stalk cell, the superficial wall of spermatangial sori was shed during the spermatangium formation, and the female plants were lacking in the life history. This family seems to be well circumscribed, not only by the above mentioned characters, but by the development of spermatangium in that the mother cells are formed by the separate type, though the other members of Rhodymeniales are the seriate type.

KYLIN (1931) divided Rhodymeniaceae into three subfamilies, Faucheoideae, Rhodymenioideae and Hymenocladioideae, while Champiaceae into two, Lomentarioideae and Champioideae. However, SPARLING (1957) recoginzed only two subfamilies in Rhodymeniaceae, and rejected the Faucheoideae because the the formation of a *tela arachnoidea* was not a distinct character. According to the present investigation, SPARLING's belief on Rhodymeniaceae is acceptable, because *C. wrightii* of Rhodymenioideae develops stellate pericarpic cells which are an intermediate form between the *tela arachnoidea* and scarcely modified one. Moreover, the intercalary occurrence of the tetrasporangia in Rhodymenioideae alows the only constant character of the Hymenocladioideae to have the tetrahedral tetrasporangia. The character seems to be, however, not so important as to separate the two subfamilies.

On the other hand, the two subfamilies of Champiaceae are fundamentally different from each other, not only in vegetative structure but in the

reproductive organs, such as the formation of medullary layer and the cellular arrangement of the septum, the sorus formation and development of tetrasporangia and the characters of cystocarp formation. Especially in cystocarp formation three-celled carpogonial branch and formation of column-like fusion cell of the carpogonial branch after the fertilization, and the carposporangia converted from almost all gonimoblast cells in Lomentarioideae are markedly different from those in the Champioideae. Therefore, I propose the elevation of the two subfamilies of Champiaceae to family rank.

As a result, the Rhodymeniales may include the following families;

Palmariaceae GUIRY (1974)

Rhodymeniaceae HARVEY (1849)

Lomentariaceae NÄGELI (1847) emend.

Syn. Lomentarioideae KYLIN (1931)

Champiaceae KÜTZING (1843) emend.

Syn. Champioideae KYLIN (1931)

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Plate I

A. *Halosaccion yendoi* sp. nov. Male plant collected at Aikappu, Akkeshi, June 26, 1967 (SAP 032338).

B. *Halosaccion yendoi* sp. nov. Tetrasporic plant collected at Aikappu, Akkeshi, Apr. 15, 1967 (SAP 032337, Holotype).

C. *Halosaccion firmum* (POST. et RUPR.) KÜTZING. Male plants collected at Erimo, Nov. 14, 1966 (SAP 032339).

D. *Halosaccion firmum* (POST. et RUPR.) KÜTZING. Tetrasporic plant collected at Erimo, Nov. 14, 1966 (SAP 032339).

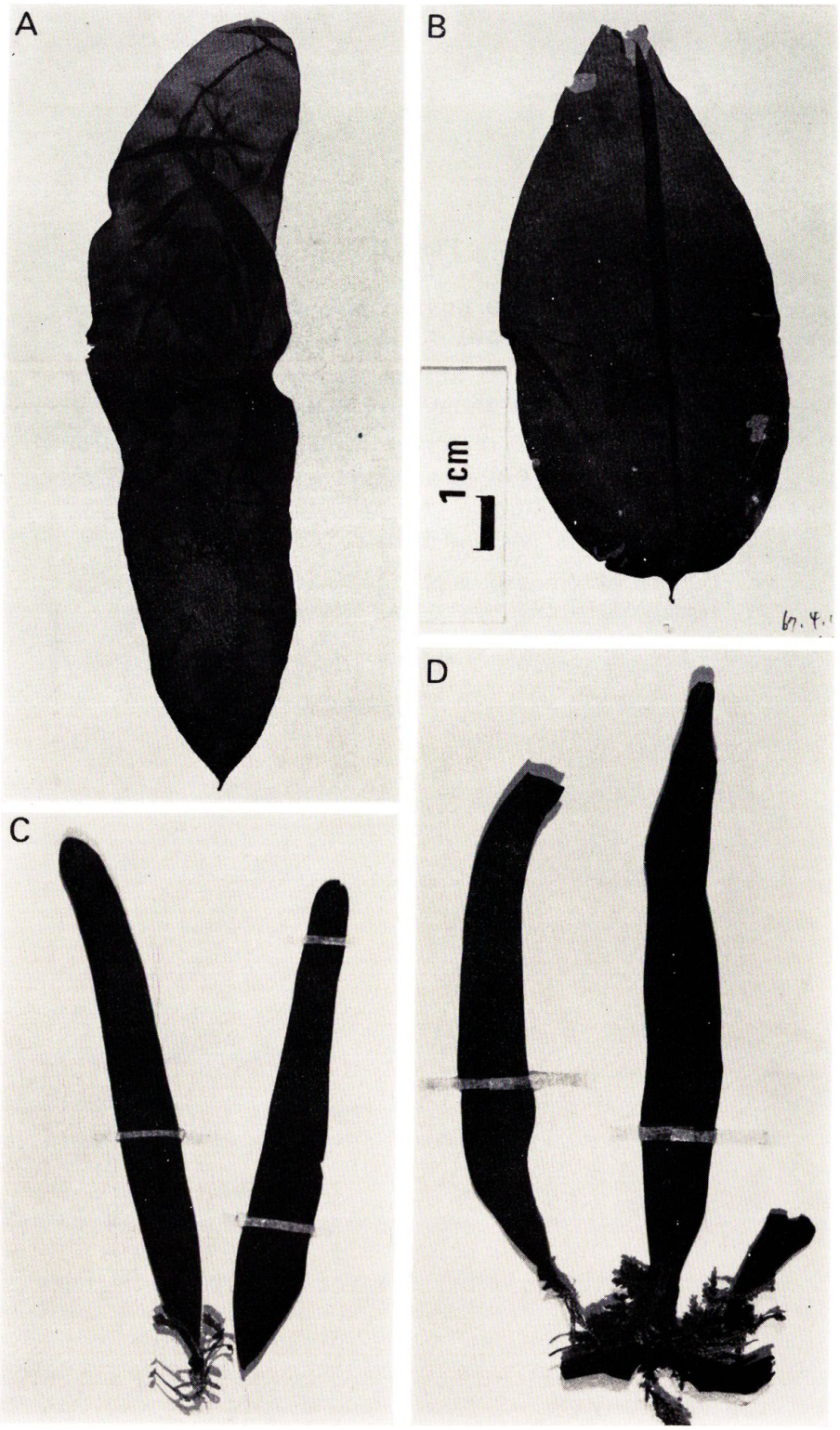
A
B
1cm
D
C

Plate II

A. *Palmaria palmata* (L.) O. KUNTZE. Male plant collected at Oshoro, Mar. 11, 1967 (SAP 032344).

B. *Palmaria palmata* (L.) O. KUNTZE. Tetrasporic plant collected at Etomo, Muroran, Feb. 21, 1968 (SAP 032343).

C. *Palmaria plamata* (L.) O. KUNTZE. Tetrasporic plant with proliferations collected at Aikappu, Akkeshi, June 21, 1966 (SAP 032345).

D. *Palmaria marginicrassa* sp. nov. Male plant collected at Aikappu, Akkeshi, Dec. 29, 1966 (SAP 032341).

E. *Palmaria marginicrassa* sp. nov. Tetrasporic plant collected at Aikappu, Akkeshi, Dec. 29, 1966 (SAP 032340, Holotype).


B
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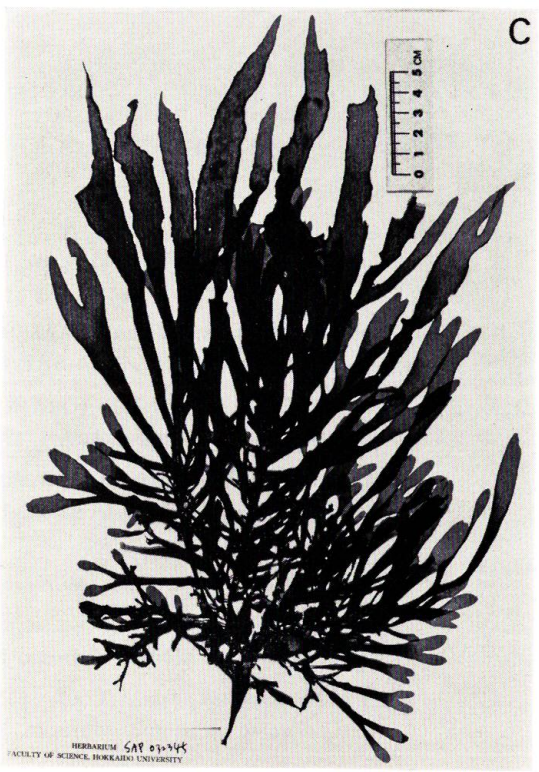
HERBARIUM SAP 032374
FACULTY OF SCIENCE, HOKKAIDO UNIVERSITY
SAP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HERBARIUM SAP 032345
FACULTY OF SCIENCE, HOKKAIDO UNIVERSITY


A
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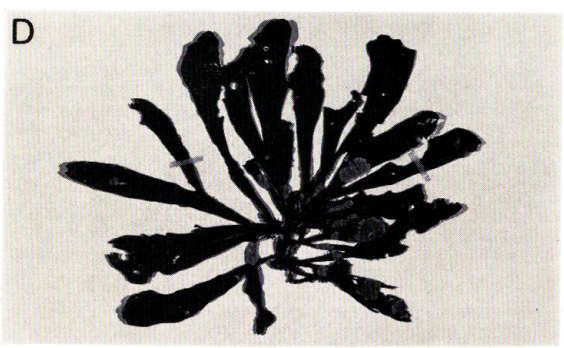
CIENCE, HOKKAIDO UNIVERSITY
SAP


D


E
0 1 2 3 4 5 CM

Plate III

A. *Rhodymenia intricata* (OKAMURA) OKAMURA. Male plant collected at Oshoro, Aug. 3, 1967 (SAP 032346).

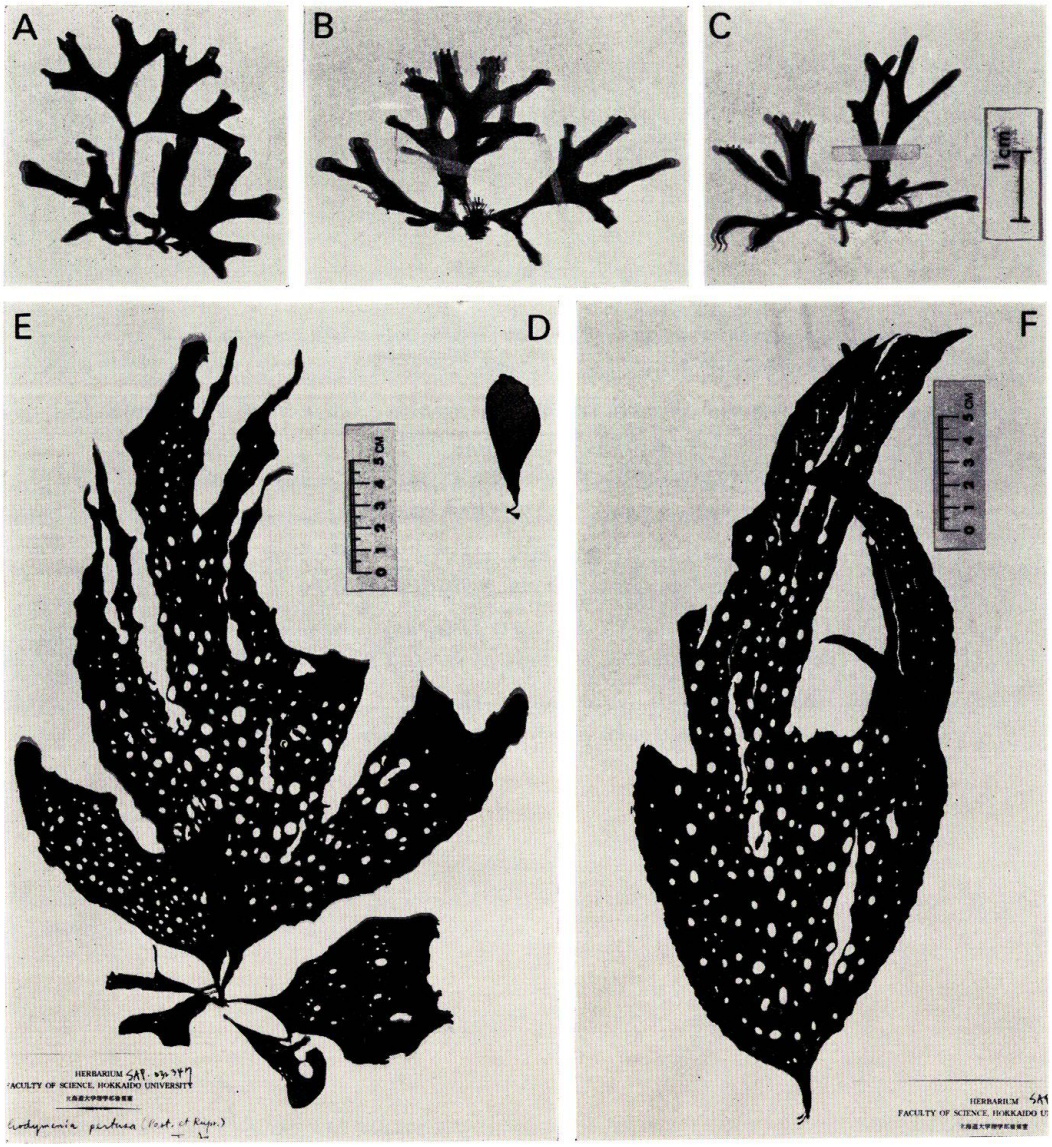
B. *Rhodymenia intricata* (OKAMURA) OKAMURA. Cystocarpic plant collected at Oshoro, Aug. 3, 1967 (SAP 032346).

C. *Rhodymenia intricata* (OKAMURA) OKAMURA. Tetrasporic plant collected at Oshoro, Aug. 17, 1967 (SAP 032346).

D. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH. Male plant collected at Charatsunai, Muroran, Mar. 2, 1967 (SAP 032347).

E. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH. Cystocarpic plant collected at Etomo, Muroran, May 23, 1966 (SAP 032347).

F. *Rhodymenia pertusa* (POST. et RUPR.) J. AGARDH. Tetrasporic plant collected at Etomo, Muroran, Mar. 30, 1967 (SAP 032347).


A
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1cm
E
D
F
HERBARIUM
FACULTY OF SCIENCE, HOKKAIDO UNIVERSITY

Plate IV

A. *Chrysymenia wrightii* (HARVEY) YAMADA. Male plant collected at Oshoro, July 7, 1967 (SAP 032349).

B. *Chrysymenia wrightii* (HARVEY) YAMADA. Cystocarpic plant collected at Oshoro, Aug. 3, 1967 (SAP 032349).

C. *Chrysymenia wrightii* (HARVEY) YAMADA. Tetrasporic plant collected at Oshoro, Aug. 19, 1966 (SAP 032350).

D. *Champia parvula* (C. AGARDH) HARVEY. Male plant collected at Charatsunai, Muroran, Aug. 19, 1967 (SAP 032353).

E. *Champia parvula* (C. AGARDH) HARVEY. Cystocarpic plant collected at Charatsunai, Muroran, Aug. 19, 1967 (SAP 032353).

F. *Champia parvula* (C. AGARDH) HARVEY. Tetrasporic plant collected at Charatsunai, Muroran, Aug. 19, 1967 (SAP 032353).

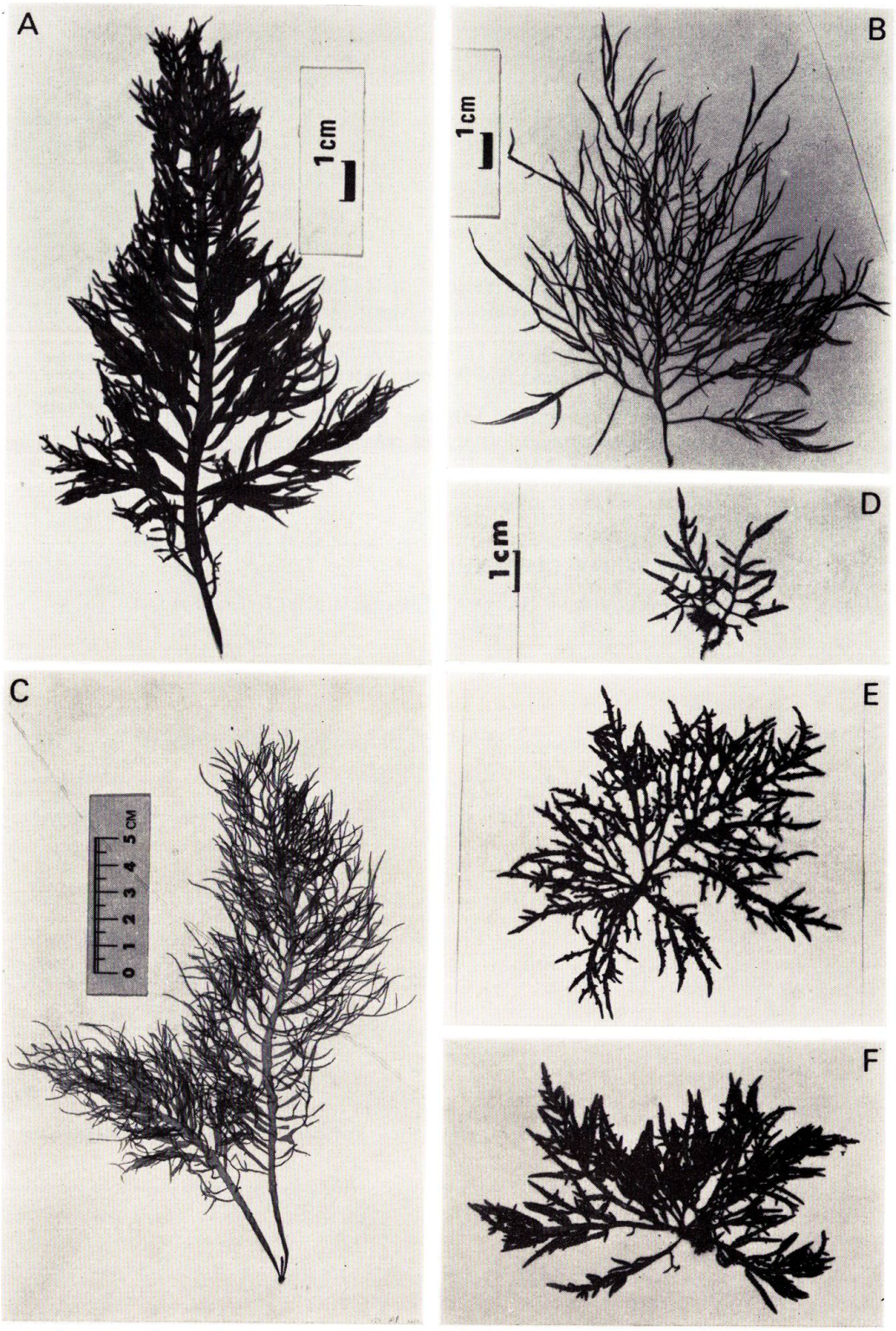
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Plate V

A. *Lomentaria hakodatensis* YENDO. Male plant collected at Charatsunai, Muroran, July 20, 1966 (SAP 032351).

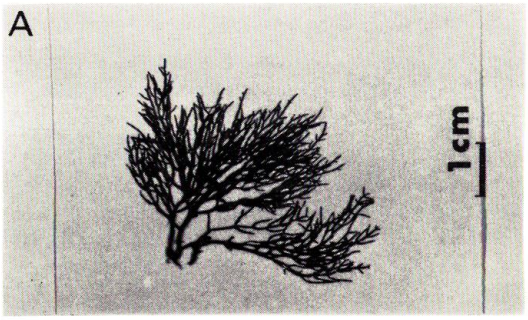
B. *Lomentaria hakodatensis* YENDO. Cystocarpic plant collected at Charatsunai, Muroran, July 20, 1966 (SAP 032351).

C. *Lomentaria hakodatensis* YENDO. Tetrasporic plant collected at Charatsunai, Muroran, July 1, 1966 (SAP 032351).

D. *Lomentaria catenata* HARVEY. Male plant collected at Oshoro, Nov. 14, 1967 (SAP 032352).

E. *Lomentaria catenata* HARVEY. Cystocarpic plant collected at Oshoro, Nov. 14, 1967 (SAP 032352).

F. *Lomentaria catenata* HARVEY. Tetrasporic plant collected at Oshoro, Dec. 18, 1967 (SAP 032352).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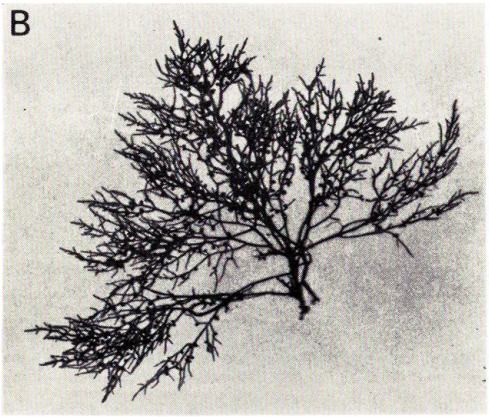
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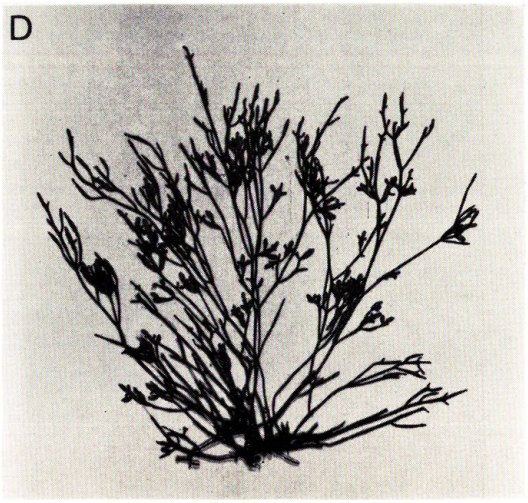
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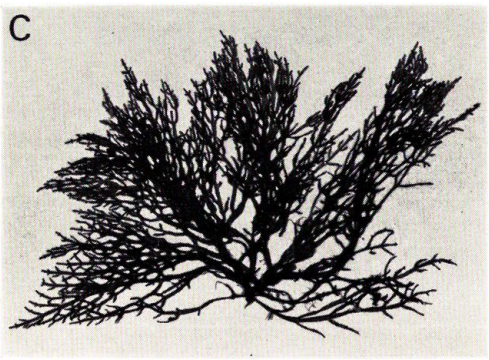
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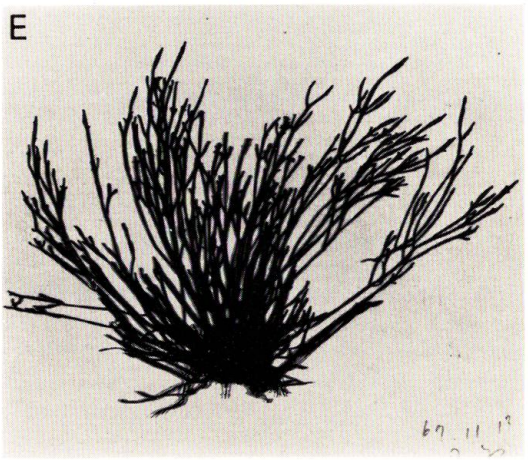
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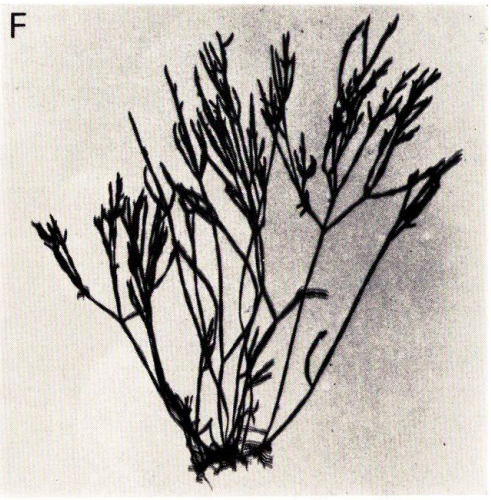
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