The Acrochaetiaceae (Acrochaetiales, Rhodophyta) in Hokkaido

By

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Introduction

Eleven species of the Acrochaetiaceae (=Rhodochortaceae) were previously described from Hokkaido: *Acrochaetium daviesii* (DILLWYN) NÄGELI, *Chantransia immersa* ROSENVINGE, *Kylinia moniliformis* (ROSENVINGE) KYLIN, *Colaconema simplex* INAGAKI, *Rhodochorton codii* (CROUAN) NAKAMURA, *Rh. hyalosiphoniae* NAKAMURA, *Rh. plumosum* DREW, *Rh. rhizoideum* DREW, *Rh. rothii* (TURTON) NÄGELI, *Rh. sessile* NAKAMURA, and *Rh. subimmersum* SETCHELL et GARDNER. Recently, *Audouinella alariae* (JÓNSSON) WOELKERLING which was epiphytic on *Alaria crassifolia or Sargassum thunbergii* (LEE & KUROGI 1983) and *Aud. kurogii* LEE et LINDSTROM which was partially endophytic in *Constantinea rosa-marina* (LEE & LINDSTROM 1979) were reported from Muroran and Nemuro, respectively. *Aud. daviesii* which was epiphytic on *Erythrocladia* species and *K. moniliformis* epiphytic on *Chondrus* species were reported from the Lake Saroma (IWAMOTO 1960). *Rh. codii* and *Rh. rhizoideum* both of which were partially endophytic in *Codium tomentosum* were reported from Akkeshi (NAKAMURA 1944). *Rh. plumosum* was epiphytic on *Sargassum* species in Esasi (NAKAMURA 1944). *C. simplex* which was endophytic in the surface wall of the thallus of *Asparagopsis hemifera* was reported from Shiwoya (INAGAKI 1935). *Rh. sessilis* and *Rh. hyalosiphoniae* both of which were epiphytic on *Hyalosiphonia caespitosa, Rh. subimmersum* endophytic in *Grateloupia turuturu* and *Rh. rothii* which has been known as *Rh. purpureum* (LIGHTFOOT) ROSENVINGE were reported from Muroran (NAKAMURA 1941). *Chantransia immersa* which was epiphytic on various red algae as *Herposiphonia, Rhodomela* and *Halymenia*, was reported from Hakodate (YENDO 1916). OHTA and KUROGI (1979) reported the monoecious and dioecious isolates of *Rh. purpureum* from Oshoro and Muroran, respectively and revealed their life cycles under culture conditions.

Although the name Rhodochortaceae NASR 1947 antedates Acrochaetiaceae, the latter name was consevated (GREUTER *et al.* 1994). There is no consensus of the generic concept in the Acrochaetiaceae (cf. WOELKERLING 1971, LEE 1980, LEE & LEE 1988). The

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taxonomic system proposed by LEE & LEE (1988) is adopted in this paper. Recently, a study on the taxonomy of the Acrochaetiaceae with the plants from the northwestern Pacific Ocean supported this taxonomic system (LEE 1993). SAUNDERS and MCLACHLAN (1991) removed *Rhodochorton spetsbergense* (KJELLMAN) KJELLMAN to a new genus *Meiodiscus* of the Rhodophysemataceae on the basis of vegetative fusions between cells of regularly radiating basal filaments, β-phycoerythrin and presence of stalk cells subtending tetrasporangia.

Acknowledgments

We wish to express our sincere gratitude to the late Professor MUNENAO KUROGI, Hokkaido University, for his constant guidance and advice during the course of this study. We are grateful to Dr. LAURENCE M. LIAO, Department of Biology, University of North Carolina at Chapel Hill, for giving us kind comments on the nomenclatural problems in this paper.

Materials and Methods

The material used for the present study was obtained in the intertidal or subtidal zones of Hokkaido coast from May 1977 to September 1978. The collecting sites are as follows: 1) southern coast; Matsumae, Shirikishinai, Muroran (Charatsunai and Nirasu), Wakanai. 2) eastern coast; Akkeshi, Daikokuzima, Nemuro (Bentenzima and Nosapumisaki). 3) western coast; Oshoro, Shiwoya. A part of the collected material is cultured in glass vessels containing PES medium (PROVASOLI 1968) or occasionally nitrate free PES medium, in low temperature incubators illuminated with cool white fluorescent lamps (ca. 1500-3000 lux) under the regimes of temperature and photoperiod combination (20°C-16 : 8 LD, 15°C-16 : 8 LD, 10°C-16 : 8 LD, 10°C-8 : 16 LD, 5°C-8 : 16 LD).

The field collected material was exclusively used for identification of species. Glycerin water (1 : 1) for mounting substance of microscopic slides, aniline blue for cell wall or reproductive structure stain, and propionocarmine (ROSOWSKI 1970) were used for pyrenoid examination. Identification was made by reference to literatures not by comparison with type collections. Therefore, the author's arbitrariness could not be eliminated in identification. All the specimens examined were preserved in the Herbarium of the Department of Biology, Cheju National University (CNU). For abbreviations of herbarium name see HOLMGREN *et al.* (1990).

Descriptions

ACROCHAETIACEAE FRITSCH ex TAYLOR 1957, p.209, 210, nom. cons.

Synonyms: Rhodochortaceae NASR 1947, p.92, nom. rej.
Audouinellaceae WOELKERLING 1971, p.22.

Plants are composed of monosiphonous, branching, heterotrichous filaments with apical growth. The erect filaments have an indeterminate growth or determinate growth due to the formation of hair or reproductive structure terminally. Erect filaments grow upwards although those of several gametophytic plants with a single cell base develop obliquely or parallely to the surface of host. The chloroplasts of the Acrochaetiaceae are various in form; laminate, stellate, discoid, ribbon-shaped, and they may be parietal or axial in position (cf. SVEDELIUS 1911). Generally, the chloroplasts of laminate form tend to include pyrenoids at margin, while a pyrenoid situates in the center of stellate chloroplast.

Asexual reproduction is effected with monospores in some taxa or tetraspores in other ones. Sexuality is monoecious or dioecious. The carposporophyte derived from a fertilized carpogonium is relatively simple or reduced. Life history is completed with mono-or diplobiontic and di- or trigenetic alternation of generations.

KEY TO THE GENERA

1. Monosporangia formed on both gametophytic and sporophytic plants ……2
1. No monosporangium formed on both gametophytic and sporophytic plants…
……*Rhodochorton*
2. Chloroplasts laminate or ribbon-shaped ……*Audouinella*
2. Chloroplasts stellate ……*Acrochaetium*

AUDOUINELLA BORY 1823, p. 340

Plants have erect filaments with indeterminate growth and laminate or ribbon-shaped chloroplasts with or without pyrenoids. Monosporangia are produced on both gametophytic and sporophytic plants. The life history is completed with isomorphic, diplobiontic, trigenetic alternation of generations. The trigenetic phases are represented with gametophytic, tetrasporophytic and carposporophytic generations. The gametophytic and the tetrasporophytic plants are similar in morphology and have a multicellular base. The carposporangial plants are of several celled filamentous structure with short branches terminating in carposporangia and not independent from the female gametangial plant. Both gametophytic and tetrasporophytic phases are duplicated by monospores.

Synonyms: *Trentepohlia* PRINGSHEIM 1862, p. 29.
Balbiania SIRODOT 1876, p. 149.
Colaconema BATTERS 1896a, p. 8.
Grania KYLIN 1944, p. 26.

Type species: *Audouinella hermanni* (ROTH) DUBY 1830, p. 972.

KEY TO THE SPECIES

1. Erect filaments reduced, monosporangia born laterally on cells of creeping filaments ····· *Aud. japonica*
1. Erect filaments well developing with indeterminate apical growth ····· 2
2. Monosporangia usually born in concatenate forms ····· *Aud. plumosa*
2. Monosporangia usually born solitarily or in pairs on a stalk cell ····· 3
3. Monosporangia born in groups on short laterals ····· *Aud. daviesii*
3. Monosporangia born in series on rather long laterals ····· *Aud. rhizoidea*

Audouinella daviesii (DILLWYN) WOELKERLING 1971, p. 2. (Text Fig. 1)

Basionym: *Conferva daviesii* DILLWYN 1802-1809, p. 73. suppl. F.

Synonyms: *Callithamnion daviesii* (DILLWYN) LYNGBYE 1819, p. 129
Trentepohlia daviesii (DILLWYN) PRINGSHEIM 1862, p. 30.
Acrochaetium daviesii (DILLWYN) NÄGELI 1861, p. 405
Chantransia daviesii (DILLWYN) THURET in LE JOLIS 1863, p. 106
Rhodochorton daviesii (DILLWYN) DREW1928, p. 172
Rhodochorton hyalosiphoniae NAKAMURA 1941, p. 287
Acrochaetium hyalosiphoniae (NAKAMURA) PAPENFUSS 1945, p. 314

Plants epiphytic or partially endophytic, tufted, composed of basal filaments and erect filaments, to 2.6mm high; basal filaments creeping on host surface or penetrating into host tissue, tortuous, branching, loosely entangled together; cells of basal filament somewhat fusiform, 5-14μm broad and 13-28μm long; erect filaments straight, more or less rigid, issuing long branches with unlimited growth and short fructiferous branchlets with limited growth; cells of erect filament cylindrical, 9-14μm broad and 14-37μm long; hairs terminal on short branchlets; chloroplasts single in a cell, parietal, laminate including pyrenoids at margin.

Monosporangia usually born in fan-shape clusters on short branchlets, ovoid to ellipsoid, 8-10μm broad and 12-14μm long.

Type locality: Bantry Bay, Ireland (HUTCHINS).
The locality for H. DAVIES collection is not given by DILLWYN (1802-1809).

Type: NMW (cf. WOELKERLING 1971, 1973).

Material examined: on *Dictyopteris divaricata* at Oshoro 17 May 1977, 10 June 1977, 11 August 1977. On *Sargassum confusum* at Oshoro 15 July 1977, 10 Decmber 1977, 18 January 1978, 17 February 1978, 11 March 1978, 11 April 1978, 9 May 1978. On *Sargassum yezoense* at Oshoro 10 June 1977. On *Laurencia* sp. at Matsumae 3 May 1977. On

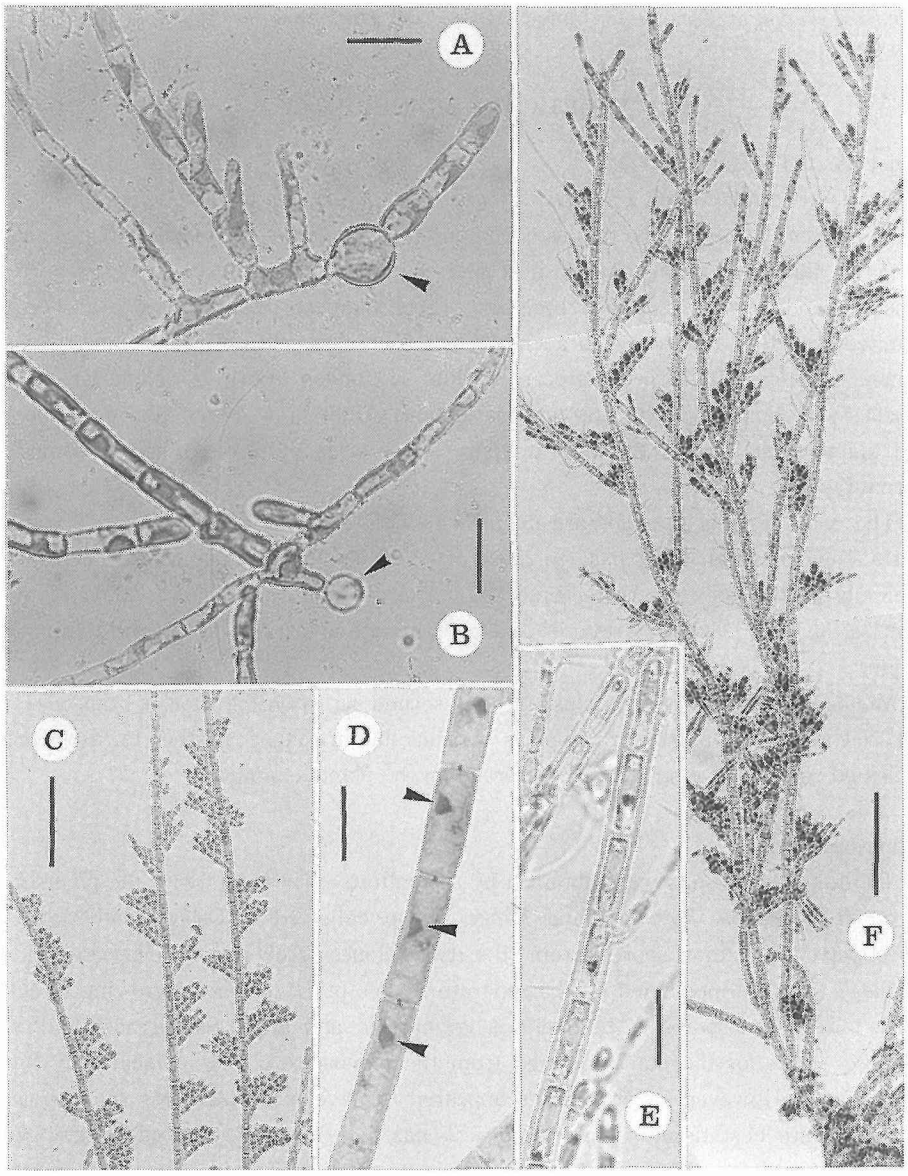

Fig. 1. *Audouinella daviesii*. A: A persistent germinating spore (arrow head). B: An empty germinating spore (arrow head). C: Erect filaments bearing monosporangial clusters in culture. D: Pyrenoids stained with propionocarmine (arrow heads). E: Cells of an erect filament. Note the parietal laminate chloroplasts with a central pyrenoid. F: Thallus bearing monosporangia. Note the characteristic branchlets bearing monosporangia. (Scale bars of Figs A-E are 20μm. Scale bar of Fig. F is 50μm.)

Chondrus yendoi at Oshoro 18 January 1978. On *Hyalosiphonia caespitosa* at Oshoro 10 June 1977.

VEGETATIVE MORPHOLOGY

Field-collected material

Plants are epiphytic on *Dictyopteris, Sargassum, Laminaria* and *Chondrus* or epi-endophytic in *Hyalosiphonia*. The thallus is composed of filamentous bases and erect filaments. The basal filaments are creeping on host surface or penetrating into host tissue, tortuous, branching and loosely entangled together. Erect filaments issue longer branches with unlimited growth. The longer branches reach to the same level as the apex of erect filament. No hair is born on erect filaments or longer branches. Numerous shorter branches with limited growth and terminated with a hair or a sporangium occur on both erect filaments and longer branches in spiral series or in the mixed form of secund and alternate mode.

The cells of erect filament are cylindrical with a rather conspicuous cell wall and mostly same in width from base to apex of erect filament. Hairs are frequently born terminally on the apex of shorter branches. The cell abutting a hair is almost same in width as the hair. Chloroplasts are parietal, laminate and including several pyrenoids at margin.

Monosporangia are born in clusters or in secund series on the shorter branches. The stalk cell abutting a monosporangium is obtriangular in shape. Neither tetrasporangium nor sexual reproductive structure is observed on the plants examined.

Cultured material

The following results were obtained by the culture experiments with the plants growing on *Hyalosiphonia caespitosa* and *Laminaria* sp. collected at Oshoro and Matsumae, respectively. The monospores from the two clones growing on *H. caespitosa* and *Laminaria* sp. were inoculated on the separate thallus of *H. caespitosa** growing in culture vessels. The monospores of both clones germinated and grew on the host thallus, *H. caespitosa*. Most of the plants derived from the monospores grew epiphytically on the host surface. However, several plants appeared to have basal filaments some of which penetrated into host tissue. Thus, *A. daviesii* has both epiphytic and endophytic nature depending upon host. Monospores germinate in unipolar mode without any previous division leaving the spore being either persistent or empty. The primary germ tube is to be a creeping filament. When the primary germ tube becomes two or three cells long, an erect filament arises from the persistent spore or from the proximal cell of the creeping

*The host plant, *H. caespitosa*, was available for this culture experiment by the courtesy of Dr. M. MASUDA, Division of Biological Sciences, Hokkaido University.

filament. Pyrenoids are not found in some cells of the plants in exhaustive culture media for a long time. Hairs occur very rarely on a younger thallus. Monosporangia are the only reproductive structure produced in the course of the culture experiment.

DISCUSSION

Although this species is known as a cosmopolitan taxon, tetrasporangial plants or gametangial plants have been little known. Recently the plants bearing sexual reproductive structures and carposporangia or tetrasporangia were reported from southern Australia and northeastern America (WOELKERLING 1971, 1973).

Hokkaido plants produce only monosporangia in both nature and culture. In April the plants growing on *Sargassum confusum* issue branches abundantly on the lower part of erect filaments, where monosporangia seem to be born in prior time. Under culture condition a certain monosporangium develops into a longer branch of unlimited growth. WEST (1968) observed a similar case in *Acrochaetium pectinatum* and interpreted it as a branch resulted by the returning of the sporangial basal cell (stalk cell) to vegetative growth. Such phenomenon may not be thought to be a kind of in situ germination because no basal creeping filament appears. Thus, it is easy to think that an immature sporangium still has a role of vegetative cell rather than reproductive cell.

Audouinella daviesii generally occurs in January, grows up vegetatively in February to March, produces monosporangia in April to May, becomes older in June, and disappears in July in the intertidal zone of Hokkaido coast. The thallus form in July and August suggests strongly that the stubbles of thallus may survive during 5 months from July to December. On the other hand, the plants of this species appear variable in the

Table 1 Comparison of morphological characters of *Rhodochorton hyalosiphoniae* and *Audouinella daviesii* in Hokkaido.

Species / Characters	*Rh. hyalosiphoniae*		*Aud. daviesii*
	Nakamura (1941)	In this study	In this study
Thallus height	0.4-1.0mm	0.9-1.3mm	1.3-2.6mm
Cell size of basal system	5-7μm broad 12-18μm long	7-16μm broad 18-28μm long	5-14μm broad 13-28μm long
Cell size of erect system	6-10μm broad 12-30μm long	8-9μm broad 22-27μm long	9-14μm broad 14-37μm long
Size of monosporangium	10-12μm broad 13-15μm	7-8μm broad 11-13μm long	8-10μm broad 12-14μm long
Germination of monospore	?	unipolar, empty or persistent spore	unipolar, empty or persistent spore

degree of development depending upon its host and locality. This fact suggests this species may change its habitat during the period from July to December.

NAKAMURA (1941) distinguished *Rhodochorton hyalosiphoniae* NAKAMURA from *Audouinella daviesii* in smaller size of thallus and endophytic nature. However, it is not reasonable to distinguish *Rhodochorton hyalosiphoniae* from *Aud. daviesii* with thallus size and endophytic nature because the latter species has also endophytic nature. In the type locality of *Rh. hyalosiphoniae*, we failed to find out the host plants, *Hyalosiphonia caespitosa*, in June and July. *Rh. hyalosiphoniae* is recognized here as the same species as *Aud. daviesii* because of no distinguishable characteristics found (cf. Table 1).

Audouinella plumosa (DREW) GARBARY 1979, p. 490. (Text Fig. 2)

Basionym: *Rhodochorton plumosum* DREW 1928, p. 173

Synonyms: *Acrochaetium plumosum* (DREW) SMITH 1944, p. 180

Colaconema plumosa (DREW) WOELKERLING 1971, p. 48

Plants epiphytic, somewhat tufted, composed of creeping filaments and erect filaments, up to 1.8mm high; creeping filaments more or less confluent each other, forming a basal monostromatic disc; cells of creeping filament cylindrical to ovoid, 4-8μm broad and ca. 8μm long; erect filaments more or less flexuous, slightly tapering toward apex, issuing numerous branches alternately or oppositely; cells of erect filament ellipsoid, 5-6μm broad and 6-13μm long at upper part, or clavate with rather thick wall, 13-16μm broad and 34-50μm long at lower part of erect filament; chloroplasts single, parietal, laminate with lobed margin, containing pyrenoids; hairs present.

Monosporangia usually born on several celled branches or occasionally on creeping filament, lateral or terminal, solitary to ternate, occasionally in concatenate form, ovoid to ellipsoid, 7-9μm broad and 10-14-16μm long.

Type locality: Fort Point, San Francisco, USA.

Type: UC 294559 (GARDNER no. 4441)

Material examined: On *Sargassum yezoense* at Oshoro 11 May 1977 (leg. T. YOSHIDA), 10 June 1977, 18 January 1978, 17 February 1978, 11 March 1978, 11 April 1978. At Shiwoya 11 April 1978.

VEGETATIVE MORPHOLOGY

Field collected material

Plants are epiphytic on *Sargassum yezoense* forming red fringes on the host surface. Creeping filaments are more or less confluent each other and form a monostromatic basal disc. In rare case short rhizoidal filaments develop from the cells in the lower part of erect filament. Erect filaments are somewhat flexuous, wavy, gradually tapering toward apex, and issue numerous branches along the whole length of erect filament. The

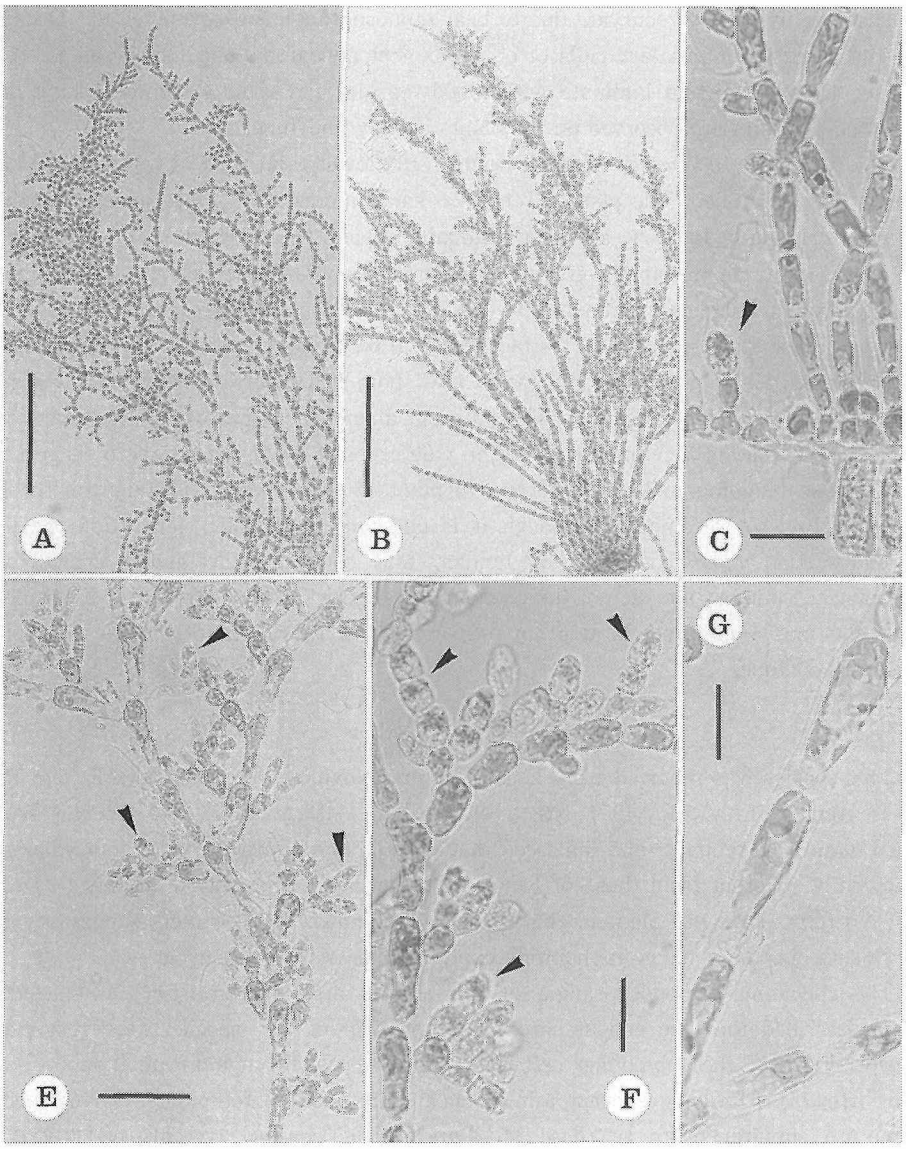

Fig. 2. *Audouinella plumosa.* A : Plants at Oshoro in April. B : Plants at Oshoro in April. C : The profile of the cells of basal system. Note a monosporangium (arrow head) on a single cell erect filament in February. E : Short branchlets bearing monosporangia (arrow heads) in March. F : Two or three concatenate monosporangia (arrow heads) in February. G : Chloroplasts in the cells of erect filament. (Scale bars of Figs A, B are 200μm. Scale bars of Figs C, F, G are 20μm. Scale bar of Fig. E is 50μm.)

branches are frequently recurvate due to bear monosporangia in secund series. Occasionally, the apical or intercalary cells of erect filament appear balloon-like in shape. Chloroplasts are parietal and laminate with lobed margin, and usually located in the distal part of cell. Hairs are observed on the plants in May and June.

The plants of *Audouinella plumosa* occur in the lower tidal zone of Oshoro, Hokkaido from January to June. The plants occur in a small mound-like appearance on the margins of host blade in January, and then gradually expand their population on host surface. The plants continue the apical growth of erect filament and increase the thallus height monthly from 0.1-0.2mm in January to 0.9-1.8mm in May. In June the plants appear decreasing their thallus height. This fact seems to be probably owing to fragmentation of erect filament. The plants in June have few short branchlets bearing monosporangia although hairs are formed on the thallus in great abundance. The vegetative cells of the plants in June contain a chloroplast being in pale greenish color. It seems to suggest that these plants are going to be senescent. No plant of *Aud. plumosa* is found on the host thallus in July to December. Although it is not confirmed which generation the plant represents, *Aud. plumosa* appears in January, and continues the apical growth with increasing the number and size of the component cells for 5 months to May. This species shows the maximum production of monosporangia in the lower tidal zone of Oshoro, Hokkaido, in June.

DISCUSSION

This species was reported from Esasi, Oshima Province and Iwagasaki, Echigo Province in April (NAKAMURA 1944, NODA 1970). NAKAMURA (1944) reported this species from Fukaura in January, and indicated that the plants of Fukaura were somewhat morphologically different from those of Esasi. This species did not occur in July to December. No tetrasporangial plant of this species was known. These facts suggest strongly that this species may change its habitats upon the phases of its life cycle.

The concatenate monosporangia of this species are characteristic. WOELKERLING (1971) described that the concatenate monosporangia of this species were resulted by transformation of the subtending cell after spore release from a terminal monosporangium. However, the monosporangia in a concatenate series of the plants at hand seem to be mature simultaneously as those of *Acrochaetium densum* (see also STEGENGA & VROMAN 1976). ABBOTT & HOLLENBERG (1976) regarded *Audouinella plumosa* conspecific with *Acrochaetium pacificum* KYLIN.

Audouinella rhizoidea (DREW) GARBARY 1979, p. 490. (Text Figs 3, 4)

Basionym: *Rhodochorton rhizoideum* DREW 1928, p. 182.
Synonym: *Acrochaetium rhizoideum* (DREW) JAO 1937, p. 102.

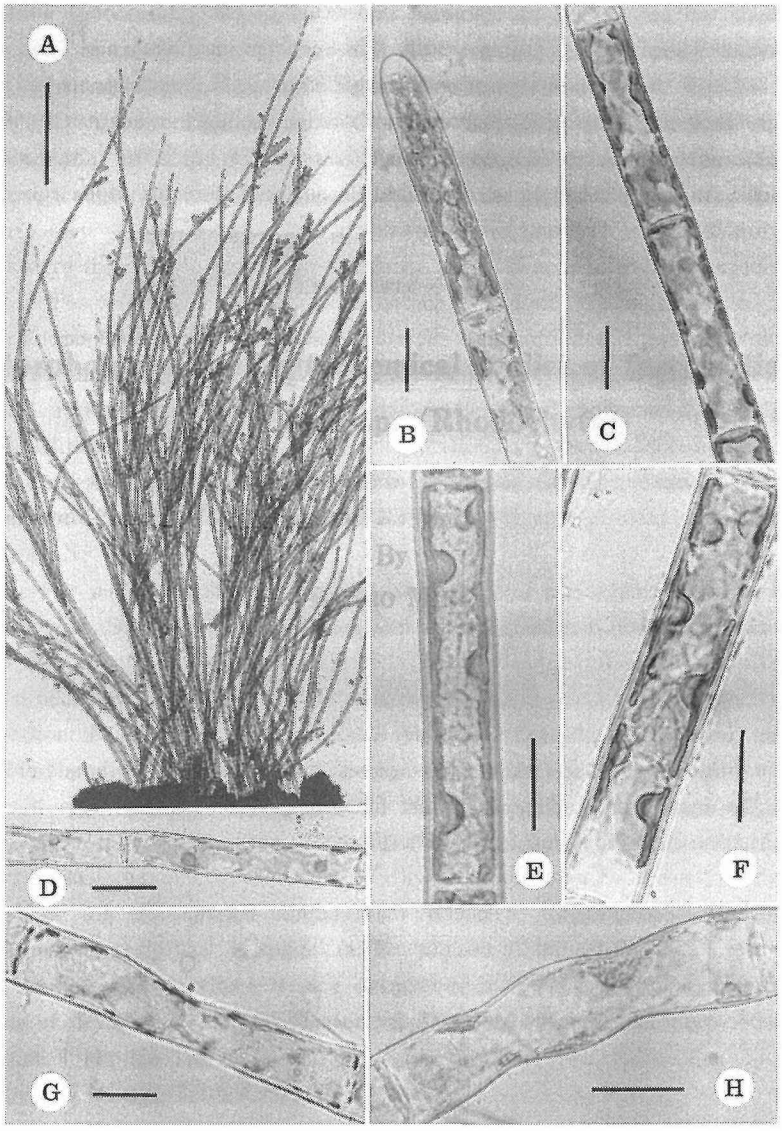

Fig. 3. *Audouinella rhizoidea.* A : Plants at Akkeshi in May. B : Chloroplast in an apical cell of creeping filament in culture. C : A reticulate form of chloroplast in the upper part of erect filament in culture. D : A patch like form of chloroplast in the creeping filament in culture. E, F : Chloroplasts in the cells of the middle part of erect filament in culture. Note many lobed pyrenoids. G : A reticulate chloroplasts in the cell of creeping filament in nature. H : A parietal laminate chloroplast in the cell of creeping filament in culture. (Scale bar of Fig. A is 500μm. Scale bars of Figs B–H are 20μm.)

Plants partially endophytic, caespitose, consisting of endophytic basal filaments and erect filaments, 4-8μm high; endophytic filaments penetrating host tissues, loosely entangled; cells of endophytic filament tortuous, with thin wall, 15-30μm broad and 80-150μm long; erect filaments more or less rigid, terminated in somewhat acute apex, branching secundly or alternately; cells of erect filament cylindrical with up to 4μm thick wall, 18-23μm broad and 36-120μm long; chloroplasts parietal, laminate with lobed margin, containing one or more pyrenoids; hairs unknown.

Monosporangia terminal or lateral on branches, solitary or in pairs on one- or two-celled stalks, ellipsoid to obovoid, 21-28μm broad and 32-36μm long; tetrasporangia rare, terminal or lateral on branches, cruciately divided, obovoid to subglobose, 25-28μm broad and 31-37μm long.

Type locality: Santa Catalina Island, California, USA.

Type: UC 294553 (DREW no. 392)

Material examined: On *Cystoseira hakodatensis* at Nemuro 2 June 1977, Akkeshi 1 June 1977, 30 June 1977, 10 May 1978 (leg. S. C. LINDSTROM), Hidaka 2 August 1977.

VEGETATIVE MORPHOLOGY

Field collected material

Plants grow on the lowermost part of the stipe of *Cystoseira hakodatensis* forming a brightly reddish violet fringe. Endophytic filaments penetrate and develop both vertically and parallel to the host surface in the cortical layers of the host. The cells of endophytic filament contain a single, parietal, laminate or several, spiral, ribbon-shaped chloroplasts. Pyrenoids are usually inconspicuous. Erect filaments arise from the cells of endophytic filament situating near host surface. Erect filaments are tufted and more or less rigid. The branches of erect filament elongate with unlimited growth and reach to the level of the apex of the erect filament. The cells of erect filament are long cylindrical without constriction at joint. Occasionally the cells in the upper part of erect filament contain a lot of small granules.

Monosporangia with one- or two-celled stalk are born in secund series on branches and erect filaments. Tetrasporangia are rarely occurred together with monosporangia.

Cultured material

The monospores of the plants from Akkeshi are filled with a lot of small granules. A bright spot usually appears on a spore being in amoeboid movement. The spot is more conspicuous after attaching to glass substrate and disappears when a germ tube is to be issued. A germinating spore issues a germ tube at first without any previous division. The germ tube always develop into a basal creeping filament.

Two types of monospore germination are found in *Audouinella rhizoidea* under culture conditions: 1) When a germinating spore issues a first germ tube, all the cell con-

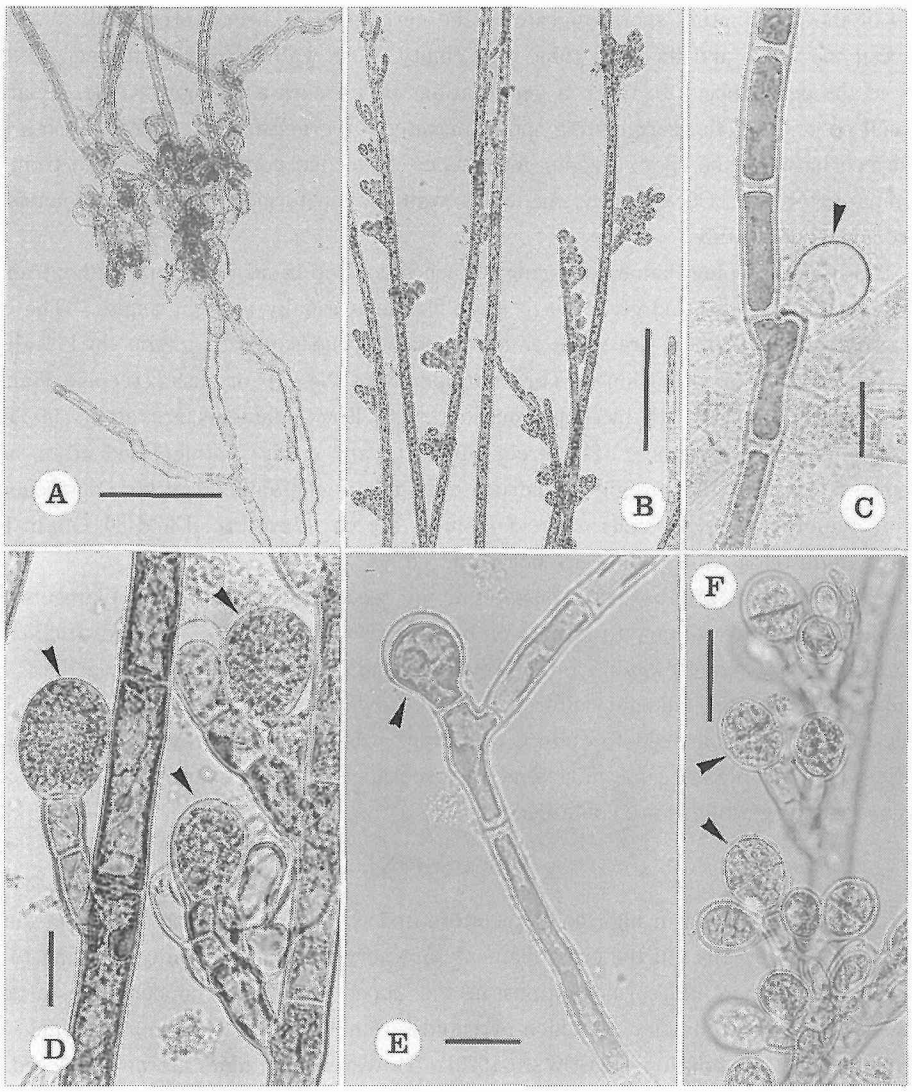

Fig. 4. *Audouinella rhizoidea.* A : Basal filaments penetrating into host tissue. B : Branches bearing monosporangia in culture. C : Empty monospore (arrow head) after germination. D : Monosporangia (arrow heads) on 2-celled stalks in culture. E : Persistent monospore (arrow head) after germination. F : Tetrasporangia (arrow heads) in culture. (Scale bars of Figs A, B are 200μm. Scale bars of Figs C–E are 20μm. Scale bar of Fig. F is 50μm.)

tents of the germinating spore migrate to the germ tube. Then, a cross wall is formed between the spore and its germ tube. An empty spore wall is resulted at the proximal part of the germ tube. 2) When a germinating spore issues a first germ tube, a part of the cell contents of the germinating spore migrate to the germ tube. Then, a cross wall is formed between the spore and its germ tube. A second germ tube is issued from the germinating spore. Occasionally, the cross wall is not formed between the persistent spore and its germ tube.

The basal creeping filaments issuing branches develop in all directions without adhering to glass substrates and give rise to erect filaments usually at right angles. The cells of basal creeping filament are more or less sinuate-cylindrical with 1-2μm thick wall, 15-17μm broad and 57-70μm long. The chloroplasts of the cell of basal creeping filament are parietal, laminate with inconspicuous outlines. Erect filaments are often simple or bearing numerous branches. The erect filaments are easily distinguished from basal creeping filament by the straight-cylindrical morphology containing a rather conspicuously outlined chloroplast. The cells of erect filament are ca. 17μm broad and 80-110μm long with ca. 3μm thick wall. Hairs are not produced.

Monosporangia are born in clusters or in secund series on erect filaments and branches. They are solitary to ternate on one- or two-celled stalks, obovoid to ellipsoid, 21-24μm broad and 29-35μm long. Tetrasporangia are rarely born together with monosporangia on the unialgal cultured plants. However, the plants with a part of host tissue transferred from field to culture conditions produce tetrasporangia in great abundance, which are almost same in size as monosporangia. Unfortunately, neither released tetraspores nor germlings are confirmed.

DISCUSSION

In the plants grown in high density culture and without refreshment of media during more than two months, all the erect filaments are very fine and gradually tapering to the apex appearing hair-like prolongations in the upper parts. The upper part of erect filament is greenish red color, in which pyrenoids are not recognized even by staining with carmine propionate solution (ROSOWSKI 1970). However, true hairs are not observed.

The morphotaxonomic characteristics of *Audouinella rhizoidea* from Hokkaido are as follows: 1) The endophytic filaments are not interwoven but loosely entangled. 2) The branches of erect filament are formed at acute angles and reach to the level of the apex of erect filament. 3) Hairs are absent. 4) Pyrenoids are one to several or absent in a cell. 5) Monospores and most vegetative cells contain a lot of small granules. WOELKERLING (1970) considered *Aud. rhizoidea* conspecific with *Aud. botryocarpa* (HARVEY) WOELKERLING. It needs further study with their type collections to confirm his opinion.

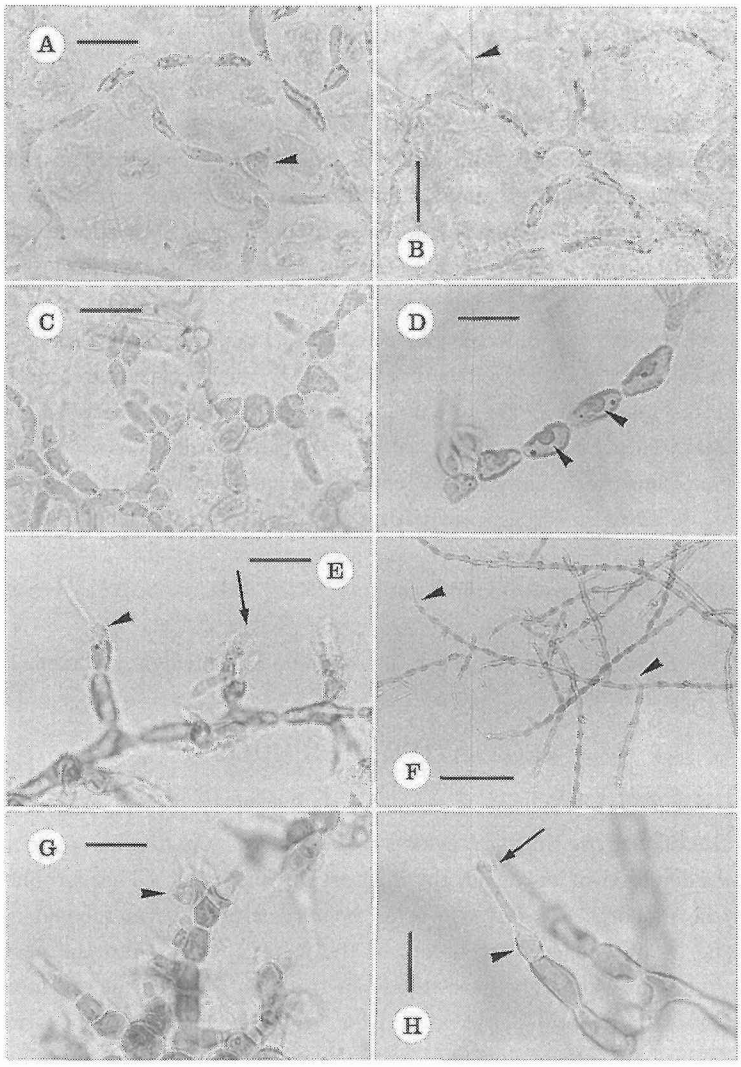

Fig. 5. *Audouinella japonica.* A : Creeping filaments of fusiform cells in the outer wall of the epidermal cells of host. Note the cup-shaped cell bearing a monosporangium (arrow head). B : Creeping filaments of thin contorted cells in the outer wall of the epidermal cells of host. Note a hair (arrow head). C : Creeping filaments of rectangular to globose cells in the outer wall of the epidermal cells of hast. D : Cells of creeping filament including a parietal laminate chloroplasts with a lobed pyrenoid (arrow heads). E : Short branches bearing a carpogonium (arrow head) or spermatangia (arrow) in culture. F : Creeping filaments bearing carpogonia (arrow heads) in culture. G : A monosporangium (arrow) on a cultured plant. H : A spermatium (arrow) on the tip of the trichogyne of a carpogonium (arrow head). (Scale bars of Figs A-E, G, H are 20μm. Scale bar of Fig. F is 50μm.)

Audouinella japonica (PAPENFUSS) GARBARY 1987. p. 97. (Text Fig. 5)

Basionym: *Acrochaetium japonicum* PAPENFUSS 1945, p. 315

Synonym: *Colaconema simplex* INAGAKI 1935, p. 44. f. 2.

Plants endophytic in outer wall-layers of host surface, composed of only prostrate filaments; prostrate filaments expanding and branching in various directions, forming networks; cells of prostrate filament fusiform to cylindrical, 3-5μm broad and 17-55μm long; chloroplasts parietal, lobed, laminate, containing pyrenoids; hairs present laterally on vegetative cells.

Monosporangia lateral on cells of prostrate filament, solitary, hemispherical to globose, 9-11μm broad and 7-10μm long; sexual reproductive structures produced under culture conditions; spermatangia born in groups on two-to several-celled branches, lateral or terminal, with a concaved stalk cell, ovoid to ellipsoid, 4-5μm broad and 5-7μm long; carpogonia born terminally on 1-3 celled branches or laterally on the cell of prostrate filament, ovoid to short fusiform with a thin and straight trichogyne, 7-8μm broad and 10-17μm long.

Type locality: Shiwoya, Hokkaido, Japan.

Type: ?

Material examined: On *Bonnemaisonia hamifera* at Shiwoya 11 April 1978, 9 May 1978.

VEGETATIVE MORPHOLOGY

Field-collected material

Plants are endophytic in the surface membrane of the thallus of *Bonnemaisonia hamifera* and composed of only endophytic prostrate filaments. The germinating spores presumed to be monospores of *Audouinella japonica* issue a germ tube in unipolar germinating mode. The whole cell contents of the spore migrate into the germ tube and leave an empty spore wall. The germ tube penetrates into the surface membrane of host thallus and leaves the empty spore wall outside. The endophytic filaments are prostrate in the wall layer between outside and epidermal cells, expanding in various directions, issuing branches from the middle part of component cells at right angles. Thus, the plants appear as a network in surface view. The cells of endophytic filaments are occasionally tortuous, fusiform to cylindrical. The cells abutting a branch usually make a protrusion at the part facing the branch. But, the cell abutting a monosporangium is concaved, showing a cup-shape, at the part facing the monosporangium. Chloroplasts are parietal, laminate and lobed with pyrenoids. Hairs occur on the plants in May, and are ca. 2μm thick and up to 45μm long. Monosporangia are born solitarily on the cells of endophytic filament and hemispherical to somewhat flatly globose.

Cultured material

Plants grow in host thallus and also on glass substrates under culture conditions. The plants issue several upright filaments stretching outwards of host surface like an erect filament of heterotrichous thallus. The plants under 15°C and 20°C long day culture conditions produce spermatangia and carpogonia in abundance as well as a few monosporangia. Spermatangia are born solitarily or in pairs on the cell of short branches. The cell abutting a spermatangium is concaved at the part facing the spermatangium. Spermatia are ca. 6μm in diameter. Carpogonia are lateral on the cell of endophytic filament or terminal on 1-2 celled branches. Trichogynes are usually born subterminally at obtuse angles to the axis of carpogonial cell, linear with a somewhat obtuse apex, slightly constricted at junction to carpogonial cell, ca. 2μm thick and up to 30μm long. The chloroplast of carpogonium cell is more or less pale in color without pyrenoid. Neither post-fertilization development nor carposporangium is observed.

DISCUSSION

This species was first described by INAGAKI (1935) as *Colaconema simplex* from Shwoya, Hokkaido. PAPENFUSS (1945) removed both species *C. simplex* INAGAKI and *Rhodochorton simplex* DREW (1928) to the genus *Acrochaetium*, and renamed the former specie to *Acrochaetium japonicum* PAPENFUSS because the latter species preoccupied the specific epithet "simplex" in this genus. GARBARY (1987) made combination to *Audouinella*.

The plants of *Audouinella japonica* collected at Shiwoya bore only monosporangia in April and May. The plants produced sexual reproductive structures together with a few monosporangia under culture conditions. However, no fertilized carpogonium appeared during the course of culture experiments.

Audouinella japonica shares some characteristics with *Colaconema asparagopsidis* CHEMIN (1926) in respects of thallus morphology, the morphology of sexual reproductive structures, and the mode of monospore germination. WOELKERLING (1971, p. 43) noted the similarity between *Aud. japonica* and *Colaconema bonnemaisoniae* BATTERS (1896a). WHITE and BONEY (1970) considered *Aud. japonica* conspecific with *Acrochaetium endophyticum* BATTERS (1896b). Thus, it needs a study on the relationship between this species and relevant taxa mentioned above on the basis of their authentic collections.

ACROCHAETIUM NÄGELI et CRAMER 1858, p. 532

Plants have erect filaments with determinate apical growth and stellate chloroplasts with a pyrenoid centrally. The apical growth of erect filaments is generally prevented by the formation of hairs or reproductive structures terminally. The life history is of heteromorphic, diplobiontic, trigenetic alternation of generations. Three generations are represented with gametophytic, tetrasporophytic and carposporophytic phases. The

gametophytic plants have a single cell base with or without a few appendage cells. The tetrasporophytic plants have a multicellular base. The carposporophytic plants develops on the thallus of female gametophytic plants. The gonimoblasts are composed of one to a few cells which bear carposporangia terminally or subterminally. Both gametophytic and tetrasporophytic plants are duplicated by monospores.

Synonyms: *Chromastrum* PAPENFUSS 1945, p. 320
Kylinia ROSENVINGE 1909, p. 141

Lectotype species: *Acrochaetium secundatum* NÄGELI et CRAMER 1858, p. 532

KEY TO THE SPECIES

1. Plants have a unicellular base (probably gametophyte) ·····2
1. Plants have a multicellular base (probably tetrasporophyte) ·····4
2. Basal cells peculiar in shape and larger than vegetative cells ·····3
2. Basal cells same in shape and size as vegetative cells ·····*Acr. catenulatum*
3. Erect filaments apparently tapering toward apex, arcuate, branching only at lower part ·····*Acr. strictum* (G)
3. Erect filaments scarcely tapering toward apex, almost straight, branching on the whole length of erect filaments ·····*Acr. alariae* (G)
4. Monosporangia born in 2-3 concatenate series·····*Acr. densum*
4. Monosporangia born solitarily or in pairs ·····5
5. Cells of erect filament obovoid to short clavate ·····*Acr. sessile*
5. Cells of erect filaments cylindrical to rectangular·····6
6. Cells of erect filaments same broad as their length ·····*Acr. humile*
6. Cells of erect filaments 2-3 times longer than their breadth ·····7
7. Erect filaments bearing long branches with short laterals, hairs absent ·····*Acr. alariae* (T)
7. Erect filaments simple or bearing only short laterals, hairs present ·····*Acr. strictum* (T)

Acrochaetium alariae (JÓNSSON) BORNET 1904, p. XIX (Text Fig. 6)

Basionym: *Chantransia alariae* JÓNSSON 1901, p. 132. f. 1.
Synonyms: *Rhodochorton alariae* (JÓNSSON) ARWIDSSON 1936, p. 137.
Kylinia alariae (JÓNSSON) KYLIN 1944, p. 13.
Chromastrum alariae (JÓNSSON) PAPENFUSS 1945, p. 320.
Audouinella alariae (JÓNSSON) WOELKERLING 1973, p. 541.
Rhodochorton repens JÓNSSON 1901, p. 147.
Acrochaetium jonssonii PAPENFUSS 1945, p. 309.

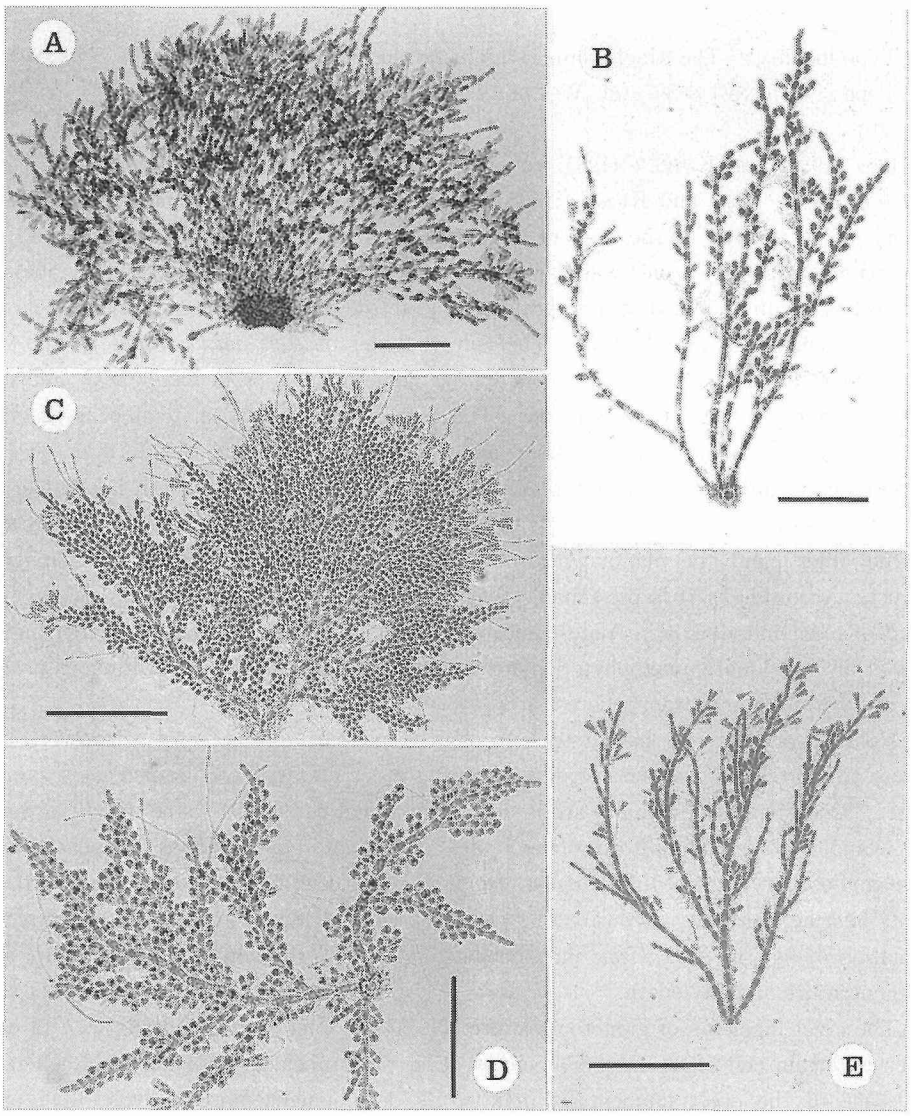

Fig. 6. *Acrochaetium alariae.* A: A tetrasporangial plant in April. B: A gametophytic plant in September. C: A gametophytic plant in June. D: A gametophytic plant in July. E: A gametangial plant in November. (Scale bars of Figs A, C, E are 200μm. Scale bars of Figs B, D are 100μm.)

Type locality: The Maelstrom, Hvammsfjordur, Iceland.
Type: C. JÓNSSON 597 (cf. WOELKERLING 1973)

LEE (1983) and KUIPER (1983) reported the life history of *Acrochaetium alariae* in Atlantic Ocean. LEE and KUROGI (1983) described the morphology, phenology and life history of *Acr. alariae* on the basis of the plants from Muroran, Hokkaido. The study on the phenology of this species was carried out by examination of every 100 individuals on several host thalli collected at a determinate site in the intertidal zone of Muroran monthly from August 1977 to July 1978. The gametopyhtes of *Acr. alariae* occur all the year round. The carposporophytes develop on the gametophytes from October to February with maximum occurrence in January. The tetrasporophytes begin to appear as germlings or younger plants in December and disappear in March. More than 90% of gametangial plants have two or three erect filaments on a basal cell. In September the appearance rate of the plants with a single erect filament on a basal cell is close to 30%. On the other hand, the plants with four erect filaments are of maximum number in August. Accordingly, it is presumable that the population of *Acr. alariae* is mostly composed of older individuals in August and of younger ones in September, although the life span of an individual gametophyte is hard to determine because of the continuous production and germination of monospores.

No hair develops on both tetrasporophytes and carposporophytes. However, hairs are usually produced on the apical cells of the erect filament and branches of gametophytes. Occasionally, two hairs are issued on an apical cell. The shape of hair is generally whipping, rarely moniliform or uncinate. The plants more than 80% appear to bear hairs in February, April, July, August, September and October. On the other hand, the plants bearing hairs are very rare in November, December and June. Consequently, the formation of hair in *Acr. alariae* may not be related with the environmental factors such as temperature and daylength.

The erect filaments of gametophyte are 300-800μm long and composed of 12-19 cells. When a certain cell of an erect filament is dead, the branch beneath the dead cell takes the place of the erect filament as making its development more actively than other branches. However, the part of erect filament above the dead cell appears very poor in growth and development. L'HARDY-HALOS (1971) reported the same phenomenon in the main axis of *Antithamnion*.

The carposporangia of *Acr. alariae* are same in size as the monosporangia of tetrasporophyte and larger than the monosporangia of gametophyte. Also, the carpospores germinate in septate mode as do the monospores of tetrasporophyte.

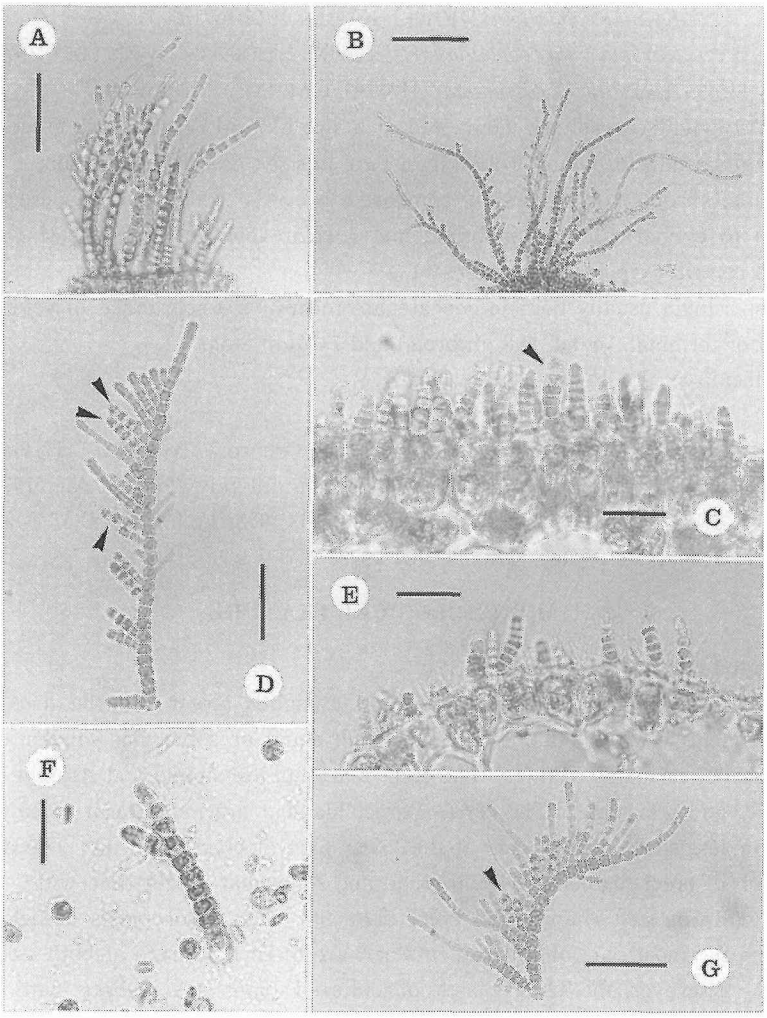

Fig. 7. *Acrochaetium catenulatum*. A: Plants in January. Note the simple and slightly arcuate form of erect filament. B: Plants in April. Note the simple and curved form of erect filament. C: Plants in June. Note the short and simple erect filament with terminal concatenate sporangia (arrow head). D: A plant with many branches in February. Note concatenate sporangia (arrow heads). E: Plants in August. F: A plant in culture. G: A plant with many branches secundly in February. Note concatenate monosporangia (arrow head). (Scale bars of Figs A, D, G are 50μm. Scale bar of Fig. B is 100μm. Scale bar of Figs C, E, F are 20μm.)

Acrochaetium catenulatum HOWE 1914, p. 84. pl. 13, f. 12-18. (Text Fig. 7)

Synonyms: *Chantransia catenulata* (HOWE) DE TONI 1924, p. 44.
Rhodochorton catenulatum (HOWE) NAKAMURA 1941, p. 273. f. 1.
Kylinia catenulata (HOWE) KYLIN 1944, p. 13.
Chromastrum catenulatum (HOWE) STEGENGA et MULDER 1979.
Audouinella catenulata (HOWE) GARBARY 1979, p. 490.

Plants epiphytic, caespitose, composed of a single basal cell and 1-3 erect filaments; basal cells globose to turbinate, 6-9μm by 6-7μm in size; erect filaments simple or secundly branching, straight or recurvate, composed of 5-34 cells; cells of erect filament moniliform to cylindrical, 4-10μm broad and 4-17μm long; chloroplasts single, stellate, including a central pyrenoid; hairs present.

Monosporangia usually born in concatenate form of 2-4 sporangia, or seldom solitarily, lateral or terminal, ovoid, 6-8μm broad and 7-10μm long.

Type locality: La Punta, Calao, Peru.

Type: NY

Material examined: On *Sargassum confusum* at Oshoro 17 May 1977, 17 Feb. 1978, 11 Apr. 1978. On *S. thunbergii* at Muroran 20 June 1977, 19 July 1977, 18 Aug. 1977, 13 Sep. 1977, 13 Oct. 1977, 11 Nov. 1977, 12 Dec. 1977, 30 Jan 1978, 13 Feb. 1978, 15 Mar. 1978, 13 Apr. 1978, 13 May 1978, 9 June 1978, 11 July 1978.

MORPHOLOGICAL FEATURE

Field collected material

The basal cell of *Acrochaetium catenulatum* is slightly larger than the vegetative cells of erect filament when the thallus is young, and equal or somewhat smaller than those when the thallus develops further. The erect filaments are simple and straight or branching secundly and recurvate. The cells of erect filament are moniliform to barrel-shaped and more or less shorter than wide at the lower part of erect filament. The cells in the upper region of erect filament are cylindrical and somewhat longer than wide. Hairs are born terminally or subterminally on erect filaments. The chloroplasts of field-collected plant covers the most part of cell contents and are often fenestrate at both side near the cross wall. However, the chloroplasts of cultured plant are stellate with a central pyrenoid.

Monosporangia are usually born in concatenate series of 2-4 sporangia. Occasionally, the monosporangia are born solitarily on one- or two-celled stalks. The terminal one of concatenate sporangia and the solitary monosporangium are ovoid, while the intercalary ones are oblong to barrel-shaped.

The plants of *Acrochaetium catenulatum* usually occur in rather dense populations on the surface of host plants. The phenological observation of *Acr. catenulatum* was carried

out with the plants monthly collected at Muroran during the period from June 1977 to July 1978. The plants occur all the year round in the intertidal zone of Muroran. Two types of thallus morphology appear in a year. One type of thallus form occurs dominantly in June to December. This type of thallus form is represented by the plants of which the erect filament is always simple, straight, gradually tapering toward the apex, often terminated by concatenate monosporangia or hairs, 18-37μm high and consisting of 5-9 cells. The basal cell of this plant type is globose and slightly larger than the vegetative cells of erect filament. The cells of erect filament of this plant type are discoid, 5-8μm broad and 3-4μm long. The other type of thallus form occurs dominantly in January to May. The latter type of thallus form is represented by the plants of which the erect filaments are increasing their height to 100-450μm in lenght, consisting of 14-34 cells and recurved by issuing branches in secund series. The cells of erect filament of the latter type are moniliform to cylindrical, 5-10μm broad and 6-17μm long. Occasionally, the erect filaments of the latter plant type show the sympodial or tortuous growth in April and May.

WOELKERLING (1971, 1972) considered that *Acrochaetium catenulatum* was conspecific with *Acr. microscopicum* (NÄGELI) NÄGELI. However, LEE (1987) concluded that *Acr. catenulatum* differs from the latter species in having monosporangia born concatenately. STEGENGA & VROMAN (1976) had drawn attention to the possibility that *Acr. catenulatum* might be the gametophytic phase of *Acr. densum* (DREW) PAPENFUSS. *Acr. catenulatum* shares some characters with *Acr. densum* such as branching mode, chloroplast morphology and formation of concatenate monosporangia. However, the two entities are recorded separately in this paper pending that the relationship of the two is clearer.

***Acrochaetium densum* (DREW) PAPENFUSS** 1945, p. 308. (Text Fig. 8)

Basionym: *Rhodochorton densum* DREW 1928, p. 168. pl. 38, f. 17-24.
Synonym: *Chromastrum densum* (DREW) STEGENGA et MULDER 1979. p. 299.
Audouinella densa (DREW) GARBARY 1979. p. 490

Plants epiphytic, caespitose, composed of basal creeping filaments and erect filaments, to 600μm high; basal creeping filaments confluent each other, forming basal discs; cells of creeping filament more or less cylindrical, 4-7μm broad and 5-10μm long; erect filaments usually arcuate, branching in secund series; cells of erect filament cylindrical with conspicuous wall, 7-11μm broad and 11-25μm long; chloroplasts single, stellate with a pyrenoid; hairs present.

Monosporangia born solitarily or in concatenate form of 2-3 sporangia, terminal or lateral on branches and erect filaments, ovoid, 7-10μm broad and 10-12μm long.

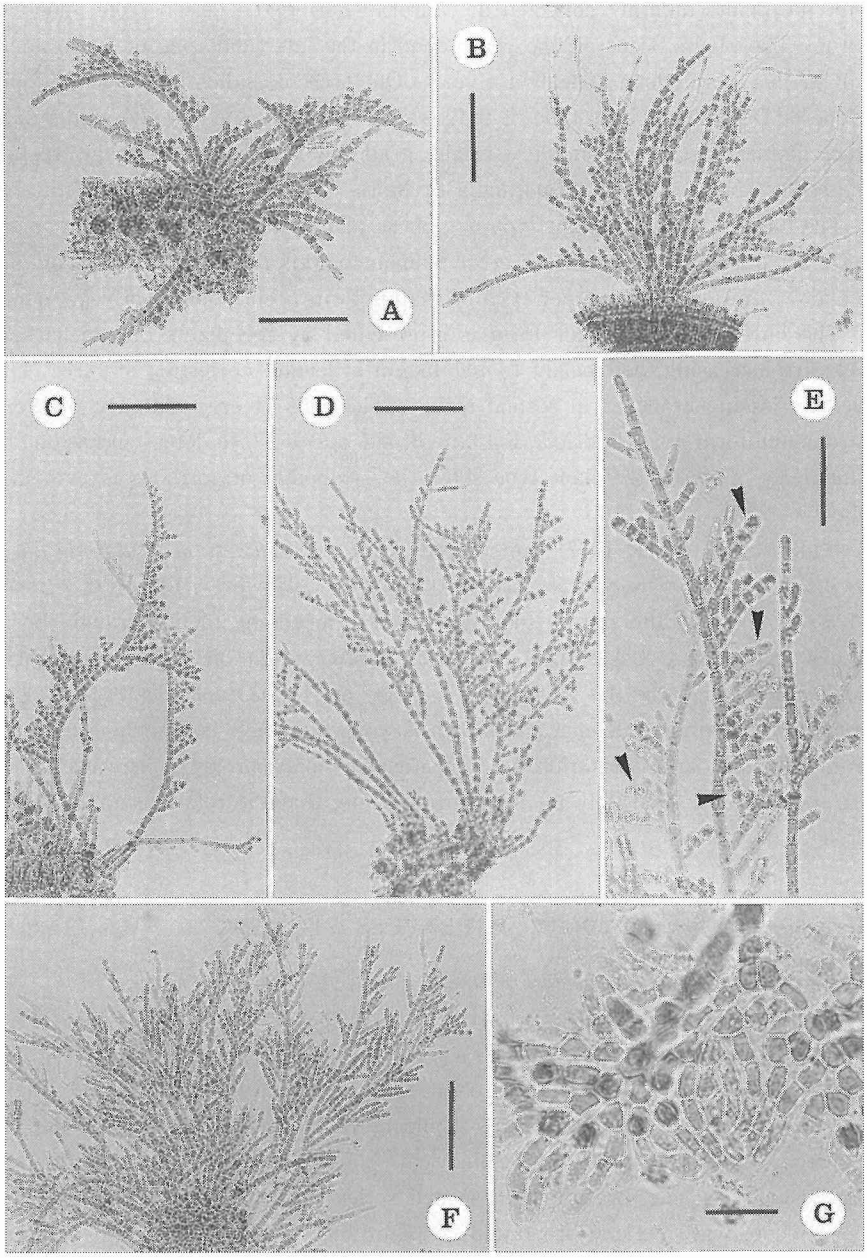

Fig. 8. *Acrochaetium densum*. A: Plants in February. B: Plants in March. C: Plants in April. D: Plants in May. E: Concatenate monosporangia (arrow heads). F: Plants in June. G: Basal creeping filaments in culture. (Scale bars of Figs A, B, C, D, F are 100μm. Scale bar of Fig. E is 50μm. Scale bar of Fig. G is 20μm.)

Type locality: Fort Point, San Francisco, America.

Type: UC, 294560 (GARDNER, no. 4607)

Material examined: On *Sargassum confusum* at Oshoro 17 May 1977, 10 June 1977, 17 Feb. 1978, 11 Mar. 1978, 11 Apr. 1978. On *Dictyopteris divaricata* at Oshoro 10 June 1977.

MORPHOLOGICAL FEATURE

Field collected material

Plants occur at Oshoro Bay, Hokkaido, in February to June. The plants increase their height monthly···about 250μm in February, 300-350μm in March, 400-450μm in April, 400-500μm in May and 450-600μm in June. The creeping filaments are more or less tightly confluent each other and forming a monostromatic basal disc. The erect filaments issue many short recurvate branches on every cells in secund series. The cells of erect filament are usually cylindrical or occasionally barrel-shaped to moniliform. Chloroplasts are parietal, usually fenestrated lamella or stellate containing a pyrenoid. Hairs appear on erect filaments in March to June.

Monosporangia are born in concatenate series of 2-3 sporangia or sometimes solitarily. The terminal one of a concatenate sporangia are ovoid as solitary ones. The intercalary ones of concatenate sporangia are barrel-shaped.

Observation of cultured material

Germinating monospores from the plants collected in June usually divide into two equal sized cells that become the rudiment of basal creeping filaments. The creeping filaments tend to be confluent each other and form a basal disc on glass substrates. Erect filaments arise from every cells at the central part of basal disc. The upper part of erect filament of the plants grown in high density culture for a long time turns to be pale green in color and eventually die. Meanwhile, new erect filaments arise from the cells of basal system.

DISCUSSION

In Dutch coast the plants of *Acrochaetium densum* were found in all seasons and occasionally produced tetrasporangia (STEGENGA & VROMAN 1976). In Oshoro Bay, Hokkaido, the plants of *Acr. densum* occur in February to June and produce only monosporangia. The plants collected in February agree quite well with the descriptions and figures of DREW (1928) and NAKAMURA (1944). But, the plants in May have erect filaments consisting of barrel-shape to moniliform cells and issuing long branches as previously observed by NAKAMURA (1944). Monosporangia are born in abundance in March to May. The plants in June produce monosporangia sparsely. However, short branches seemingly like the precursors of concatenate monosporangia appear luxuriantly. This fact suggests that June in Oshoro Bay may be a favorable season for vegetative growth

rather than for reproduction of *Acr. densum*. Under culture conditions the basal disc of the plants survives with reduced erect filaments even though their longer and older erect filaments are degenerative.

Acrochaetium humile (ROSENVINGE) BØRGESEN 1915, p. 23. (Text Fig. 9)

Basionym: *Chantransia humilis* ROSENVINGE 1909, p. 117. f. 44-45.

Synonyms: *Rhodochorton humile* (ROSENVINGE) DREW 1928, p. 151.
Chromastrum humile (ROSENVINGE) PAPENFUSS 1945, p. 323.
Kylinia humilis (ROSENVINGE) PAPENFUSS 1947, p. 437.
Colaconema humilis (ROSENVINGE) WOELKERLING 1971, p. 44.
Audouinella humilis (ROSENVINGE) GARBARY 1979.

Plants epiphytic, tufted, composed of basal creeping filaments and erect filaments, 120-150(-200)μm high; basal creeping filaments expanding radiately, forming monostromatic basal discs; cells of creeping filament cylindrical to roundish polygonal in shape, 6-8μm broad and 8-13μm long; erect filaments usually simple or occasionally branching, consisting of 1-6 (-13) cells; cells of erect filament quadrate through cylindrical to ellipsoid, 7-10μm broad and 9-12μm long; Chloroplasts stellate, including a central pyrenoid; hairs present.

Monosporangia born terminally or laterally on erect filaments, with one- or two-celled stalks, globose to short ellipsoid, 10-11μm broad and 11-14μm long.

Type locality: Spodsbjerg, Langeland, Denmark.

Type: C. (cf. WOELKERLING 1973, p. 570).

Material examined: on *Codium yezoense* at Nemuro, 2 June 1977.

MORPHOLOGICAL FEATURE

Field collected material

Plants occur in a dense bundle on the tip of the utricle of *Codium yezoense*. The presumable monospores of the plants divide into two equal sized cells when germinating, each of which issue a basal creeping filament. Occasionally, a germling has only the development of basal disc without issuing erect filaments. The creeping filaments expand coherently and adhere rather tightly on the host surface. The cells of creeping filament are more or less variable in shape in the central region and cylindrical in the marginal region of the basal disc. The terminal cell of creeping filament is tortuous. Erect filaments arise in dense bundle from basal cells, usually simple and consisting of 1-6 cells. Occasionally, one to a few erect filaments consisting of up to 13 cells protrude beyond the bundle of the erect system. Hairs are common, terminal and up to 120μm long.

Cultured material

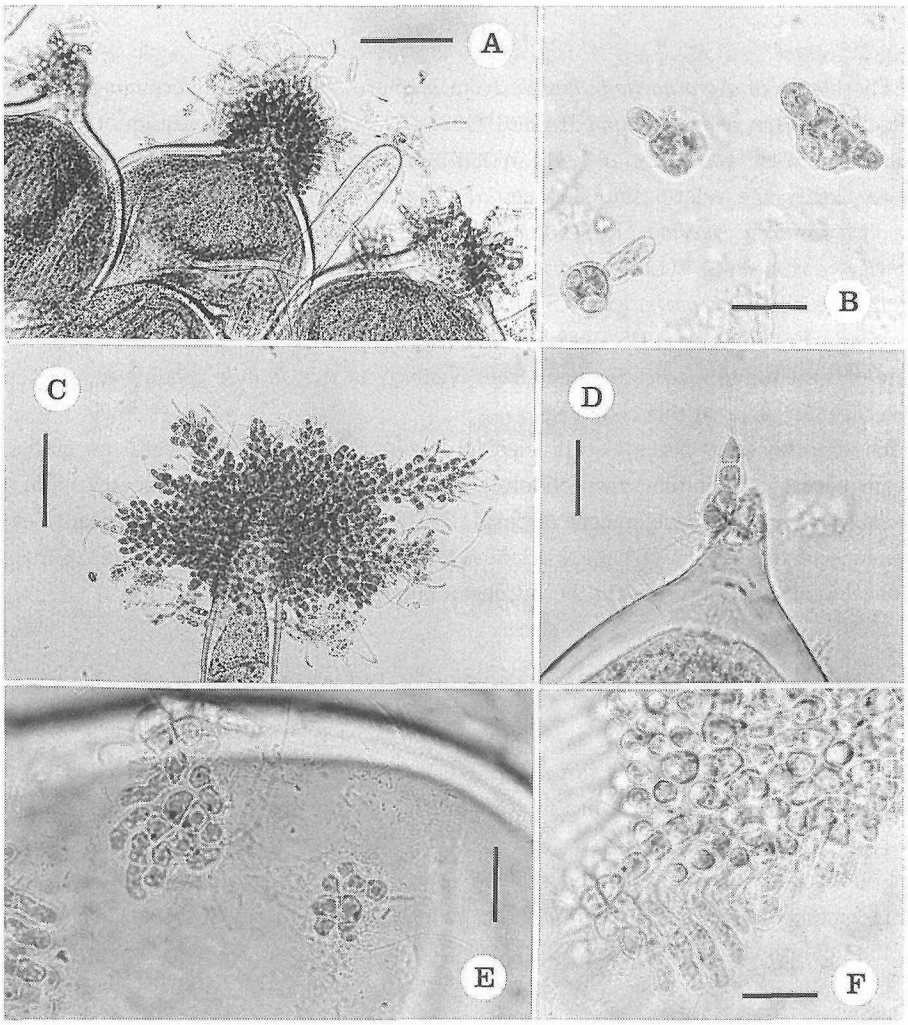

Fig. 9. *Acrochaetium humile.* A, C: Habits. B: The mode of monospore germination in culture. D, E: Germlings on the utricles of Codium *yezoense* in nature. Note the persistent germinating spores. F: Monostromatic disc of basal system. Note most of the cells of basal system except marginal ones issue erect filaments. (Scale bars of Figs A, C are 50μm. Scale bars of Figs B, D, E, F are 20μm.)

Germinating monospores usually divide into two to several unequal sized cells and develop into a small roundish disc. The cells of the disc give rise to several filaments slantwise to decunbently. The filaments are slightly tortuous, composed of barrel-shaped to globose cells with a thick wall, and often branching in various directions.

DISCUSSION

The plants of *Acrochaetium humile* from Nemuro, share some morphological characteristics with *Acr. mahumetanum* HAMEL (1927; 1928b). Several investigators (LEVRING 1935; 1940; 1942; BAARDSETH 1941; WOELKERLING 1971; 1973) pointed out the necessity to clarify the relationship between *Acr. humile* and other morphologically similar taxa; *Chantransia macula* ROSENVINGE (1909), *Ch. reducta* ROSENVINGE (1909), *Acr. pulchellum*, BØRGESEN (1915), *Acr. cymopoliae* BØRGESEN (1927), *Acr. mahumetanum* HAMEL (1928b), *Acr. boergesenii* SCHIFFNER (1931), *Acr. radiatum* JAO (1936), *Acr. duboscquii* FELDMANN (1935, 1938-1939), and *Acr. subreductum* LEVRING (1953). We agree with them and record the plant from Nemuro as *Acr. humile* pending more accumulation of knowledge on this complex.

The germinating spores also divided into two equal sized and several unequal sized cells in nature and cultuer, respectively. The plants growing on the acute tip of host utricles showed lesser development of basal disc than those growing on the broadly expanding plane of the utricle. STEGENGA and VROMAN (1976) observed the similar mode of the development of basal disc in the European plants of *Acr. densum*.

Acrochaetium kurogii (**LEE et LINDSTROM**) **LEE et LEE** 1988. p. 128. (Text Fig. 10)

Basionym: *Auduinella kurogii* LEE et LINDSTROM 1979. p. 115. f. 1-9. F. A-L
Synonym: *Chromastrum kurogii* (LEE et LINDSTROM) KUIPER 1983, p. 139.
Type locality: Nosappu Misaki, Nemuro, Hokkaido.
Type: SAP 034552.

Following to the classification scheme proposed by LEE & LEE (1988), this species was recombined to the genus *Acrochaetium* owing to producing monosporangia and having a stellate chloroplast.

Acrochaetium sessile (**NAKAMURA**) comb. nov. (Text Fig. 11)

Basionym: *Rhodochorton sessile* NAKAMURA 1941, p. 278. f. 4.
Synonyms: *Chromastrum sessile* (NAKAMURA) PAPENFUSS 1945, p. 323.
Kylinia sessilis (NAKAMURA) PAPENFUSS 1947, p. 437.
Audouinella sessilis (NAKAMURA) GARBARY 1979, p. 490.

Plants epiphytic, caespitose, composed of basal creeping filaments and erect filaments, 200-260μm high; creeping filaments occasionally confluent together, forming monostromatic basal discs; cells of creeping filament cylindrical or variable in shape, 5-8μm broad and 6-10μm long; erect filaments simple or rarely branching, composed of 20-30 cells; cells of erect filament short clavate to obovoid, 5-7μm broad and 7-12μm long;

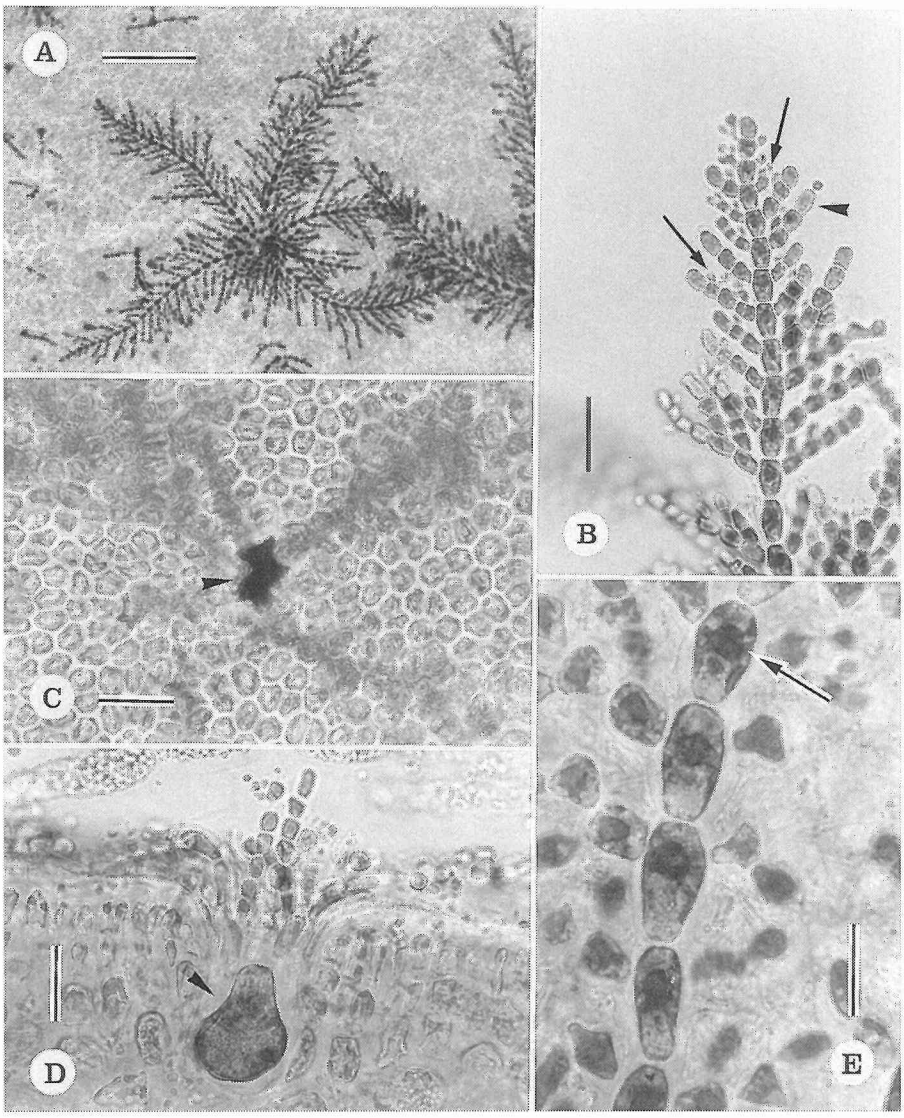

Fig. 10. *Acrochaetium kurogii*. A: A plant on host surface. Note the starfish form of plant having four or five horizontally stretching filaments with pinnate branches. B: The upper part of filament bearing spermatangia (arrows) and carpogonia (arrow head). C: Upper view of a basal cell (arrow head) immersed into host tissue. D: Profile of a basal cell (arrow head) immersed into host tissue. E: Stellate chloroplasts with a central pyrenoid (arrow). (Scale bar of Fig. A is 50μm. Scale bars of Figs B-D are 20μm. Scale bar of Fig. E is 10μm.)

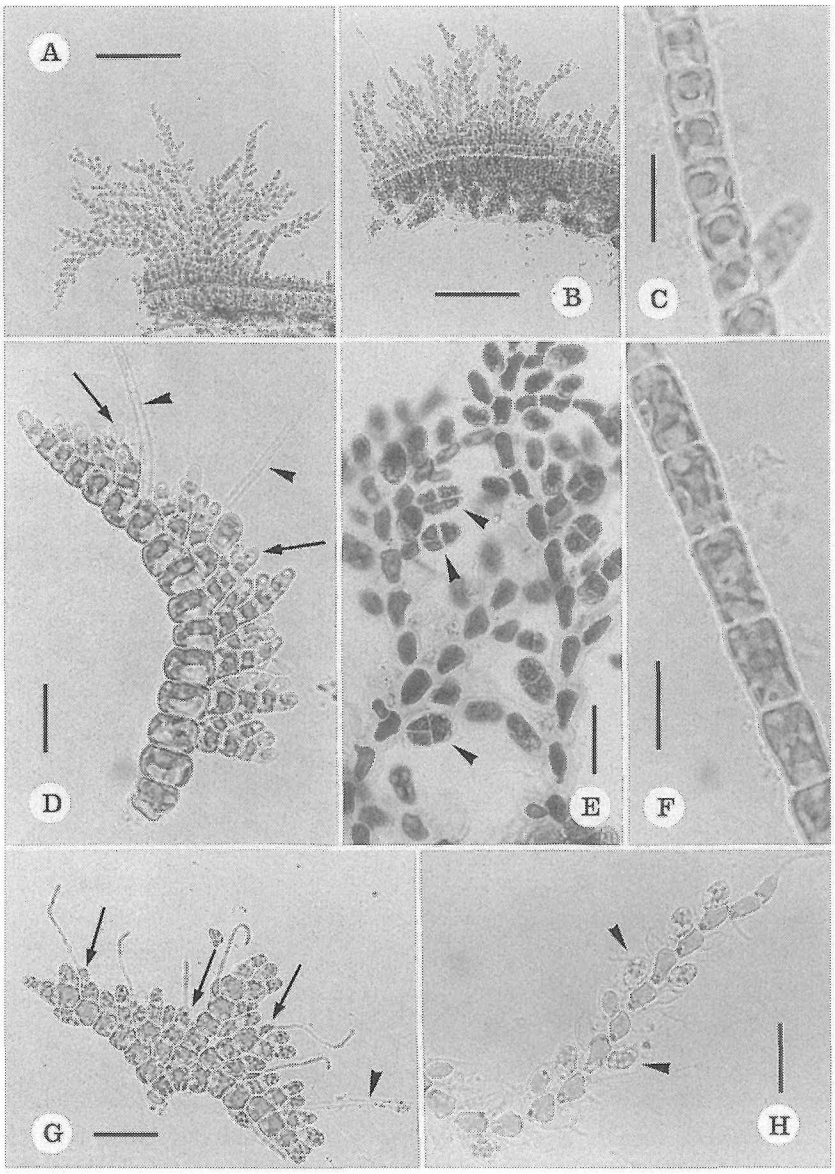

Fig. 11. *Acrochaetium sessile*. A, B: Plants on host in June. C, F: Cells of erect filament including a stellate chloroplast. D: A male plant bearing spermatangia (arrows) and hairs (arrow heads). E: Erect filaments bearing tetrasporangia (arrow heads) as well as monosporangia in May. G: A female plant bearing carpogonia (arrows) and a hair (arrow head). H: An erect filament bearing sessile monosporangia (arrow head) in May. (Scale bars of Figs A, B are 100μm. Scale bars of Figs C, F are 10μm. Scale bars of Figs D, E, H are 20μm. Scale bar of Fig. G is 30μm.)

chloroplasts single stellate with a central pyrenoid; hairs common, terminal or subterminal, 3-4μm thick, up to 200μm long. Monosporangia lateral or terminal, solitary or in pairs, ovoid, 7-9μm broad and 12-14μm long; tetrasporangia lateral, cruciately divided, ellipsoid, 10-11μm broad and 15-17μm long.

Type locality: Muroran, Hokkaido, Japan.

Type: SAP (Slide)

Material examined: On *Cladophora* sp. at Muroran 18 June 1977. On *Sargassum confusum* at Muroran 20 June 1977, at Oshoro 17 May 1977, 11 April 1978, at Shiwoya 11 April 1978. On *Dictyopteris divaricata* at Oshoro 17 May 1977.

MORPHOLOGICAL FEATURE

Field collected material

Plants are epiphytic on other algae forming a bright red felt on the host surface. The creeping filaments of the plant expand flexuously in various directions on the host surface and are confluent together in the central region of basal system. The erect filaments are usually simple or rarely branching, arcuate, and usually terminating in hairs or sporangia. The cells abutting a monosporangium become concave at the part facing the monosporangium, but convex after shedding a spore. The vegetative cells of erect filament are short clavate to obovoid with constriction at cross wall. However, the apical cells of erect filament are longish cylindrical to fusiform. Hairs are very common on erect filaments and branches terminally or laterally. In rare case, one or more septa -like structures are formed in a hair cell.

Monosporangia are born laterally on the cells of erect filament in secund or pinnate series and usually sessile or occasionally with a one-celled stalk. Tetrasporangia are born together with monosporangia.

Cultured material

Tetrasporophyte: Germinating monospores of the plants from nature divide into two equal sized cells after settled down to the glass substrate. Each daughter cell resulted by the division of germinating monospore issues creeping filaments and erect filaments. The creeping filaments are confluent together and form a monostromatic basal disc on the glass substrate. However, the creeping filaments of the plants growing in the nitrate free medium (ESP defective in $NaNO_3$) are not confluent together and extend separately. Long and mature erect filaments occur in the central part of the basal disc. Chloroplasts are stellate with a central pyrenoid.

Hairs occur in great abundance on a well grown thallus or even on the daughter cells of germinating spore. All the plants under 15°C long day culture conditions produce hairs by 10 days after germination. On the other hand, only the plants less than 50% under 10°C short day conditions produce hairs by 20 days after germination. Generally, hairs of

the plants of *Acrochaetium* sessile produced earlier and more under long day conditions than those under short day conditions. In nitrate free medium hairs are very long and produced on most of cells of erect system. However, septum-like structure is not observed in hair cell of the plants in culture.

Monosporangia are sessile and solitary in secund series or in pairs on one-celled stalk in pinnate series on erect filaments. Plants begin to release monospores since 10 days after germination under 15°C long day (16 hr light : 8 hr dark), 15 days under 10°C long day, 20 days under 10°C short day (8 hr light : 16 hr dark), and 35 days under 5°C short day conditions. Tetrasporangia are rarely produced on the plants under 10°C long day culture conditions.

Unfortunately, tetraspores could not be isolated because monospores was shedded simultaneously. However, several new plants with a single cell base occurred in the proximity of the plants bearing tetrasporangia. The plants with a single cell base produce male and female reproductive structures together with monosporangia under 10°C short day culture conditions.

Gametophyte : Germinating monospores of the gametophytic plants issue a germ tube that is becomes an erect filament. The gametophytic plants are composed of a single cell base and one to three erect filaments, up to 250μm high. The gametophytic plants produce spermatangia or carpogonia together with monosporangia on separate thallus. The basal cell of gametophytic plants is globose to ellipsoid, more or less smaller than the vegetative cells of erect filament in a well grown thallus, 9-10μm broad and 8-9μm long. The erect filament of gametophytic plants is upright to oblique or occasionally recurvate owing to branching in secund series. The cells of erect filament are moniliform to polygonal in shape, 10-13μm broad and 9-11μm long. Chloroplasts are single, stellate and situating in the distal part of cells. Hairs occur on both male and female plants.

Spermatangia are born in pairs or often solitarily on spermatangial branches that are composed of 2-4 small cells, ovoid to ellipsoid, 3-5μm long. Spermatia are ca. 4μm in diameter. Carpogonia are lateral or terminal on short branches, containing an inconspicuous chloroplast, flask-shaped, 4-5μm broad and 6-7μm long. Trichogyne is issued from the acute apex of a carpogonium, somewhat constricted at junction, straight or occasionally tortuous, ca. 1μm thick and up to 50μm long. The carpogonia are produced plentifully under 10°C short day culture conditions. However, the female plants produce only monosporangia under the same conditions when the medium is refreshed frequently. No fertilized carpogonium is observed. Monosporangia are born on both male and female plants together with sexual reproductive structures.

DISCUSSION

NAKAMURA (1941) described this species growing on the apices of the lamuli of *Hyalosiphonia caespitosa* at Muroran, Hokkaido. The host plant was not found at the

type locality during the period of this study. The plants examined in this study grew on *Cladophora* sp., *Dictyopteris divaricata* and *Sargassum confusum* at both Muroran and Oshoro, Hokkaido.

It is known by the culture experiments that the plants of *Acrochaetium sessile* described by NAKAMURA (1941) represent the tetrasporophytic phase. The tetrasprophytic plants have a multicellular discoid base and produce tetrasporangia together with monosporangia. The gametophytic plants have a single cell base and produce male or female reproductive structures together with monosporangia.

AZIZ (1965 p. 156) recombined *Rhodochorton sessile* NAKAMURA to the genus *Acrochaetium*. But, *Acrochaetium sessile* (NAKAMURA) AZIZ is invalid under the Article 29 of the ICBN (International Code of Botanical Nomenclature).

Acrochaetium strictum (**ROSENVINGE**) **HAMEL** 1927, p. 101. (Text Figs 12, 13)

Basionym: *Chantransia stricta* ROSENVINGE 1909, p. 108.

Plants epiphytic, caespitose, composed of creeping filaments and erect filaments, 300-500 μm high; creeping filaments branching secundly, confluent together, forming monostromatic discs, tightly adhering to substrate; cells of creeping filament cylindrical, contortive, 7-9μm broad and 9-18μm long; erect filaments straight, issuing only short branchlets alternately or oppositely, usually terminating in hairs; cells of erect filament cylindrical, occasionally with slight constriction at cell septum, 8-11μm broad and 13-30μm long; chloroplasts single, stellate with a central pyrenoid; monosporangia born solitarily or in pairs on 1-3 celled branchlets, subterminal or lateral on erect filaments, ellipsoid to ovoid, 10-11μm broad and 15-17μm long; other reproductive structures unknown.

Type locality: In depths of 7-12 meters, Off Gjerrild Klint, Kattegat, Denmark.

Type: C (?).

Material examined: On *Spongomorpha* sp. at Akkeshi 30 June 1977.

MORPHOLOGICAL FEATURE

Field-collected material

The presumable gametophytic plants occurred together with tetrasporophytic plants on *Spongomorpha* sp., even though the former plants were in rather sparse populations. There is no direct evidence that the gametophytic plants are to be the same species as the tetrasporophytic plants. However, the gametophytic plants are attributed to *Acrochaetium strictum* in several respects including that it has the same habitats with the sporophytic plants, simple erect filaments with 1-2 celled short branchlets bearing carpogonia or spermatangia, and with stellate chloroplasts.

Gametangial plants monoecious, epiphytic, caespitose, consisting of unicellular base and two or three erect filaments, 300-500μm high; basal cells hemispherical with wall ca.

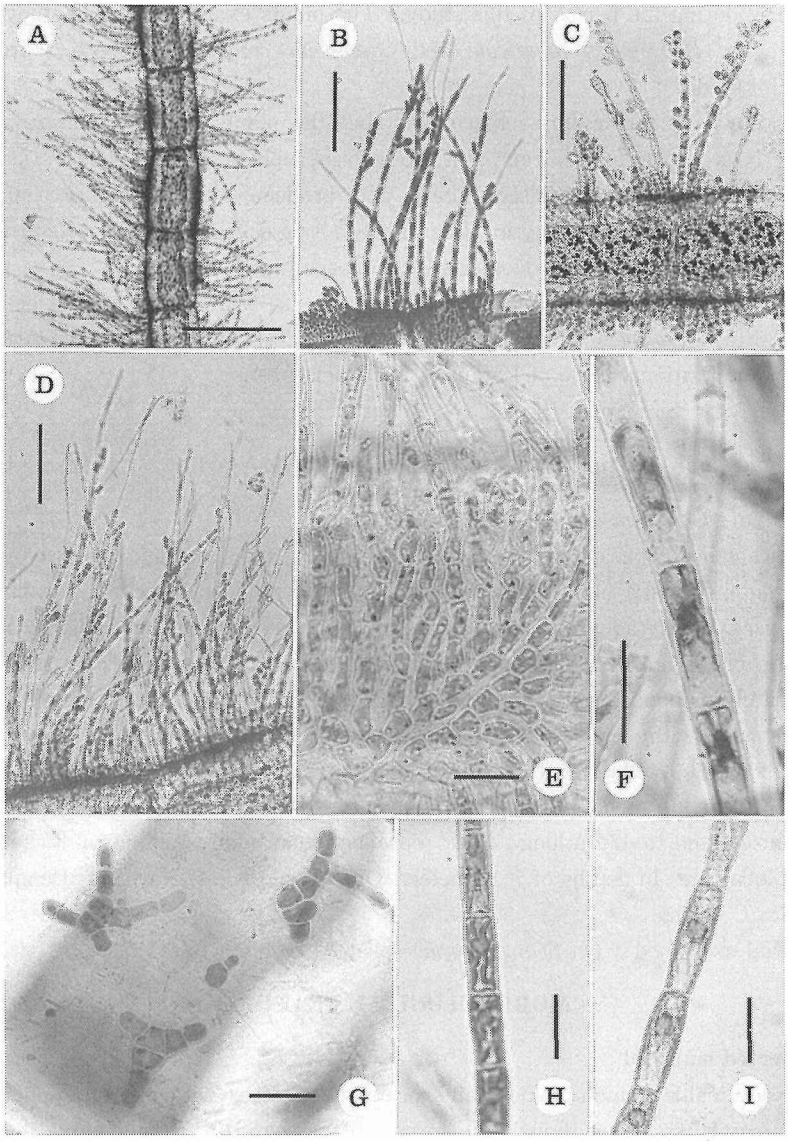

Fig. 12. *Acrochaetium strictum*. A: Habit on the plant of *Spongomorpha* sp. in nature. B, D: Erect filaments with terminal hairs. Note the simple and straight form of erect filament. C: Erect filaments bearing lateral or terminal monosporangia. Note the simple and straight form of erect filament. E: Basal creeping filaments on host plant. F: Cylindrical cells including a parietal laminate or stellate chloroplast in nature. G: Germlings on host surface in nature. H, I: Cylindrical or longish barrel-shaped cells of erect filament in culture. Note stellate chloroplasts with a central pyrenoid. (Scale bar of Fig. A is 300μm. Scale bars of Figs B-D are 100μm. Scale bars of Figs E-I are 20μm.)

10μm thick, 18-28μm in diameter; erect filaments gradually tapering toward apex, usually simple and arcuate or seldom issuing branches alternately or secundly and straight; cells of erect filament barrel-shaped to cylindrical, 11-16μm broad and 24-29μm long; chloroplasts stellate with a pyrenoid; hairs present; spermatangia usually born on the abutting cell of carpogonium or on one-or two-celled branchlets, 3-4μm in diameter; carpogonia terminal or occasionally lateral, solitary or in groups on one- to four-celled branchlets, ca. 7μm broad and 9-10μm long, issuing trichogynes subterminally; trichogynes papillate to spatulate, up to 7μm long; fertilized carpogonia giving rise to 3-4 carposporangia on distal part; carposporangia ellipsoid to ovoid, 9-10μm broad and 15-18μm long; monosporangia terminal or lateral on branches, ca. 9μm broad and ca. 13μm long.

Presumable younger gametophytic plants generally issue short branches on the lower part of erect filament. Spermatangia are usually born on the abutting cell of carpogonium or occasionally on small-celled branchlets. Spermatangia are produced in close proximity of carpogonium. Carpogonia are generally born terminally or seldom laterally on one-to three-celled branchlets, and solitary or in pairs. Fertilized carpogonia elongate distally, and then cut off 3-4 carposporangia subterminally. Monosporangia are produced laterally or terminally on the erect filaments of presumably older plants.

Germinating spores that are presumed to be the monospores of the sporophyte usually divide into equal sized cells. Each cell give rise to creeping filaments as well as erect filaments. The two cells derived by the first division of the germinating spore are recognizable even in fairly grown plants. The creeping filaments of the sporophyte expand radiately and are confluent together to form a monostromatic basal disc. The erect filaments of the sporophyte arise from the daughter cells of germinating spore as well as from the cells of creeping filament. The erect filaments are straight, usually issuing few-celled short branchlets, and terminating in hairs or monosporangia. Monosporangia of the sporophyte are born in opposite or alternate series on erect filaments.

Cultured material

The germinating monospores of the sporophyte issue germ tubes after unequal sized division or equal sized division. A filamentous basal system develops from the former mode and a discoid one from the latter mode. However, both types of the basal system develop into a pseudoparenchymatous monostromatic disc in the well grown plants. The erect filaments are also simple and issuing only 1-2 celled branchlets. Thus, the simple and straight erect filaments are characteristic in this species. Under short day conditions the plants grow very slowly and have erect filaments consisting of short and barrel-shaped cells. On the other hand, the plants show a rapid growth and have erect filaments consisting of long and cylindrical cells under long day conditions. Chloroplasts are parietal laminate with a maringal pyrenoid or stellate with a central pyrenoid. Hairs

appear in great abundance even at the early stage of thallus development in both ESP and nitrate free ESP ($NaNO_3$ free) media under long day conditions.

Monosporangia are born solitarily or ternately, terminally or laterally on erect filaments or on 1-3 celled branchlets, somewhat longish ellipsoid, 9-10μm broad and 18-21μm long; other reproductive structures are not found.

DISCUSSION

Acrochaetium strictum is characterized by its straight erect filaments which are unbranched, and most of the branchlets which are unicellular or two-celled and bear two sporangia (ROSENVINGE 1909). Hokkaido plants agree well with the plants from Denmark in simple erect filaments with 1-3 celled branchlets, branching mode, abundance of hairs, the size of cell and monosporangium. However, the plants at hand differ from the type collections in chloroplast morphology. ROSENVINGE (1909) described that this species had a parietal laminate chloroplast. STEGENGA & VAN WISSEN (1979) reported this species as the tetrasporic phase of *Kylinia rosulata* ROSENVINGE. However, the tetrasporophytic plants, which are cultured, issue abundant branches (see STEGENGA & VAN WISSEN 1979, p. 110 figs 79, 80) and differ from the cultured ones derived from monospores of Hokkaido plants. The cells of erect filament of the plants from Hokkaido issue branchlets or monosporangia without changing their cylindrical shape. The presumable gametophytic plants are also different from *K. rosulata* in most respects. The presumable gametophytic plants of *Acr. strictum* are somewhat related to the gametophytic plants of *Acr. alariae* in the morphologies of basal cell, carpogonium, and carposporophyte, the mode of spermatangium formation. However, the former differs from the latter in the erect filament morphology and the branching pattern.

RHODOCHORTON NÄGELI 1861 p. 355

Plants are epilithic, epiphytic, epizoic, endophytic or endozoic. This taxon does not produce monosporangia. Asexual reproduction is performed with tetraspores which are formed apomeiotically. Chloroplasts are various in form, i.e., stellate, discoid, ribbon-shape or parietal laminate. A fertilized carpogonium develop into a filament which is composed of several cylindrical cells. The filament produces tetrasporangia terminally and laterally, or gives rise to an erect filament which grows up into a large thallus producing tetrasporangia. Therefore, the carposporophytic generation is reduced. The life history is completed with diplobiontic (sporophyte and gametophyte) and digenetic (sporophyte and gametophyte) alternation of generations.

Synonym: *Thamnidium* THURET in LE JOLIS 1863, p. 110.

Type species: *Rhodochorton purpureum* (LIGHTFOOT) ROSENVINGE 1900, p. 75.

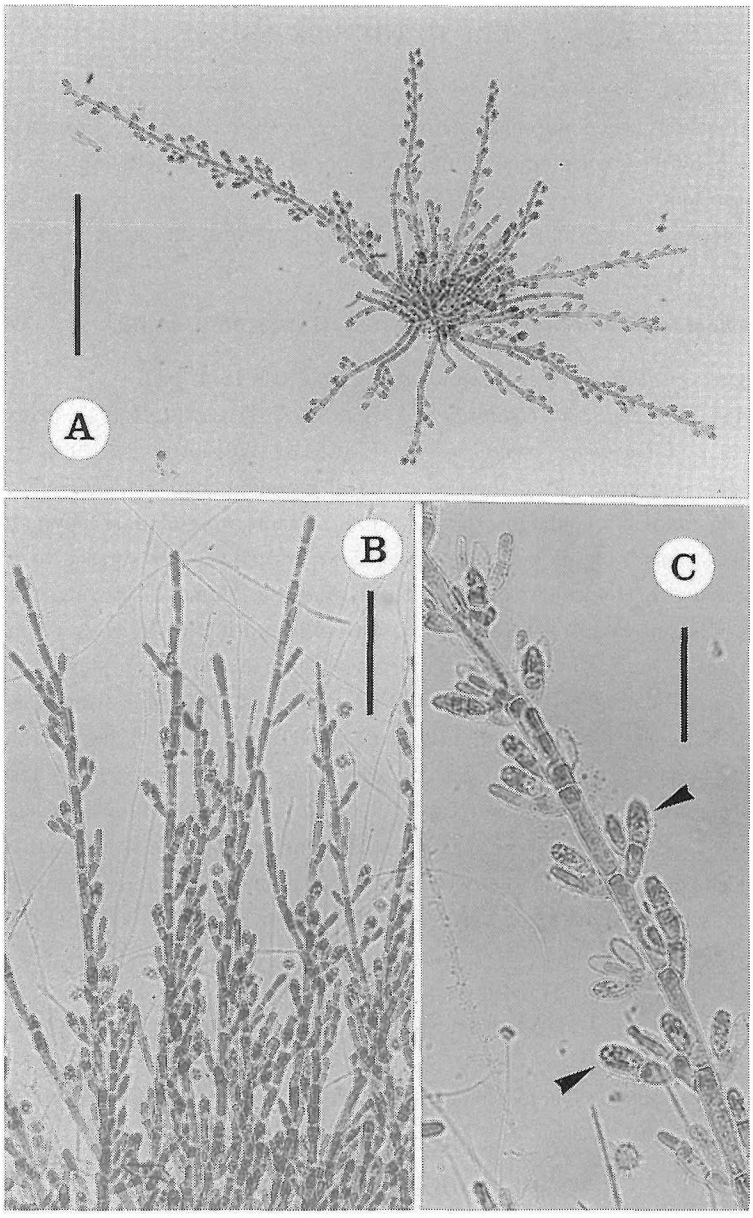

Fig. 13. *Acrochaetium strictum*. A: A plant in culture. Note simple and straight form of erect filaments. B: Erect filaments in culture. C: Monosporangia (arrow heads) born solitarily or in pairs on a stalk cell. (Scale bar of Fig. A is 200μm. Scale bar of Fig. B is 100μm. Scale bar of Fig. C is 50μm.)

KEY TO THE SPECIES

1. Basal system filamentous ·····2
1. Basal system pseudoparenchymatous ·····*Rh. membranaceum*
   2. Endophytic, erect filament simple, composed of several cells, up to 50μm long ·····*Rh. subimmersum*
   2. Saxicolous, erect filament branching, usually several mm long ·····*Rh. purpureum*

Rhodochorton membranaceum (MAGNUS) HAUCK 1879, p. 312. **(Text Fig. 14)**

Basionym: *Callithamnion membranaceum* MAGNUS 1874, p. 67.

Synonyms: *Audouinella membranacea* (MAGNUS) PAPENFUSS 1945, p. 326.
Colaconema membranacea (MAGNUS) WOELKERLING 1973, p. 566.

Plants epi- and endozoic, composed of basal creeping filaments and erect filaments; basal creeping filaments confluent and branching, forming pseudoparenchymatous monostromatic plates; basal plates laminate with 3-5 layers from outer surface to inner site of chitinous perisarc of hydroids; cells of basal creeping filament showing various shape with sinuate margins in surface view, globose to ellipsoid in side view, 3-14μm broad, ca. 10μm long and 3-15μm thick; erect filaments arising in groups on superficial layers of basal plate, usually simple, composed of 3-6 cells, equal in width from base to apex; cells of erect filament cylindrical, slightly constricted at junctions, 6-10μm broad and 8-12 (-20)μm long; chloroplasts several per cell, discoid or ribbon-shape; hairs absent.

Spermatangial filaments born in tufts on superficial plate of basal discs branching dichotomously; spermatangia terminal on spermatangial filaments, solitary or in pairs, ellipsoid to globose, 5-7μm in diameter; carpogonia unknown; tetrasporangia produced in groups on superficial plate of basal discs, sessile or with one-celled stalk, cruciately divided, 15-16μm broad and 17-20 (-24)μm long.

Type locality: Between Sprogoe and Corseor, Denmark.

Lectotype: Original illustration (MAGNUS 1874, pl. 2, fig. 8. cf. DIXON & IRVINE 1977, p. 101).

Material examined: On hydroids at Oshoro 9 May 1978; at Nemuro 5 Sept. 1978 (leg. S. C. LINDSTROM).

MORPHOLOGICAL FEATURE

Field-collected material

The hydroids bearing the plants of *Rhodochorton membranaceum* were cast ashore at Nemuro, while those attached to the thallus of *Gelidium* sp. at Oshoro. The basal creeping filaments are confluent with branches and form a monostromatically layered expansion on and in the chitinous perisarc of hydroids. The cells of basal creeping filament are

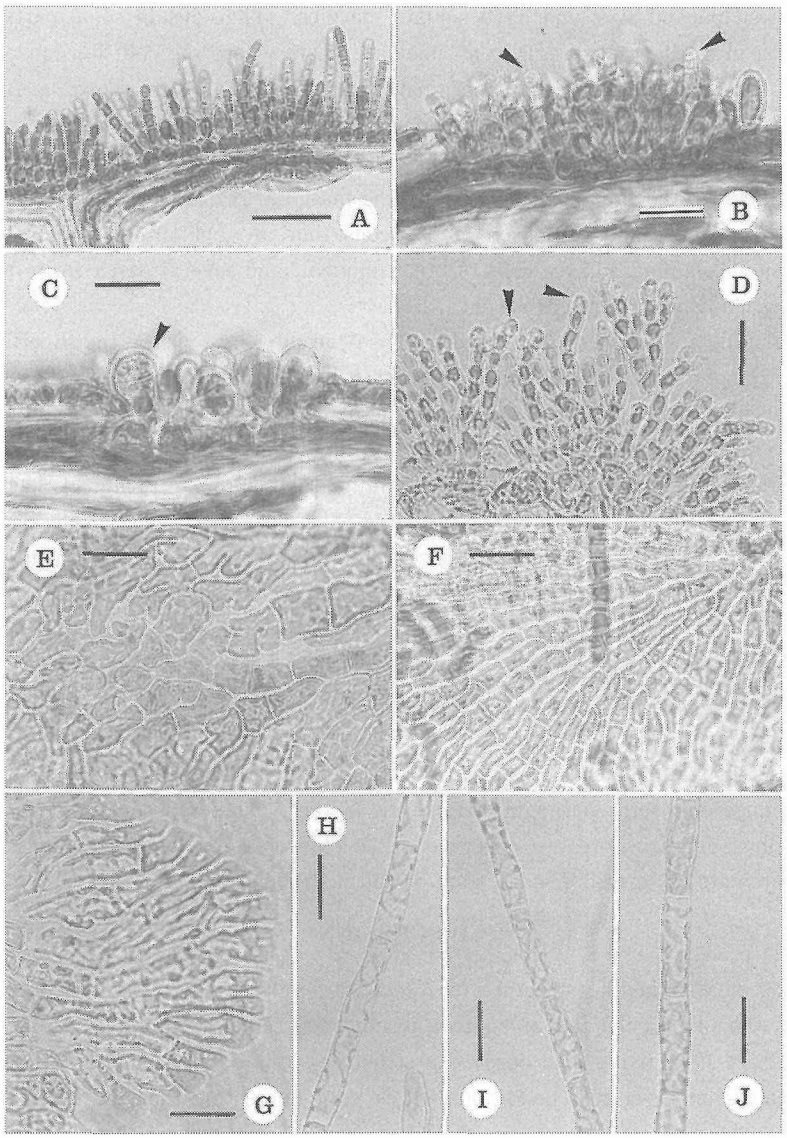

Fig. 14. *Rhodochorton membranaceum*. A: Habit on the perisarc of hydroids. Note multi layers of the basal system in the perisarc. B: Spermatangial cluster born on the superficial layer of basal system. Note the spermatangium (arrow heads). C: Tetrasporangia born on the superficial layer of basal system. Note the tetrasporangium (arrow head). D: Spermatangial branches bearing a spermatangium (arrow heads) terminally. E: The cells of basal system having an irregularly folded cell wall. F: Sinuate form cells of basal system having an wave margin. G: A margin of basal system. H, I, J: Chloroplasts in the cells of erect filament in culture. (Scale bar of Fig. A is 50μm. Scale bars of Figs B–J are 20μm.)

various in shape and size, and have sinuate margins. The cells in some parts of basal disc have a inwardly folded wall in an uncinate form, where the cell division occur (see MAGNUS 1847, pl. II, fig. 8). The marginal region of basal disc shows a fan-shaped expansion. Occasionally the marginal region of basal disc issues erect filaments or reproductive structures such as spermatangial branches or tetrasporangia. Erect filaments arise in groups on the superficial layer or on the marginal region of basal disc. The erect filaments are simple and composed of 3-6 cells that are cylindrical. Chloroplasts are parietal, single, laminate in the cells of erect filament, and several patch-form in the cells of creeping filament. Hairs are absent.

Spermatangial branches are formed in dense caespitose groups on the superficial layer or the marginal region of basal disc. Occasionally the spermatangial branches are formed on the immersed layer of basal disc at the place exposed by the crevices of chitinous perisarc. The spermatangial branches diverge dichotomously. The cells of spermatangial branch are fusiform to cylindrical, ca. 5μm broad and 7-8μm long. Spermatangia are terminal, solitary or in pairs on the apical cell of spermatangial branch. Carpogonia are unknown. Tetrasporangia are produced directly on the cells of the superficial layer of basal disc or on the immersed layer at the crevices of the chitinous perisarc.

Cultured material

The erect filaments of the plants collected at Oshoro were used for the unialgal culture experiments. The basal creeping filaments develop from the erect filaments do not form a pseudoparenchymatous basal disc, but adhere loosely to glass substrate. The plants produce only tetrasporangia. However, neither sexual reproductive structures nor the germlings of tetraspore are observed. The chloroplast of cultured plants is single, parietal laminate or several discoid, even or spiral, ribbon-shaped.

DISCUSSION

The spermatangia-like structure of *Rhodochorton membranaceum* was previously reported on the plant collected at southeasternmost Greenland (PEDERSEN 1976). WEST (cf. PEDERSEN 1976, p. 17) also obseved a structure similar to spermatangia on the plant of this species under culture conditions. It is very interesting that the spermatangia of this species are produced together with tetrasporangia on the same thallus in nature, but no carpogonium is observed. The spermatangia as well as tetrasporangia on the same thallus were reported in *Rh. spetsbergense* (KJELLMAN) KJELLMAN (ROSENVINGE 1923-1924) and *Rh. floridulum* (DILLWYN) NÄGELI (KNAGGS 1965a). Some presumable interpretations on the productions of tetrasporangia and spermatangia on the same thallus in this species can be summarized as follows: (1) The plants bearing spermatangia and tetrasporangia may be the male gametophyte recycling by apomeiotic tetrasporangia like *Rh. concrescens* DREW (WEST 1970a). (2) The plants produce carpogonia somewhat ear-

lier than the production of spermatangia, and then appear in bearing spermatangia together with carpotetrasporangia resulted from fertilized carpogonia as does in *Rh. subimmersum* SETCHELL et GARDNER (LEE & KUROGI 1978). (3) The plants produce both carpogonia and spermatangia simultaneously. But, the carpogonia are overlooked owing that their morphology is a certain form hitherto unknown.

Rhodochorton purpureum (LIGHTFOOT) ROSENVINGE 1900, p. 75.

(Text Figs 15, 16)

Basionym: *Byssus purpurea* LIGHTFOOT 1777, p. 1000.

Synonyms: *Conferva purpurea* (LIGHTFOOT) DILLWYN 1802-1809, pl. 40.
Trentepohlia purpurea (LIGHTFOOT) C. AGARDH 1824, p. 36.
Callithamnion purpureum (LIGHTFOOT) HARVEY 1841, p. 116.
Audouinella purpurea (LIGHTFOOT) WOELKERLING 1973, p. 536.
Conferva violacea ROTH 1797, p. 190.
Conferva rothii TURTON in DILLWYN 1802-1809, p. 73.
Callithamnion rothii (TURTON) LYNGBYE 1819, p. 129.
Ceramium rothii (TURTON) C. AGARDH 1824, p. 133.
Trentepohlia rothii (TURTON) PRINGSHEIM 1862, p. 30.
Rhodochorton rothii (TURTON) NÄGELI 1861, p. 356
Thamnidium rothii (TURTON) THURET in LE JOLIS 1863, p. 111.

Plants saxicolous, caespitose, forming velvety expansions, composed of basal creeping filaments and erect filaments, 1.5-7 mm high; creeping filaments tortuous, entangled, forming more or less massive basal systems, occasionally confluent together, showing pseudoparenchymatous structures; cells of creeping filament tortuously cylindrical or various in shape, 6-25μm broad and 17-60μm long; erect filaments rather rigid, slightly tapering toward apices, branching at acute angles; cells of erect filament cylindrical with somewhat thick walls, 15-45μm broad and 10-75μm long; hairs absent; chloroplasts several, laminate or discoid; tetrasporangia born in clusters on apical region of erect system, globose to obovoid, 8-20μm broad and 17-28μm long; other reproductive structures not found in nature.

Type locality: Ruined Abbey, Island of Iona, Scotland.

Type: ? (cf. DIXON 1959, CONWAY & KNAGGS 1966).

Distribution: Cosmopolitan.

Material examined: On rocks at Daikokuzima, Akkeshi 2 July 1977; at Bentenzima, Nemuro 2 June 1977; at Nirasu, Muroran 9 June 1978; at Oshoro 9 May 1978.

Rhodochorton purpureum is variable in morphology and habit according to locality and habitat. All the plants in both nature and culture are described separately on the

basis of localities.

NEMURO STRAIN : The plants occur in the intertidal zone of Bentenzima, Nemuro. The plants attach to a rock substrate with loosely entangled creeping filaments. Occasionally some basal creeping filaments develop upwards among erect filaments. The cells of creeping filament are contorted, 15-25μm broad and 30-45μm long. Rhizoids are, unlike the creeping filaments, free from the basal structure, gradually tapering toward apex, and occasionally forming branches in uncinate mode. The rhizoids are also distinguished from the branches of erect filament in the development at various angles and the flexuous profile. The rhizoids are also issued from branches and erect filaments under culture conditions. The erect filaments are more or less rigid, straight, branching irregularly, and issuing rhizoids plentifully along the whole length. Occasionally, the apical part of some erect filaments is morphologically transformed into a rhizoid. Thus the erect system is crowded with entanglement of erect filaments, branches, rhizoids, basal creeping filaments developing upwards and the fragments of erect filaments. The cells of erect filament are cylindrical, 11-15μm wide and 30-75μm long.

Neither tetrasporangia nor sexual reproductive structures are observed in both nature and culture. LEE (1985) described probable ways of vegetative reproduction in this strain.

AKKESHI STRAIN : The plants occur on rocks, forming a broad velvety expansion in the supralittoral zone of Daikokuzima, Akkeshi. The plants are caespitose, 1-1.2mm high. The basal creeping filaments are entangled together and forming a massive basal plate that is ca. 200μm thick. Some creeping filaments under culture condition are free from the basal plate without attaching to substrate and produce tetrasporangia on short laterals.

The plants in nature produce no reproductive structures. However, tetrasporangia are produced luxuriantly on the apical region of erect filament and on the short laterals of free creeping filaments. Most of the tetrasporangia contain binary partitions showing the stage after the first division of the sporangium. In rare case, a sporangium divide in unequally zonate mode. No plants bearing sexual reproductive structures are observed in both nature and culture.

MURORAN STRAIN : The plants grow on rocks, forming a broad velvety expansion in the intertidal zone of Nirasu, Muroran. The creeping filaments are tortuous or contorted, tightly entangled or confluent together and forming a thick, massive basal disc. Occasionally, some creeping filaments develop upward and produce tetrasporangia on short laterals. Such creeping filaments deviated from the basal disc also appear under culture conditions. The erect filaments are somewhat flexuous, issuing long branches at

the middle region.

Tetrasporangia are born in clusters on the apical region of erect filament. Occasionally, some sporangia are born on short erect filaments or one-to three-celled laterals of the creeping filaments being free from basal discs. Several aberrant sporangia including two or four globular bodies are observed. A germinating spore presumed to be the tetraspore of the plant is observed in nature. Regeneration occurs frequently in empty or abortive sporangia or even in the stumps of sporangium. Under culture conditions the tetraspores from the plants derived the fragments of field material develop into gametophytes. The gametophytes frequently issue rhizoids from the lowermost cells of the branches of erect filament. The rhizoids are composed of flexuously cylindrical cells morphologically similar to the creeping filaments of germlings.

The description of the gametophyte and reproductive structures has been given by LEE (1985). Spermatangia are born in spherical to hemispherical clusters on the upper part of branch, solitary to ternate on the distal part of stalk cell, obovoid to ellipsoid, ca 5μm broad and 7μm long. The spermatangial branches develop on erect filaments, creeping filaments or even on a persistent germinating spore. Carpogonia are born on the cells of a creeping filament, an erect filament or on a persistent germinating spore, longish fusiform, 6-7μm broad and 30-40μm long. Trichogynes are about 300μm long and scarcely constricted at junction of a carpogonium. The tetrasporangia on gametophytes are ellipsoid to obovoid, cruciately or decusately divided, 15-17μm broad and 22-28μm long. Fertilized carpogonia are elongated distally, somewhat inflated, divided by transverse walls twice to four times, composed of 3-5 cells, longish clavate, 16-24μm broad and 135-170μm long. The terminal cell of the longish clavate filament (gonimoblast filament?) is abruptly attenuated at its distal end, from which a thin filament, 8-11μm wide, develops. Occasionally, such thin filaments develop laterally from the intercalary cell of the longish clavate filament. The longish clavate filament issues rhizoids from its proximal end. The rhizoids are rather thick, tortuous, composed or cylindrical or uncinate cells that are 8-10μm broad and 35-50μm long.

OSHORO 1 STRAIN : The plants grow on rocks of the wall of a small cave forming a broad velvety expansion in the supralittoral zone. The erect filaments are up to 1mm high, more or less rigid, 5-10μm broad, branching alternately or secundly at middle to upper region. Tetrasporangia are born on short branches at the middle to upper region of erect filaments in nature.

All the plants derived from the fragments of the field material in culture produce tetrasporangia. Under culture conditions tetrasporangia are produced plentifully on the apical parts of erect filaments. However, no plant bearing sexual reproductive structures are observed.

Table 2 Comparison of the strains of *Rhodochorton purpureum* in Hokkaido on the basis of dimensions of some characters.

Strains		Cells of creeping filament (μm)		Cells of erect filament (μm)		Tetrasporangium (μm)	
		Breadth	Length	Breadth	Length	Breadth	Length
Field	Nemuro	15-25	30-45	11-15	30-75	-	-
	Oshoro II	15-20	25-35	14-17	14-30	17-20	25-28
	Akkeshi	11-14	17-37	10-12	15-22	-	-
	Muroran	10-17	50-60	11-20	22-37	19-20	22-26
	Oshoro I	6-11	20-25	5-10	13-35	8-11	17-20
Culture	Nemuro	6-13	38-52	10-13	30-50	-	-
	Muroran (T)	8-10	35-50	11-15	21-58	19-21	26-28
	Oshoro II (T)	14-18	20-35	9-16	17-31	17-21	25-33
	Oshoro II (G)	7-9	40-50	7-10	29-50	11-17	25-30
	Akkeshi	5-10	38-48	7-12	20-40	13-14	24-25
	Muroran (G)	5-10	17-46	8-13	16-30	15-17	22-28
	Oshoro I	?	?	7-10	31-53	12-13	17-21

OSHORO 2 STRAIN: The plants grow together with OSHORO 1 STRAIN. The erect filaments are 2.5-2.7mm high, more or less rigid, 14-17μm broad, branching dichotomously or subdichotomously at the apical region. Tetrasporangia are born in clusters, usually on the apical region of erect filaments. Regeneration occurs frequently in the stump of sporangia.

The plants derived from the fragments of field material in culture produce tetrasporangia plentifully. The plants derived from the germination of tetraspores are distinguished into three types on the basis of the morphology of erect filaments; Type-1) erect filaments long and bearing few branches, Type-2) erect filaments short and simple, and Type-3) erect filaments short and bearing numerous branches. The plants of Type-1 and Type-2 are usually sterile and show the morphology similar to the plants of OSHORO 1 STRAIN in culture. In rare case, spermatangia are produced in small clusters on the apical parts of the erect filament of Type-2. The plants of Type-3 bear tetrasporangia plentifully. However, most of the tetrasporangia but a few aberrant sporangia are abortive before or after the first division. The aberrant sporangia are round in shape and occasionally showing in situ germination.

Fig. 15. *Rhodochorton purpureum*. A: Thallus of Muroran strain. B: Thallus of Oshoro 1 strain. (Scale bar of Fig. A is 1mm. Scale bar of Fig. B is 200μm.)

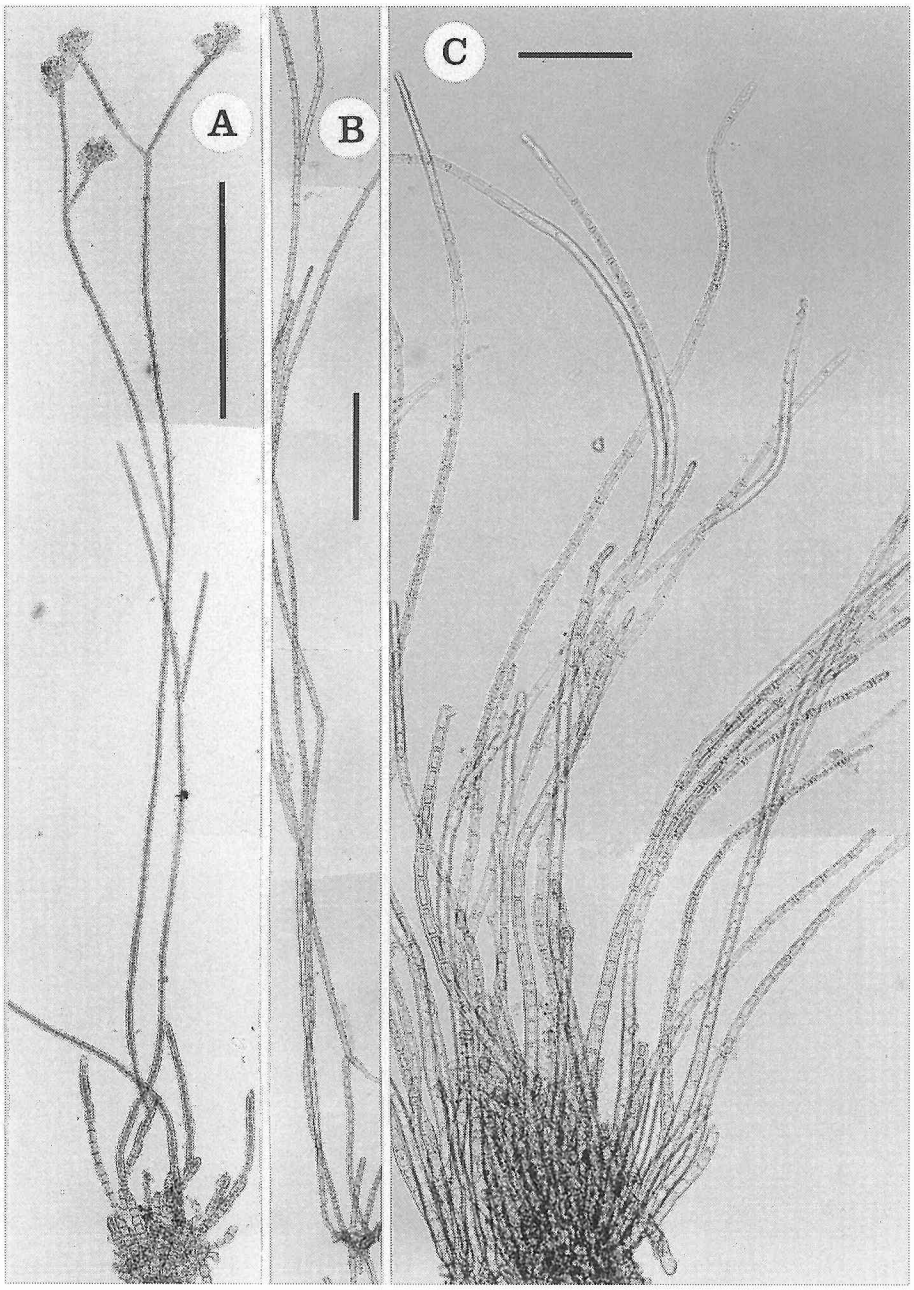

Fig. 16. *Rhodochorton purpureum*. A: Thallus of Oshoro 2 strain. B: Thallus of Nemuro strain. C: Thallus of Akkeshi strain. (Scale bar of Fig. A is 500μm. Scale bar of Fig. B is 300μm. Scale bar of Fig. C is 100μm.)

DISCUSSION

KNAGGS (1965b, 1966a, 1966c) reported that the thallus of *Rhodochorton purpureum* was very polymorphic. Other characteristics of *Rh. purpureum*, such as the formation of sporangia and the spore germination, were also known variable according to environmental conditions (KLAVESTAD 1957, KNAGGS 1966b, CONWAY & KNAGGS 1966, WEST 1969, 1972, 1974). The plants of *Rh. purpureum* in Hokkaido showed a great variation in morphology and multiplication according to habitats.

It was regarded that *Rhodochorton purpureum* probably propagated itself by means of fragmentation of its thallus (KNAGGS 1966c, WEST 1974, PEARLMUTTER & VADAS 1978). Thus, the vegetative propagation by means of fragmentation of thallus has been used for unialgal culture studies of this species (KNAGGS 1966c, 1968, WEST 1969, 1970b, 1972, PEARLMUTTER & VADAS 1978, STEGENGA 1978 etc.). PEARLMUTTER & VADAS (1978) suggested with the results of culture experiments that the propagation of *Rh. purpureum* might be effected by thallus fragmentation in intertidal habitats. LEE (1985) suggested the possible modes of propagation by means of thallus fragmentation in *Rh. purpureum*, supporting the suggestion of PEARLMUTTER & VADAS (1978).

CONWAY & KNAGGS (1966) reported that the first division of the tetrasporangium of *Rhodochorton purpureum* was meiotic. However, WEST (1970a) reported that the tetrasporangia of *Rh. concrescens* DREW were produced mitotically. Tetrasporangia were produced together with male or female reproductive structures on the male and female gametophytes of Muroran strain, although most of them were abortive. It must be an important fact that tetrasporangia are born on the gametophytes of *Rh. purpureum*, although the fate of the tetraspore is unknown yet. STEGENGA (1978) thought the tetrasporangium on a female gametophyte as a "functionless" structure. However, it is possible that the tetrasporangia born on gametophytes of *Rh. purpureum* are produced mitotically and have a role of self-duplication of the gametophytes as the function of the monosporangia produced by the species of *Audouinella* and *Acrochaetium*. It must be cytological interests whether the formation of tetrasporangium on gametophytes is mitotic or meiotic as well as whether or not mitotic tetrasporangia on tetrasporophytes of *Rh. purpureum* are produced together with meiotic tetrasporangia.

As a tetrasporophyte resulted from a fertilized carpogonium grows up and issues rhizoids on the female gametophyte, the latter plant gives its place to the former plant, i. e., the gametophyte is difficult to be recognized by a well grown bunch of the tetrasporophyte in culture. On the other hand, a male gametophyte continues to grow up as being an independent plant in culture. Consequently, it is postulated that the thallus of male gametophyte may grow up and lose the ability to produce spermatangia due to ages or some environmental factors in nature. Thus, it is suggested that the male gametophyte of *Rh. purpureum* may be easy to overlooked by tetrasporophytes because of bearing

mitotic tetrasporangia but spermatangia.

Rhodochorton subimmersum SETCHELL et GARDNER 1903, p. 347. pl. 17.

Synonyms: *Acrochaetium subimmersum* (SETCEHLL et GARDNER) PAPENFUSS 1945, p. 318.

Audouienlla subimmersa (SETCHELL et GARDNER) GARBARY et RUENESS 1980, p. 22

Plants partially endophytic, composed of endophytic filaments immersed in host tissues and erect filaments protruding on host surface; endophytic filaments developing in cortical layers of host; cells of endophytic filament tortuously cylindrical with thin wall, 3-6μm broad and 20-60μm long; erect filaments usually simple composed of 2-10 cells, 10-50μm long, slightly tapering toward apex; cells of erect filaments cylindrical to barrel-shaped, 3-6μm broad and 4-7μm long; chloroplasts single parietal laminate without pyrenoids; hairs absent; monoecious; spermatangia lateral on the cells of surface creeping endophytic filaments or terminal on erect filaments, solitary, globose, 3-4μm in diameter; carpogonia lateral on the cells of surface creeping filaments or terminal on one-or two-celled erect filaments, flask to conical in shape, 3-4μm broad and 5-10μm long; trichogynes terminal, slightly constricted at junctions, 2-3μm broad and to 16μm long; fertilized carpogonia divided by transverse walls once to several times, developing into simple or branched gonimoblast filaments with terminal or lateral tetrasporangia; cells of gonimoblast filaments oblong to cylindrical, 5-6μm broad and 3-6μm long; tetrasporangia obovoid to ellipsoid, cruciately divided, 10-12μm broad and 15-19μm long.

Type locality: Whidbey Island, Washington.

Type: UC no. 96094 (GARDNER, no. 289!, cf. DREW 1928).

Hosts: *Grateloupia filicina* (LAMOUROUX) C. AGARDH, *Gr. turuturu* YAMADA.

The morphology and life history of this species was described by LEE & KUROGI (1978) and LEE (1987).

General Discussion

GENERAL FEATURE

Host specificity

The plants of the Acrochaetiaceae in Hokkaido are epiphytic (*Acrochaetium alariae, Acr. densa, Acr. catenulata, Acr. strictum, Acr. sessile, Acr. humilis, and Audouinella plumosa*), epi- and partially endophytic (*Aud. daviesii*), partially endophytic (*Aud. japon-*

ica, Acr. kurogii, Aud. rhizoidea, and *Rhodochorton subimmersum*), partially endozoic (*Rh. membranaceum*), and lithophytic (*Rh. purpureum*). The plants of *Aud. daviesii* develop no endophytic filaments on brown algal hosts, but some parts of basal filaments of the plants penetrate into the cortical layer of *Hyalosiphonia caespitosa* in culture as well as in nature. Thus, the term "partially endophytic" means that the basal filaments are immersed in host tissues and the erect filaments issue out of the host thallus. Although most epiphytic forms examined in this study have no any host specificity, the gametophytic plants of *Acr. alariae* occur only on the thallus surface of *Alaria crassifolia* in nature whereas the tetrasporophytic plants of the species occur on various algae, such as *Alaria crassifolia, Sargassum thunbergii* and *Chondrus yendoi*. However, it does not indicate the host specificity of the gametophytic plants of *Acr. alariae* since the plants grow on a glass substrate under culture conditions. *Rh. subimmersum* is partially endophytic in *Grateloupia filicina* and *Gr. turuturu*. The plants of *Rh. subimmersum* show neither vegetative growth nor spore germination under host-free culture conditions. Consequently, it may be suggested that *Rh. subimmersum* has some obligate relationship with the hosts.

ROSENVINGE (1909, p. 82) suggested that several endophytic species might have rather specific host requirement. Many authors laid stress on host specificity to circumscribe species of audouinelloid algae (e. g., DAWSON 1953, TAYLOR 1960, DIXON & IRVINE 1977). However, most epiphytic forms of audouinelloid algae have been known to grow on more than one kind of host, e. g., *Acrochaetium robustum* BØRGESEN epiphytic on *Sargassum vulgare* (India, BØRGESEN 1915), on *Turbinaria ornata* (Japan, NAKAMURA 1941), on *Sargassum* sp. (Hong Kong, TSENG 1945; Vietnam, DAWSON 1954), on *Gracilaria foliifera* (Virginia, USA, AZIZ 1965), and on *Sargassum thunbergii* (Korea, LEE & KIM 1977). Even several endophytic forms have been also known to grow in various hosts according to localities, e. g., *Acr. nemalionis* (DE NOTARIS) BORNET endophytic in *Nemalion multifidum* (Denmark, ROSENVINGE 1909), in *Liagora farinosa* (Canary Islands, BØRGESEN 1927), and in *Tamaris* sp. (British Isles, DIXON & IRVINE 1977). Moreover, recent culture studies of audouinelloid algae revealed indirectly that most species had no host-specificity because they grew on glass substrates. WOELKERLING (1971, p. 11) wrote that "…… taxonomic limits based on host specificity are probably arbitrary and unrealistic". It would be best not to set importance excessively to host specificity for species determination.

Spore germination and basal system

The plants of audouinelloid algae except *Rhodochorton subimmersum* can grow on glass substrates under culture conditions. When the monospores of *Acrochaetium alariae* (tetrasporophyte), *Acr. densum, Audouinella plumosa, and Acr. sessile* (tetrasporophyte) germinate on glass substrates, they usually divide into two equal-sized cells which become the initials of creeping filaments. Such creeping filaments attach to the substrates rather

tightly with confluent branches and result in a monostromatic basal disc. The component cells of the basal disc give rise to erect filaments. The germinating monospores of *Acr. humile* divide into more than two cells. The plants of *Aud. plumosa* have a more expansion of basal system than that of erect system under 10°C short-day culture conditions.

The germinating monospores of *Audouinella daviesii, Aud. rhizoidea* and *Aud. simplex* issue a germ tube without previous division. When the spores issue a germ tube, they are either persistent with cell contents or nonpersistent with empty spore wall. The germ tube becomes an initial of creeping filaments. The creeping filaments resulting from the germ tube expand without adhering to glass substrates and issue branches which are not confluent but entangled together. The creeping filaments of *Aud. rhizoidea* penetrate into an agar substrate at the beginning of spore germination and are scarcely entangled together. When the carpospores of *Acrochaetium alariae* germinate, they divide into two equal-sized cells as the same mode of germination as that of the monospores of tetrasporangial plants.

The germinating monospores of *Acrochaetium alariae* (G), *Acr. sessile* (G), and *Acr. catenulatum* are persistent and give rise to one to three erect filaments directly without producing any accessory cells for the basal system. Thus, the plants derived from the monospores have a single-celled base. The tetraspore of *Acr. alariae* germinates in the same mode as the germination of the monospores of gametophytic plants. The monospores of *Acr. alariae* (T), *Acr. densum, Acr. humile, Audouinella plumosa*, and *Acr. sessile* (T) show neither the mode of germination of the monospores in *Aud. daviesii, Aud. simplex*, and *Aud. rhizoideae*, nor that in *Acr. alariae* (G), *Acr. catenulatum*, and *Acr. sessile* (G), and vice versa. Consequently, the mode of spore germination and the morphology of resultant basal system are to be species constant (sensu lato).

Audouinelloid algae may fall into four groups based on the mode of spore germination and the morphology of basal system as follows: 1) Both gametophytic and tetrasporophytic plants have a multicellular base derived from an aseptate and persistent or nonpersistent spore, e. g., *Audouinella asparagopsidis* (MAGNE 1977), *Aud. botryocarpa* (WOELKERLING 1970), *Aud. dasyae* (STEGENGA & BORSJE 1976), *Aud. daviesii* (WOELKERLING 1971, 1973), *Aud. efflorescens* (ROSENVINGE 1909, KYLIN 1906), *Aud. hermanni* (DREW 1935 as *Rhodochorton violaceum*, ISRAELSON 1942), *Aud. investiens* (SWALE & BELCHER 1963), *Aud. thuretii* (KYLIN 1907, WOELKERLING 1971), and *Aud. dotyi* (ABBOTT 1962). 2) Tetrasporophytic plants have a multicellular base derived from the septate germination of spore, and gametophytic plants have a unicellular base, e. g., *Acrochaetium alariae* (LEE & KUROGI 1983), *Acr. densum* (STEGENGA & VROMAN 1976), *Acr. hallandicum* (STEGENGA & BORSJE 1977), *Acr. collopodum* (STEGENGA & MULDER 1979), *Acr. moniliforme* (STEGENGA & MULDER 1979), *Acr. sessile* (in this study), and *Acr. virgatulum* (BORSJE 1973). 3) Both gametophytic and tetrasporophytic plants have

a unicellular base. SCHIFFNER (1931) reported tetrasporangia on the thallus of *Acr. microscopicum* from Adriatic Sea. However, AZIZ (1965) and WOELKERLING (1972) opposed to the SCHIFFNER's report after observations of many collections of the species. STEGENGA & MULDER (1979) revealed *Acr. microscopicum* to be a gametangial phase vs. the tetrasporophytic phase having a multicellular base. It may be interested curiously in examining the SCHIFFNER'S plant and its gametophytic phase. No example for this mode is known. 4) Tetrasporangial plants have a unicellular base, and gametangial ones have a multicellular base. No example for this mode is also known.

Several species do not fit completely to the mode of spore germination and the morphology of basal system. Although the mode of spore germination in *Audouinella liagoraе* was described by ABBOTT (1962) and WOELKERLING (1971), it was unclear to which phase the plants were referred. Moreover, the mode of spore germination differed in descriptions between the two authors such as "septate" or "aseptate." The basal system of the tetrasporophytic plants of *Aud. pectinata* is formed by the aseptate germination of spore, and adheres to a glass substrate tightly showing a monostromatic basal disc (WEST 1968). The tetrasporangial plant of *Kylinia rosulata* was known to have a multicellular base, but no information on the mode of spore germination for its basal system was given (BOILLOT & MAGNE 1973). *Acrochaetium affine* (HOWE & HOYT 1916) and *Acr. opetigenum* (BØRGESEN 1915) have a unicellular base which occasionally issues one or more accessory cells or short creeping filaments. *Aud. australis* usually has a unicellular base and occasionally a multicellular base derived from the septate germination of spore (WOELKERLING 1971). *Acr. robustum* usually has a several-celled base and occasionally a unicellular base (NAKAMURA 1941). The tetrasporophytic plants of *Rhodochorton purpureum, Rh. subimmersum*, and *Rh. floridulum* are not derived from free carpospores but from fertilized carpogonia directly. Consequently, our knowledge of the mode of spore germination and the basal system morphology is still insufficient to allow the characters to be used for generic criteria of the Acrochaetiaceae. LEVRING (1953) regarded that it was artificial and unfeasible to use the structure of basal system for generic circumscription of the Acrochaetiaceae. WOELKERLING (1971) had an opinion that basal system morphology was to be untrustworthy as a systematic criterion.

Many authors have attached basal system morphology and the mode of spore germination to systematic importance in the Acrochaetiaceae since BORNET (1904, p. XVIII). CHEMIN (1937) proposed that the Acrochaetiaceae should be raised to ordinal status on the basis of the mode of spore germination. KYLIN (1944, 1956) and STEGENGA (1979) adopted the morphology of basal system and the mode of spore germination as generic criteria in the Acrochaetiaceae. However, the morphology of basal system has been known to be variable according to substrates, e. g., *Rhodochorton concrescens* (WEST 1970a), *Audouinella botryocarpa* (WOELKERLING 1970, 1971), *Aud. daviesii* (BORSJE 1973, in this study), and *Acrochaetium densum* (STEGENGA & VROMAN 1976). PAPENFUSS

(1947, p. 434) expressed that "…… the basal structure must be suspected of being, at least in some degree, adaptive to the substratum." WOELKERLING (1971) emphasized that the mode of spore germination and the morphology of basal system were not reliable for specific criteria.

Erect system

Erect filaments: The term "erect filament" is used in this paper for the filament arising from the basal system no matter whether the filament develops vertically or horizontally. The erect filaments of *Audouinella daviesii, Aud. rhizoidea* and *Rhodochorton purpureum* show a tendency toward unlimited growth under culture conditions. The erect filaments produce no hairs under the all culture conditions examined and even in unrefreshed medium for a long time or in nitrate-free medium. However, hairs are produced on short branchlets terminally in the field-collected plants of *Aud. daviesii*. The erect filaments of *Acrochaetium alariae* (G), *Acr. catenulatum, Acr densum, Acr. humile, Acr. sessile*, and *Aud. plumosa* show a limited growth by means of terminating in hairs or reproductive structures under the culture conditions. The plants having a unicellular base develop erect filaments in decumbent, oblique, or horizontal way as well as upright way, e. g., *Aud. baltica* (ROSENVINGE 1909, as *Chantransia baltica*), *Aud. kylinii* (ROSENVINGE 1909, as *Kylinia rosulata*), *Acr. trifilum* (BUFFHAM 1892), and *Acr. scapae* (LEE 1987). The erect filaments of *Acr. alariae* (G), *Acr. catenulatum*, and *Acr. sessile* (G) appear in upright, oblique or occasionally horizontal way under the culture conditions. *Acr. kurogii* is characteristic in having a horizontal development of erect filament on host surface (LEE & LINDSTROM 1979).

HAMEL (1927, 1928a) paid attention to the number of erect filament arising from a unicellular base for distinguishing some relevant taxa. On the other hand, WOELKERLING (1972) recorded some variation in the number of erect filament of *Acrochaetium microscopicum*. The number of erect filament in Hokkaido plants is (1-) 2-3 (-4) in *Acr. alariae*, 1-3 in *Acr. catenulatum*, 4-6 in *Acr. kurogii*, 2-3 *Acr. strictum* (G), and 1-2 in *Acr. sessile*. Consequently, it is also suggested that the number of erect filament arising from a unicellular base may be species specific.

Branches: In the Acrochaetiaceae branches are of subordinate filaments derived from erect filaments. There is also no morphological difference between the component cells of a branch and those of an erect filament. All the taxa examined in this study, except *Audouinella japoncia*, have branches born secundly, pinnately, alternately, oppositely, or irregularly on erect filaments. The branching pattern in most species shows a mixed mode of secund, alternate and irregular. The erect filaments of *Rhodochorton subimmersum* and *Rh. membranaceum* are simple. *Aud. daviesii* and *Aud. rhizoidea* have numerous short and long branches at rather acute angles. The long one of them elongates and reaches to the same level as the apex of the erect filament. On the other hand, the short

one has a limited growth and generally terminates in hairs or sporangia. The branch of *Acrochaetium kurogii* are born oppositely on erect filaments and develops on a plane parallel the host surface. All the branches are terminated in reproductive structures. In *Acr. catenulatum* and the gametophyte of *Acr. sessile*, erect filaments give rise to short branches in secund series and become arcuate on the opposite side of the branches.

Many authors used the degree of branching and the branching pattern as taxonomic criteria (e. g., COLLINS 1906, ABBOTT & HOLLENBERG 1976, DIXON & IRVINE 1977, etc.). STEGENGA & BORSJE (1976) discovered through the culture study of *Acrochaetium dasyae* that the degree of branching varied in response to light intensity and temperature and that branching pattern was independent of either factor and was always secund.

Cells: In Hokkaido plants, the cells of erect filament are cylindrical, barrel-shaped or fusiform. The cells of erect filament in *Acrochaetium catenulatum* and *Audouinella rhizoidea* are hardly modified in shape when they support branches or reproductive structures. In *Aud. daviesii, Acr. densum, Acr. strictum, Aud. plumosa, Rhodochorton membranaceum, Rh. purpureum*, and *Rh. subimmersum* the cells bearing branches slightly protrude toward the portion abutting the branches. On the other hand, the cells of erect filament in *Acr. alariae, Acr. humile*, and *Acr. kurogii* are slightly concaved at the portion abutting branches. The cells abutting on a monosporangium in *Aud. simplex* and *Acr. sessile* are deeply concaved.

The dimensions of cell have been used as one of taxonomic criteria in the Acrochaetiaceae. According to STEGENGA & BORSJE (1977), the cell width in *Audouinella polyblasta-Aud. hallandica* complex appears as a rather stable character in response to various environmental factors such as daylength, temperature and light intensity. However, it may not have a significance for the dimensions of cell to be used as an absolute criterion for species discrimination, since the range of the cell dimensions shows an interspecific overlapping.

Chloroplasts: *Acrochaetium alariae, Acr. kurogii, Acr. strictum,* and *Acr. sessile* have a single stellate chloroplast with a central pyrenoid. In some cells of the lower plants of *Acr. alariae* the chloroplasts have thin and long arms and show a spiral band form. The chloroplasts of *Acr. catenulatum* and *Acr. densum* in nature are parietal laminate in shape with a central pyrenoid, usually fenestrated at both ends, and appearing in a stellate form. *Audouinella rhizoidea* has various forms of chloroplast, i. e., the cells of erect system have a parietal laminate chloroplast with one or more pyrenoids appearing marginally, while those of basal system have spiral ribbon-shaped chloroplasts with or without pyrenoids as well as parietal laminate ones. In nature the cells of erect filaments of *Rhodochorton membranaceum* and *Rh. purpureum* are full with a chloroplast appearing in

a parietal laminate form. However, numerous discoid chloroplasts occur in some cells of the plants of *Rh. purpureum* in culture. Under culture conditions *Rh. membranaceum* has spiral ribbon-shaped chloroplasts in the cells of the upper half of an erect filament and discoid ones in the cells of the lower half.

Since REINKE (1889) paid attention to the chloroplast morphology of the Acrochaetiaceae, many authors attached the chloroplast morphology to systematic significance (e. g., KUCKUCK 1897, KYLIN 1906, WOELKERLING 1971, DIXON & IRVINE 1977, LEE 1987 etc.). The presence or absence and the number of pyrenoid in a chloroplast have also been used for species discrimination and even a generic criterion. DREW (1928) indicated the difficulty in observation of distinct pyrenoids unless the material was preserved very carefully. WOELKERLING (1971) said that pyrenoids may be found in future to have a generic significance.

Hairs: In Hokkaido the plants of *Acrochaetium catenulatum, Acr. sessile, Acr. strictum, Acr. densum, Audouinella daviesii, Acr. humile, Aud. japonica,* and *Aud. plumosa* produce hairs. The gametophytic plants of *Acr. alariae* generally produce hairs whereas its tetrasporophytic plants do not. Occasionally, a septum-like structure is observed in a hair cell of *Acr. sessile. Aud. daviesii* produces hairs on short branches. The hairs of *Aud. daviesii* appear in a multicellular form owing that the cell abutting on a hair is attenuated as that of the hair.

BERTHOLD (see ROSENVINGE 1911) suggested that hairs play a role in protecting the plants from intense radiation. WEST (1971) said that hairs may serve a role in scattering visible radiation rather than acting as a physical barrier to illumination because of lack of evident pigments in hairs to serve as the agents of light absorption. ROSENVINGE (1911) assumed that hairs take part in absorbing nutrients because of their thin cell wall and their contents consisting of a great deal of cell sap. KYLIN (1917) also concluded through the culture experiments of *Dumontia filiformis* using both nitrate-rich and nitrate-free media that the hairs of the species serve as the structure of nutrient absorption from the environment surrounding the plant. More and longer hairs occur on the tetrasporophytic plants of *Acrochaetium sessile* in nitrate-free medium (ESP-$NaNO_3$) than in normal ESP medium. Hairs also occur plentifully on the gametophytic plants of *Acr. sessile* in the medium circulated by a stirrer. WEST (1971) indicated that it would be a doubtful interpretation that nutrient limitation might stimulate hair formation because the culture medium used in the experiment of *Acr. proskaueri* contained nitrate-nitrogen at a hundred times the quantity found in sea water. An interpretation on hair formation in the Acrochaetiaceae is made that the occurrence of a terminal hair on an erect filament or a branch may interfere with the apical growth of the filament, and consequently serve an indirect role for stimulating the production of branches or reproductive structures laterally.

Reproductive structure

Monosporangia: Monosporangia are generally born terminally or laterally on the cell of erect filaments and branches. The cells abutting on monosporangia in the tetrasporophyte of *Acrochaetium* sessile show a cup-like shape as those in *Audouinella japonica*. However, the cup-like shape of the former disappear after liberation of monospores. The monosporangia of *Aud. daviesii* are born solitarily on a stalk cell which is obtriangular in shape and morphologically distinguishable from other vegetative cells. Concatenate sporangia are produced in *Acr. catenulatum, Acr. densum* and *Aud. plumosa*. The terminal one of concatenate sporangia is released by means of a rupture in the distal portion of the sporangium whereas the intercalary one is released through a rupture in the side of the sporangium. Monosporangia on the gametophyte of *Acr. alariae* show no seasonal variation in width. The arrangement and the shape of monosporangia have been used in species discrimination (BØRGESEN 1915, HAMEL 1927, 1928a, DREW 1928, TAYLOR 1957, 1960, CHAPMAN 1963, WOELKERLING 1971, ABBOTT & HOLLENBERG 1976, LEE 1987).

Tetrasporangia: Tetrasporangia in the Acrochaetiaceae are generally cruciately divided. *Acrochaetium* alariae, *Acr. sessile*, *Audouinella rhizoidea, Rhodochorton purpureum, Rh. membranaceum,* and *Rh. subimmersum* are known to produce tetrasporangia in Hokkaido. Gametophytic generations are derived from tetraspores of *Acr. alariae* and *Acr. sessile* under culture conditions. However, no gametophytic generation appeared during the culture experiments of *Aud. rhizoidea* even though tetrasporangia were produced together with monosporangia on the same plant. WEST (1971) considered that the lack of a gametophyte in *Acr. proskaueri* was due to the loss of its ability to reproduce sexually and it now recycled only through accessory non-sexual sporangia.

Oshoro I and Akkeshi strains of *Rhodochorton purpureum* produced numerous tetrasporangia under 10°C short day culture condition. *Rh. membranaceum* also produced many tetrasporangia under culture conditions. However, the new plants derived from the tetraspores produced no sexual reproductive structures. WEST (1970a) suggested for such case in *Rh. concrescens*, which also repeated the generation bearing only tetrasporangia in culture, that the tetrasporangia might be formed apomeiotically. Both male and female gametophytes of Muroran strain and the male gametophyte of Oshoro II strain of *Rh. purpureum* produce tetrasporangia together with male or female reproductive structures on the same thallus. *Rh. floridulum* was also known to produce tetrasporangia together with carpogonia on the female gametophytes (STEGENGA 1978). Consequently, it is suggested that the species of *Rhodochorton* may produce tetrasporangia apomeiotically by the spores of which the plants are duplicated.

Spermatangia: The spermatangia of *Acrochaetium alariae, Acr. kurogii*, and *Acr.*

strictum are born in pairs laterally at the distal region of a carpogonial stalk cell underneath the trichogyne of the carpogonium. The spermatangia of *Acr. sessile* are born in pairs or solitarily on rather smaller vegetative cells. In *Audouinella japonica*, spermatangia are born in pairs on a few celled branchlet occurring in clusters. In *Rhodochorton subimmersum*, spermatangia are born solitarily on creeping filaments laterally and erect filaments terminally. The spermatangia of *Rh. purpureum* and *Rh. membranaceum* are binate or ternate, lateral or terminal on the cells of spermatangial branch which is usually constructed with somewhat smaller cells. The spermatangial branch issues many lateral branches corymbosely and shows a hemispherical to spherical cluster of spermatangia.

Audouinella rosulata and *Aud. investiens* have a speramtangial branches which are constructed with the cells rather differentiated in morphology. There are several suggestions for generic discrimination on the basis of spermatangia formation and the morphology of spermatangial stalk cells (ROSENVINGE 1909, FELDMANN 1962, MOESTRUP, *et al.* 1975, ABBOTT & HOLLENBERG 1976). LEVRING (1953) and WOELKERLING (1971) indicated that generic segregation based on the presence or absence of "androphore cell" (ROSENVINGE 1909) was unsound.

Carpogonia: The carpogonia of *Acrochaetium alariae, Acr. kurogii*, and *Acr. strictum* are somewhat ovoid in shape with a short papillate trichogyne which is always inserted subterminally in the distal region of the carpogonium. In *Audouinella japonica, Acr. sessile*, and *Rhodochrton subimmersum*, carpogonia are flask-shaped with a rather longer filamentous trichogyne which is slightly constricted at the joining part to the distal end of the carpogonium. The carpogonia of *Rh. purpureum* are fusiform to bottle-shaped with a long trichogyne. FELDMANN (1962) suggested that the Acrochaetiaceae might be raised to ordinal rank on the basis of the lack of carpogonial branch.

Carposporangia: Carposporangia occurred in three species, *Acrochaetium alariae, Acr. kurogii*, and *Acr. strictum* in Hokkaido. The carposporangium is somewhat obpyriform and more or less larger than the monosporangia of gametophyte. In *Acr. alariae* carposporangia are identical with the monosporangia of tetrasporophyte in terms of the dimensions of sporangia and the mode of spore germination. Thus, the relationship of the two kind of sporangia gives a useful tool for detecting gametophytes or tetrasporophytes of a species. Furthermore, the presence of carposporangia in a species suggests the presence of monosporangia in the species and contribute as a main criterion to discrimination of genera in the Acrochaetiaceae.

Carpotetrasporangia: It is known in the species of *Rhodochorton* that a fertilized carpogonium develops into a plant producing tetrasporangia instead of carposporangia. The plant was named as a "carpotetrasporophyte" (BODARD 1971). The spore develops into a plant producing sexual reproductive structures. Therefore, a carposporophytic phase is

reduced in the life history of the species of *Rhodochorton*.

PHENOLOGY

During the period of this study, the growth of 14 species of the Acrochaetiaceae were confirmed in the intertidal and subtidal zones of Hokkaido. *Audouinella plumosa* occurs in January and grows until May, being senescent in June. *Aud. plumosa* produces monosporangia during its entire life. *Acrochaetium densum* occurs in February and grows up until June producing monosporangia luxuriantly in March to May. *Acr. catenulatum* occurs all the year round although it appears in rather different morphology in July to November. *Acr. catenulatum* shows a maximum growth and production of monosporangia in April and May. The life span of *Aud. daviesii* is not confirmed clearly because this species occurs without a homogeneous population on various hosts. *Acr. kurogii* produces sexual reproductive structures and carposporangia in quantities in June and disappears gradually in summer. The tetrasporophyte of *Acr. sessile* produces tetrasporangia as well as monosporangia in nature and culture. *Aud. japonica* occurs in April and May and produces only monosporangia. The gametophyte of *Acr. alariae* produces monosporangia all the year round and shows the maximum production of monosporangia in July and of sexual reproductive structures and carposporangia in October to February. The tetrasporophyte of *Acr. alariae* occurs in December, corresponding with the production of carposporangia in quantities, and produces tetrasporangia in March to May and disappears in June. *Rhodochorton subimmersum* occurs in October to March and produces sexual reproductive structures in November to January, and the consequent production of carpotetrasporangia is made in December to February. The plants of *Rh. subimmersum* are of only creeping filaments in March and then erect filaments develops when carpos-tetrasporangia are produced. *Rh. purpureum* shows a great variation in thallus morphology and spore production according to localities (LEE 1985).

The phenological examinations and culture experiments of them are summerized in Figure 17.

SPECIES EXCLUDED FROM THE ACROCHAETIACEAE

Rhodochorton spetsbergense (KJELLMAN) KJELLMAN (1883) was removed to a new genus *Meiodiscus* in the Rhodophysemataceae by SAUNDERS & MCLACHLAN (1991) on the basis of vegetative fusions between cells of regullary radiating basal filaments, β-phycoerythrin and stalk cells of tetrasporangia. However, this species could be described here because of being examined in this study and known to be new to Japan.

Meiodiscus spetsbergensis **(KJELLMAN) SAUNDERS et MCLACHLAN** 1991. P. 284. f. 1-51. (Text Fig. 18)

Basionym: *Thamnidium spetsbergense* KJELLMAN 1875, p. 31.

Species	Phase	Nature / Month Ja. Fe. Mr. Ap. My. Jn. Jl. Au. Se. Oc. No. De.	Culture
Au. davi.	?	▤▤▤▤▤▤▤▤▤▤▤▤ ▨▨	▤▤
Au. japo.	G	▤▤▤▤	▤♡
Au. plumo.	?	▤▤▤▤▤▤▤▤▤▤▤▤	▤▤
Au. rhizo.	?	▤▤▤▤▤▤▤▤	▤◐
Ac. alari.	G C T	▤♡▤♡▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤♡▤♡▤♡ ▣▣▣▣ ▣▣▣▣▣▣ ▤▤▤▤▤◐▤◐▤◐ ▨▨	▤♡ ▣▣ ▤◐
Ac. caten.	?	▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤▤	▤▤
Ac. dens.	T	▤▤▤▤▤▤▤▤▤▤▤	▤▤
Ac. humi.	?	▤▤	▤▤
Ac. kuro.	G C	▤♡ ▨▨ ▤▣	
Ac. stric.	G C T	▤♡ ▣▣ ▤▤	 ▤▤
Ac. sessile	G T	 ▤▤▤◐▤▤	▤♡ ▤◐
R. memb.	TG	◐◐ ◐♡	◐◐
R. purpur.	G T	 ◐◐◐◐	◐♡ ◐◐
R. subim.	GT	◐♡◐◐▨▨ ▨▨♡♡◐♡	

Fig. 17. Seasonal occurrence of the species of the Rhodochortaceae in Hokkaido during the period from May 1977 to September 1978
▨: sterile plant, ▤: monosporangia, ◐: tetrasporangia, ♡: male and female reproductive structures, ▣: carposporangia, G: gametophyte, T: tetrasporophyte, C: carposporophyte

Synonyms: *Audouinella spetsbergensis* (KJELLMAN) WOELKERLING 1973, p. 585.
Rhodochorton spetsbergense (KJELLMAN) KJELLMAN 1883, p. 187.

Plants epizoic, composed of basal creeping filaments and erect filaments, up to 400μm high; basal creeping filaments confluent together, forming monostrmatic discs; cells of basal creeping filaments usually cylindrical, occasionally having vegetative fusions between cells, 5-8μm broad and 8-16μm long; erect filaments arising in groups from central parts of basal disc, usually simple, straight; cells of erect filament cylindrical, with thick wall (to 2μm), 10-14μm broad and 12-16μm long; chloroplasts single parietal laminate, or several irregular in shape; hairs absent.

Tetrasporangia terminal on erect filament, cruciately divided, globose to obovoid, 17-19μm broad and 22-26μm long.

Type locality: Fairhaven, Spitzbergen, Norway.

Type: UPS (cf. WOELKERLING 1973)

Material examined: On hydroids at Nemuro 5 September 1978.

VEGETATIVE MORPHOLOGY

Field collected material

The basal creeping filaments are confluent together in running parallel and forming a monostromatic expansion. The basal creeping filaments branch dichotomously. The cell of creeping filament issuing a branch is concaved at the part facing tha branch. On the other hand, the most proximal cell of the branch is convexed at the part facing the subtending cell. It is characteristic of this species that a connecting bridge is occasionally formed between cells. The erect filament is composed of cylindrical cells which are usually longer than broad. However, certain cells of erect filament appear as long as broad or shorter than broad. Such cells are always in pairs. It suggests that the erect filaments of this species may elongate by means of intercalary cell division as well as apical growth.

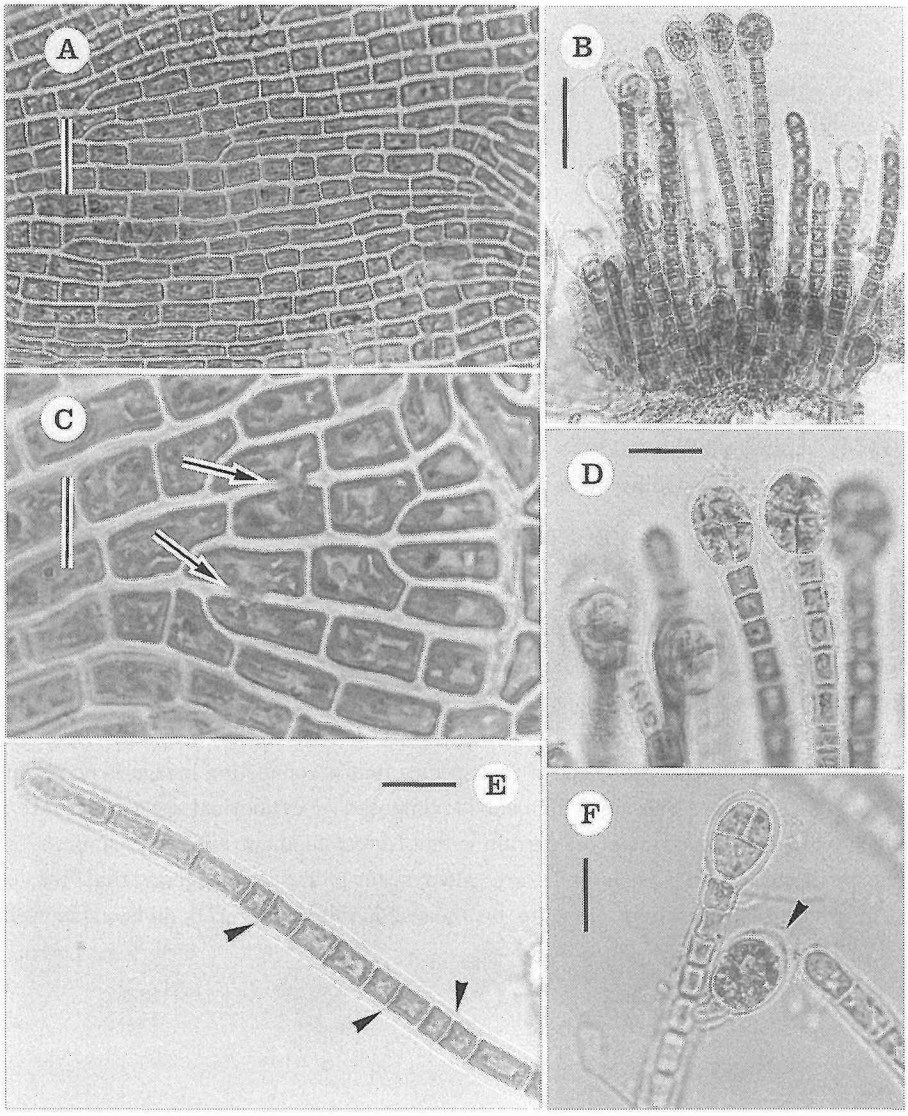

Fig. 18. *Meiodiscus spetsbergensis*. A: Basal system. Note a monostromatic membraneous basal system with cylindrical cells. B: Erect filaments bearing a tetrasporangium terminally. C: Cells of basal system with fusions between neighbors (arrows). D: Tetrasporangia born terminally on erect filaments. E: An erect filament showing an presumable intercalary growth. F: A tetrasporangium born laterally on a single cell stalk. (Scale bars of Figs A, D-F are 20μm. Scale bar of Fig. B is 50μm. Scale bar of Fig. C is 10μm.)

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