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Author(s)	LEE, Yong Pil; KUROGI, Munenao
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**The life history of *Audouinella alariae* (JÓNSSON)  
WOELKERLING (Rhodophyta, Acrochaetiaceae)  
in nature and culture**

**Yong Pil LEE\* and Munenao KUROGI**

Two species of acrochaetioid algae, identified as *Audouinella alariae* (JÓNSSON) WOELKERLING and *Rhodochorton repens* JÓNSSON (= *Acrochaetium jonssonii* PAPENFUSS), were collected from the southern coast of Hokkaido, Japan. They are shown to be the gametophyte and tetrasporophyte respectively in the life history of the same species. Both the plants are heteromorphic in the basal system. The gametophyte is characterized by a unicellular base, and production of spermatangia, carpogonia and monosporangia on the same thallus. The tetrasporophyte has a multicellular filamentous base, and produces tetrasporangia and monosporangia.

The fertilized carpegonium produces a rather simple carposporophyte with a few carposporangia. The mature carposporophyte consists of a central cell and 3-4 carposporangia which are cut off from the former terminally and laterally.

The gametophyte occurs throughout the year, the carposporophyte from October to February, and the tetrasporophyte from December to May.

Recently some species of the Acrochaetiaceae have been shown to have a diplobiontic life history in culture (WEST 1968; BOILLOT and MAGNE 1973; BORSJE 1973 b; STEGENGA and VROMAN 1976; STEGENGA and BORSJE 1976, 1977; STEGENGA and VAN ERP 1979; STEGENGA and MULDER 1979; STEGENGA and VAN WISSEN 1979). BORSJE (1973 a) suggested that some taxa are incorrectly recorded as separate species but are actually the alternate generation of another species. Some phycologists have attempted to search for entities which represent the alternate generation of a particular species by means of a comparative study between field-collected and cultured materials (STEGENGA and VROMAN 1976; STEGENGA and BORSJE 1977; STEGENGA and MULDER 1979; STEGENGA and VAN WISSEN 1979). However, for most *Audouinella* taxa the entities of the alternate generations remain unknown and reproduction by means of other than monospore remains undiscovered.

Since *Audouinella alariae* was first described from Iceland as *Chant-ransia alariae* JÓNSSON (1901), it has gone through combinations with various

\* Present address: Department of Botany, Faculty of Agriculture, Cheju University, Jeju 590, Korea.

genera, with *Acrochaetium* by BORNET (1904), *Rhodochorton* by ARWIDSSON (1936), *Kylinia* by KYLIN (1944), *Chromastrum* by PAPENFUSS (1945), and *Audouinella* by WOELKERLING (1973). In this paper the name *Audouinella alariae* (JÓNSSON) WOELKERLING is used, because *Audouinella* represents the oldest generic name available for this species complex (WOELKERLING 1971), until generic concepts for the Acrochaetiaceae become more comprehensively and appropriately established. *A. alariae* hitherto has been known to produce only monosporangia. In the course of this study it was found that *A. alariae* represented only the gametophytic phase. The tetrasporophytic phase which alternates with *A. alariae* has a multicellular filamentous base and is provisionally identified as *Rhodochorton repens* JÓNSSON (= *Acrochaetium jonssonii* PAPENFUSS, 1945).

### Materials and Methods

Materials used for the present study were collected in the lower intertidal zone at Muroran and Shirikishinai, Hokkaido, Japan (Fig. 1), monthly from May 1977 to July 1978 as follows.

Gametophyte: on *Alaria crassifolia* KJELLMAN at Muroran August 18, September 13, October 13, November 11, December 12, 1977; January 30, February 13, March 15, April 13, May 13, June 9, July 11, 1978.

Tetrasporophyte: on *Laurencia* sp. at Shirikishinai May 5, 1977; on *Alaria crassifolia* at Muroran December 12, 1977; January 30, February 13,

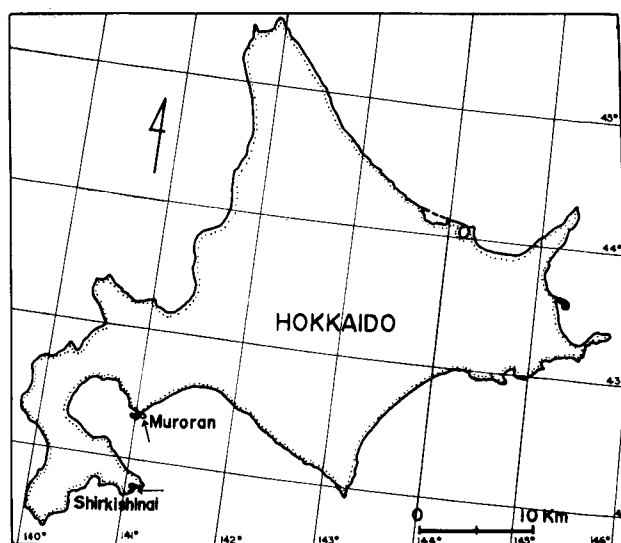


Fig. 1. Map of the Hokkaido showing the localities.

1978; on *Sargassum thunbergii* (MERTENS) O. KUNTZE at Muroran March 15, April 13, May 13, 1978; on *Chondrus yendoii* YAMADA et MIKAMI at Muroran March 15, April 13, May 13, 1978.

For culture experiment, a part of the field-collected material was fragmented after washing of thallus two to three times with sterilized seawater. The fractions of the apical part of erect filament were selected and transferred in culture vessels containing PES medium (PROVASOLI 1968) in freezer incubators illuminated with coolwhite fluorescent light (ca. 1500–3000 lux) in the laboratory of Department of Botany, Faculty of Science, Hokkaido University. When the fragments developed and produced monospores, unialgal culture experiments were begun with their monospores under the following sets of conditions; 5°C SD (8 hr light/16 hr dark), 10°C SD, 10°C LD (16 hr light/8 hr dark), 15°C LD.

The dry specimens were deposited in the Herbarium of the Department of Botany, Faculty of Science, Hokkaido University (SAP). Their duplicates and slide specimens were deposited in the private herbarium of the first author.

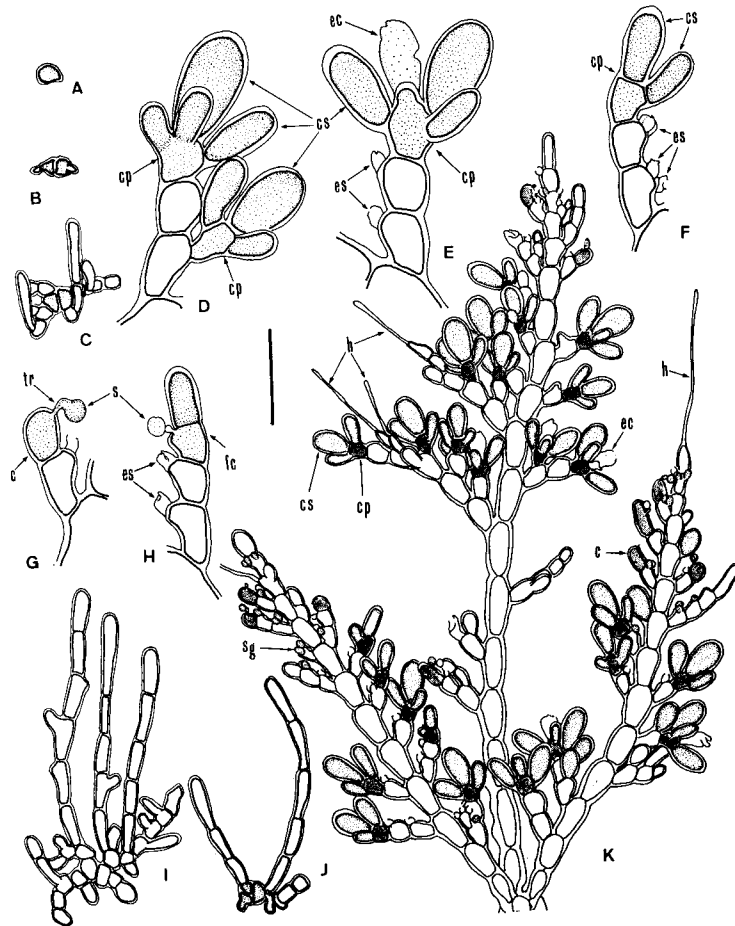
### Morphological Observations on Field-Collected Materials

#### *Gametophyte (Audouinella alariae)*

The gametophyte, epiphytic on the blades and sporophylls of *Alaria crassifolia*, is composed of a single basal cell and 1–3(–4) erect filaments 0.3–0.8(–1.2) mm long. The basal cell is easily distinguishable from other vegetative cells by its thick (to 10  $\mu\text{m}$ ) wall and hemispherical profile 27–50  $\mu\text{m}$  diam. and 12–20  $\mu\text{m}$  high. Erect filaments are composed of 12–29 (–34) cells, gradually attenuated upwards and produce alternate or opposite branches (Figs. 2–K, 3–A). The cells of erect filaments are slightly constricted at their juncture, barrel-shaped to cylindrical, 8–17  $\mu\text{m}$  wide and 25–50  $\mu\text{m}$  long. Plastids are stellate with a central pyrenoid, and are located in the distal part of the cell (Fig. 4–E and cf. 5–H). Hairs develop terminally or subterminally in the apical region of the erect filaments (Figs. 2–K, 3–A, 4–L).

Monosporangia are solitary to ternate and terminal or lateral near the distal ends of the cells of the erect filament. They are obovoid, 10–11  $\mu\text{m}$  wide and 14–19  $\mu\text{m}$  long (Fig. 3–A). Sometimes the monospores are observed germinating *in situ* (Fig. 4–J). Spermatangia are borne in groups of 2–3 near the distal ends of the cells subtending carpogonia or on somewhat small-celled adjacent branches (Figs. 2–F, H, K, 4–A, B). They are globose to ovoid, 4–5  $\mu\text{m}$  wide and 5–6  $\mu\text{m}$  long. Spermatia attached to trichogynes are 4–5  $\mu\text{m}$  in diameter (Figs. 2–G, H, 4–A, B). Carpogonia

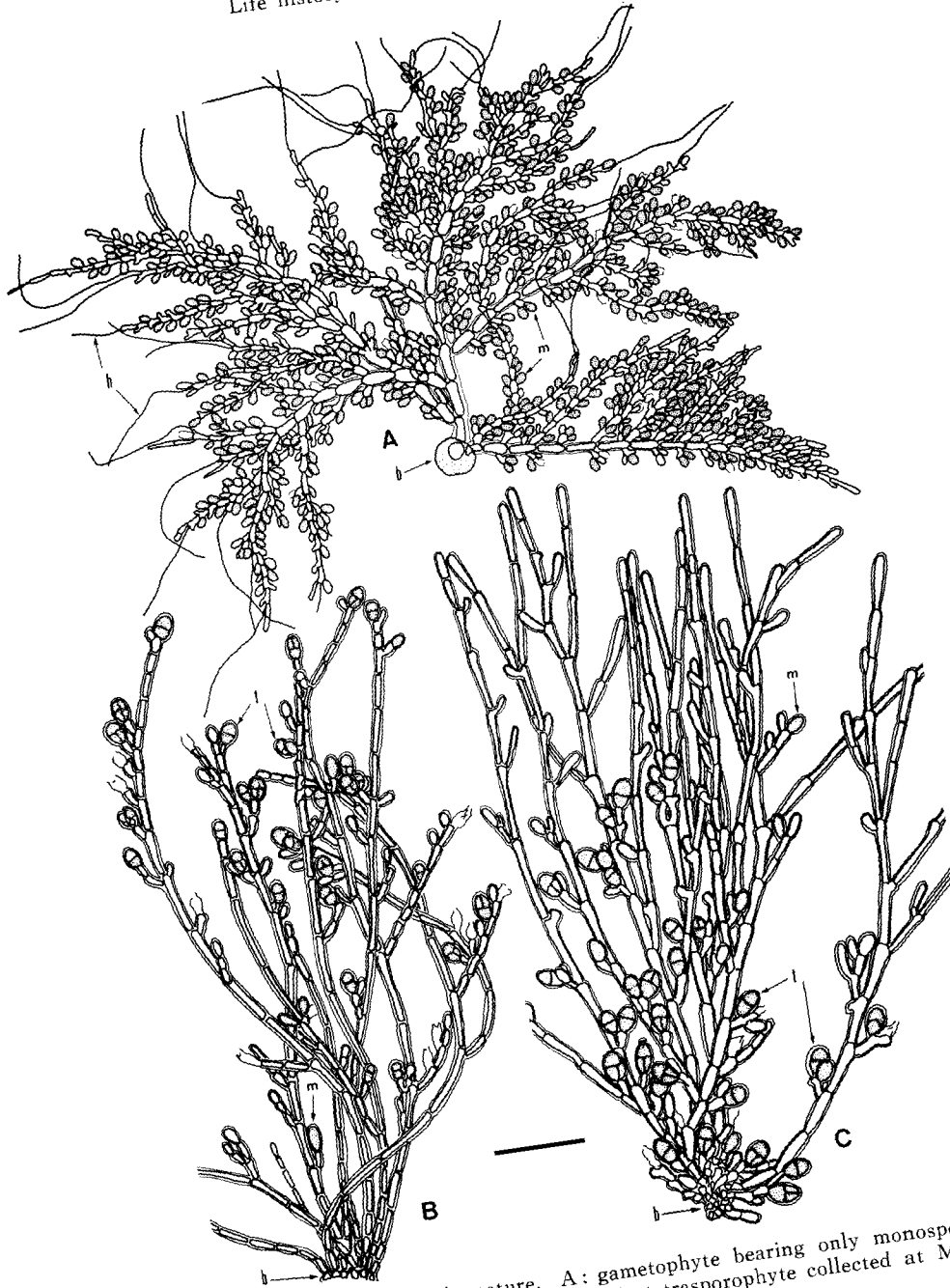
are terminal on short laterals and rather light in color compared to vegetative cells, ellipsoid,  $7-8\ \mu\text{m}$  wide and  $9-11\ \mu\text{m}$  long. Trichogynes always develop subterminally and adaxially near the distal end of a carpogonium, and are about  $3\ \mu\text{m}$  thick and to  $8\ \mu\text{m}$  long (Figs. 2-G, 4-A, B). The trichogyne is initially papillate and later spatulate with a short and narrow stalk.



**Fig. 2.** *Audouinella alariae* in nature. A-C, I-J: Germlings of carpospores developing into tetrasporophyte found in nature, D-H: postfertilization development, K: gametophyte bearing sexual reproductive structures and carposporophytes collected at Muroran in January.

h: hair, c: carpogonium, tr: trichogyne, s: spermatium, sg: spermatangium, es: empty spermatangium, fc: fertilized carpogonium, cp: carposporophyte, cs: carposporangium, ec: empty carposporangium.

Scale bar: A-C, I-K =  $50\ \mu\text{m}$ , D-H =  $20\ \mu\text{m}$ .

Life history of *Audouinella alariae*

**Fig. 3.** *Audouinella alariae* in nature. A: gametophyte bearing only monosporangia (stippled) collected at Murooran in July, B-C: tetrasporophyte collected at Murooran in May (B) and March (C).  
 b: basal cell, m: monosporangium, t: tetrasporangium, h: hair.  
 Scale bar: A-C = 100  $\mu$ m.

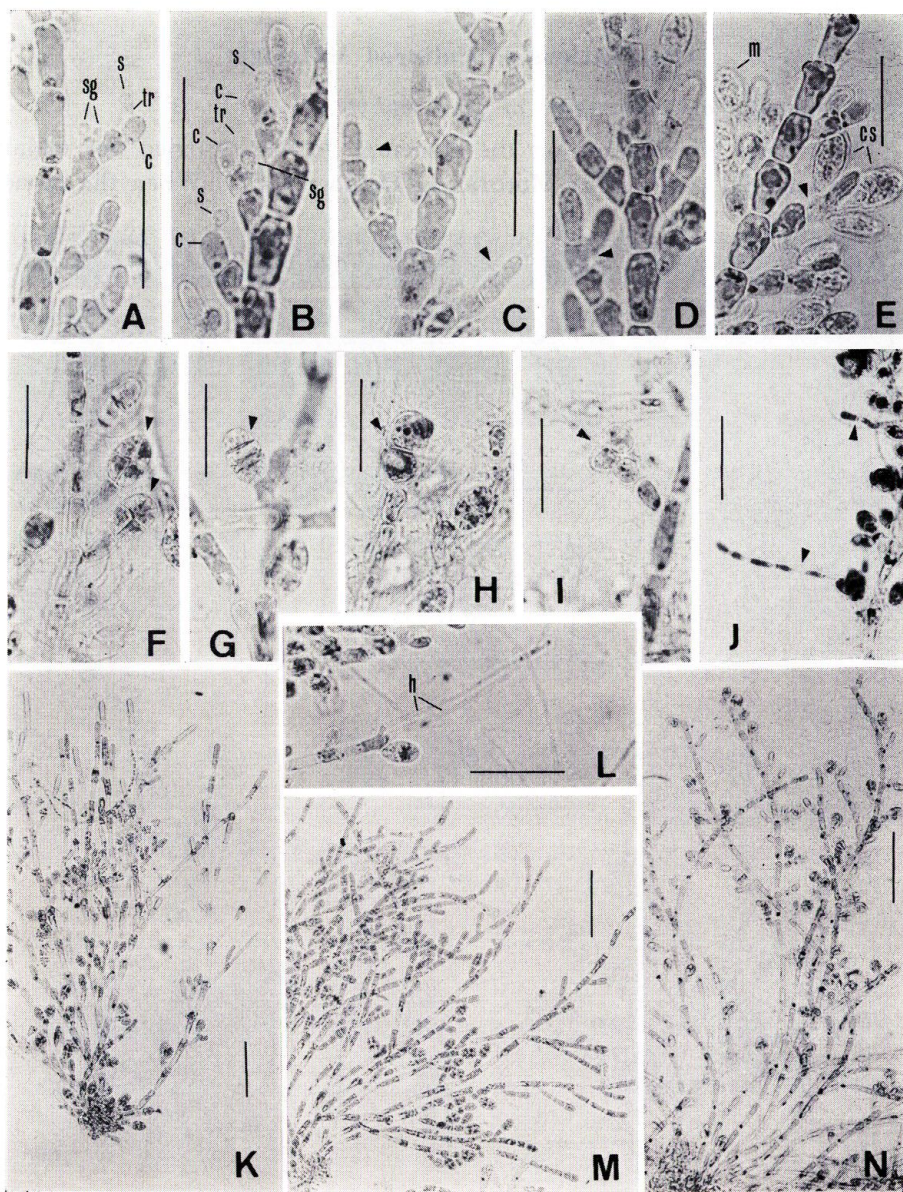
*Carposporophyte*

The carposporophyte is initiated from the fertilized carpogonium. A fertilized carpogonium elongates and divides transversely near the point where the trichogyne occurred (Figs. 2-H, 4-C). The distal cell derived from the cleavage of the fertilized carpogonium is transformed into a carposporangium (Figs. 2-F, 4-D), the proximal cell gives rise to 2-3 lateral cells which also become carposporangia (Figs. 2-D, E, 4-E). Proximal cells retain their characteristic light color similar to unfertilized carpogonia. Rarely the distal or lateral cells of the proximal cell produce 2-3 carposporangia instead of being transformed into carposporangia. Carposporangia are obpyriform, 10-13  $\mu\text{m}$  wide and 18-25  $\mu\text{m}$  long. Regeneration can occur in an empty carposporangium.

*Tetrasporophyte (Rhodochorton repens sensu JÓNSSON)*

The tetrasporophyte, like the gametophyte, is epiphytic on *Alaria crassifolia* as well as *Sargassum thunbergii*, *Chondrus yendoi*, and *Laurencia* sp., although it grows associated with *Audouinella catenulata* (HOWE) GARBARY on the latter hosts. It is composed of a multicellular filamentous base and erect filaments 0.6-1.2 mm long (Figs. 3-B, C, 4-K, M, N). Basal creeping filaments develop from septation of a presumable germinating carpospore and give rise to branches forming a basal plate (Fig. 2-A, B, C, I, J). Erect filaments arise from most cells of creeping filaments except for the cells in the marginal fringe of the basal plate, and form a tuft, branching secundly or alternately. The cells of erect filaments are generally elongate-cylindrical, of nearly the same width throughout, 12-13  $\mu\text{m}$  wide and 50-90  $\mu\text{m}$  long. Plastids are stellate, situated in the distal half of the cell, containing a pyrenoid (cf. Fig. 5-J). Hairs are not observed.

Monosporangia are borne singly or in pairs and terminally or laterally on short laterals. They are ovoid to ellipsoid, 11-14  $\mu\text{m}$  wide and 18-23  $\mu\text{m}$  long. Tetrasporangia are borne singly or in pairs and terminally or laterally on short laterals and erect filaments. They are cruciately divided or rarely zonate, decussate or tetrahedral (Fig. 4-F, G). They are ellipsoid, 17-20  $\mu\text{m}$  wide and 24-29  $\mu\text{m}$  long. Some aberrant sporangia, which seem to be transformed tetrasporangia, were also encountered (Fig. 4-H, I). Older plants tend to bear tetrasporangia in the upper region of thalli (Fig. 8, cf. Figs. 3-B, C, 4-K, M, N).

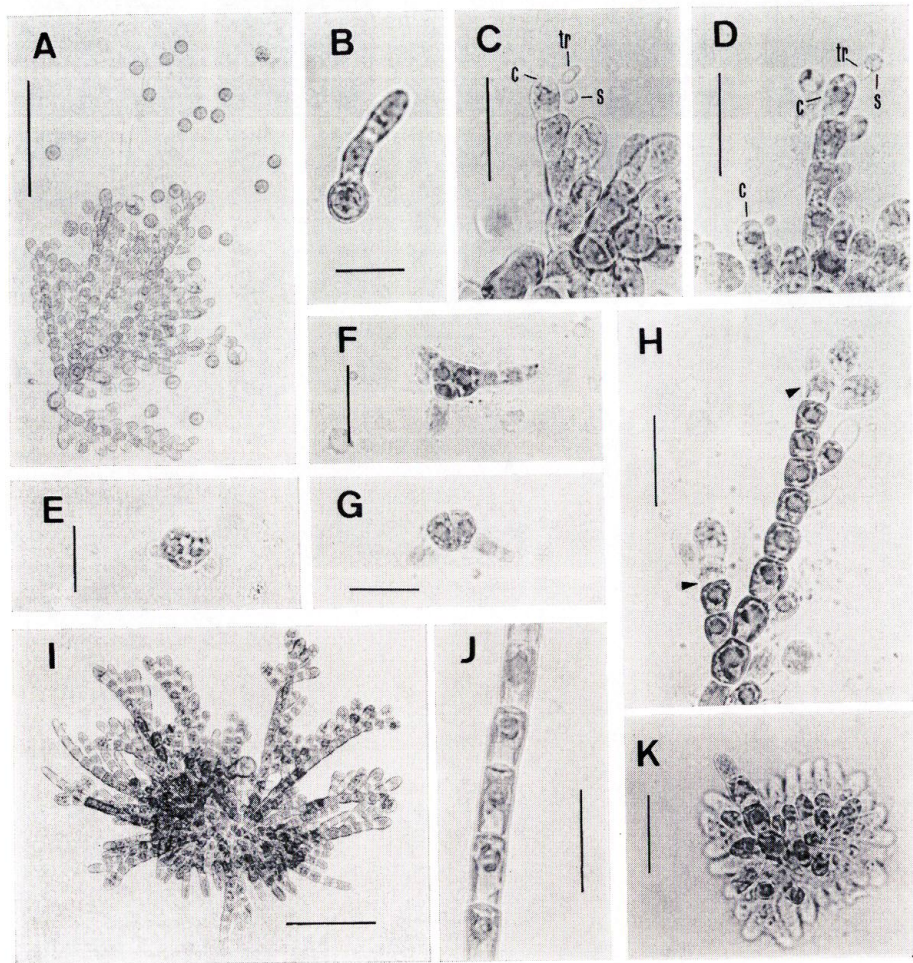


**Fig. 4.** *Audouinella alariae* in nature. A-E, J, L: gametophyte; A, B: spermatangia and carpogonia developing terminally on short laterals, C, D: postfertilization development (arrows), showing elongation and transverse division of fertilized carpogonia (C), and initial branching of carposporophyte (D), E: mature carposporophyte (arrow), F: *in situ* germination of monospores (arrows), L: terminal and subterminal hairs. F-I, K-N: tetrasporophyte; F: cruciately divided tetrasporangia (arrows), G: zonately divided tetrasporangium (arrow), H, I: aberrant sporangia (arrows), K, M, N: tetrasporophyte collected at Muroran in March (K), April (M) and May (N), note the basal (K), middle (M) and upper (N) regions of erect filaments where tetrasporangia occur. For abbreviation see Figs. 2 & 3. Scale bars: A-E = 30  $\mu$ m, F-I, L = 40  $\mu$ m, J = 50  $\mu$ m, K, M, N = 100  $\mu$ m.

### Observations on Cultured Materials

#### *Culture started from monospore of gametophyte*

The culture experiments on the gametophyte were carried out mainly with the material collected at Muroran in October 1977. When the mono-



**Fig. 5.** *Audouinella alariae* in culture. A-D, H: gametophyte derived from monospore of gametophyte; A: gametophyte producing only monospores, B: germling of monospore, C, D: mature carpo-gonia, H: mature carposporophyte on gametophyte (arrows). E-G, I-K: tetrasporophyte derived from carpospore; E-G, K: germination and development of carpospore, I: mature tetrasporophyte bearing tetrasporangia and monosporangia, J: showing plastid in vegetative cell.

For abbreviation see Figs. 2 & 3.

Scale bars: A=100  $\mu$ m, B, E, F, G=20  $\mu$ m, C, D, H, J, K=30  $\mu$ m, I=200  $\mu$ m.

spore of a gametophyte germinates, it develops erect filaments directly and itself becomes the single basal cell of the thallus without the development of any basal creeping filaments (Fig. 5-A, B). Usually 1-3 separate erect filaments arise from a single basal cell. The resulting plant produces only monosporangia under 10°C and 15°C long day conditions. However, the plant produces male and female reproductive structures as well as monosporangia under 5°C and 10°C short day conditions (Fig. 5-C, D). Hairs are more common under long day conditions.

Although the actual fertilization of a carpogonium was not confirmed, certain cells of the gametophyte appeared to be the derivatives of the fertilized carpogonium by their rather light color compared to vegetative cells and by the fashion of the sporangia production (Fig. 5-H). The cells bore 3-4 carposporangia terminally and laterally. Carpospores germinated differently from the monospores of the gametophyte. They divided into 2 or more cells and then produce creeping filaments from the each cell forming a basal disc, from which erect filaments arise (Fig. 5-E, F, G, K). The plants derived from the germinating carpospores in turn produced tetrasporangia as well as monosporangia under 10°C and 15°C long day conditions (Fig. 5-I).

#### *Culture started from monospore of tetrasporophyte*

The culture experiments on the tetrasporophyte were carried out chiefly with plants growing on *Laurencia* sp. collected at Shirikishinai in May, 1977. The monospores germinate in the same fashion as carpospores mentioned above. Creeping filaments first develop from each cell of the septate monospore. They are often confluent and form a basal disc on a glass surface. Erect filaments arise on the cells of creeping filament as well as of the septate monospore. The plant resulting from the germination of a monospore from a tetrasporophyte produces tetrasporangia as well as monosporangia under 10°C and 15°C long day conditions. Hairs were not found in culture conditions under which plants were grown.

Tetrasporangia are cruciately or rarely zonately divided. The other pattern of division seen in nature, decussate and tetrahedral patterns, were not seen in culture. Although tetraspores could be neither confirmed nor isolated because they were released simultaneously with monospores, two kinds of plants appeared in the culture vessel under 10°C and 15°C long day conditions. One has a unicellular base and only monosporangia, and the other a multicellular base and both tetrasporangia and monosporangia. The former was considered to be gametophytes derived from tetraspores, and it produced male and female reproductive structures as well as mono-

TABLE 1. Morphological characteristics of *A. alariae* in nature and culture

generation	characteristics	nature		culture	
		original description (JÓNSSON 1901)	Hokkaido material	started from tetrasporophyte	started from gametophyte
gametophyte ( <i>A. alariae</i> )	thallus height	0.5-1 mm	0.3-0.8 (-1.2) mm		
	basal system	unicellular	unicellular	unicellular	unicellular
	erect filament				
	number	1-2	1-3 (-4)	1-3	1-3
	branch	opposite, alternate or secund	alternate or opposite	—	—
	cell shape	—	barrel-shaped to cylindrical	—	—
	cell size (width×length)	7-23 $\mu\text{m}$ ×20-72 $\mu\text{m}$	8-17 $\mu\text{m}$ ×25-50 $\mu\text{m}$	—	—
	hair	present	present	present	present
	spermatangia				
	development	—	near carpogonia	near carpogonia	near carpogonia
	shape	—	globose to ovoid	globose to ovoid	globose to ovoid
	size (w×l)	—	4-5 $\mu\text{m}$ ×5-6 $\mu\text{m}$	4-5 $\mu\text{m}$ ×4-6 $\mu\text{m}$	3-4 $\mu\text{m}$ ×4-6 $\mu\text{m}$
	carpogonia				
	shape	—	ellipsoid	ellipsoid	ellipsoid
	size (w×l)	—	7-8 $\mu\text{m}$ ×9-11 $\mu\text{m}$	6-8 $\mu\text{m}$ ×8-10 $\mu\text{m}$	7-8 $\mu\text{m}$ ×9-13 $\mu\text{m}$
	trichogyne				
	development	—	subterminal	subterminal	subterminal
	shape	—	papillate-spatulate	papillate-spatulate	papillate-spatulate
	size (w×l)	—	2 $\mu\text{m}$ ×to 8 $\mu\text{m}$	2-3 $\mu\text{m}$ × to 10 $\mu\text{m}$	2-3 $\mu\text{m}$ × to 10 $\mu\text{m}$
	monosporangia				
shape	obovoid-ellipsoid	obovoid	obovoid	obovoid	
size (w×l)	10-11 $\mu\text{m}$ ×17-22 $\mu\text{m}$	10-11 $\mu\text{m}$ ×14-19 $\mu\text{m}$	9-10 $\mu\text{m}$ ×13-15 $\mu\text{m}$	8-10 $\mu\text{m}$ ×12-14 $\mu\text{m}$	
germination	—	aseptate	aseptate	aseptate	

generation	characteristics	nature		culture	
		original description (JÓNSSON 1901)	Hokkaido material	started from tetrasporophyte	started from gametophyte
carposporophyte	cell number	—	4-5 (-11)	4-5	4-5
	carposporangia				
	number	—	3-4 (-8)	3-4	3-4
	shape	—	obpyriform	obovoid-obpyriform	obovoid-obpyriform
	size (w×l)	—	10-13 μm×18-25 μm	9-13 μm×16-18 μm	10-11 μm×15-18 μm
	germination	—	septate	septate	septate
tetrasporophyte ( <i>R. repens</i> )	thallus height	c. 1 mm	0.6-1.2 mm	—	—
	basal system	multicellular, filamentous	multicellular, filamentous	multicellular, filamentous	multicellular, filamentous
	erect filament				
	branch	alternate, opposite, corymbose	secund-alternate	—	—
	cell shape	—	elongate-cylindrical	—	—
	cell size (w×l)	8-13 μm×16-65 μm	12-13 μm×50-90 μm	—	—
	hair	—	absent	absent	absent
	tetrasporangia				
	shape	ovoid, obovoid or ellipsoid	ellipsoid	obovoid-ellipsoid	obovoid-ellipsoid
	size (w×l)	14-17 μm×20-27 μm	17-20 μm×24-29 μm	14-16 μm×20-26 μm	15-19 μm×19-25 μm
	germination	—	—	aseptate	aseptate
	monosporangia				
	shape	—	ovoid-ellipsoid	ovoid-obovoid	ovoid-obovoid
size (w×l)	—	11-14 μm×18-23 μm	10-12 μm×16-19 μm	10-12 μm×15-18 μm	
germination	—	—	septate	septate	

sporangia under 5°C and 10°C short day conditions. The latter was considered to be tetrasporophyte derived again from monospores.

*Morphological comparison between gametophyte and tetrasporophyte in nature and culture*

Table 1 compares some of the morphological characteristics of each generation of *Audouinella alariae*; gametophyte, carposporophyte and tetrasporophyte. There are no differences in morphology between field-collected materials and cultured ones of gametophyte and tetrasporophyte.

### Phenological Observations

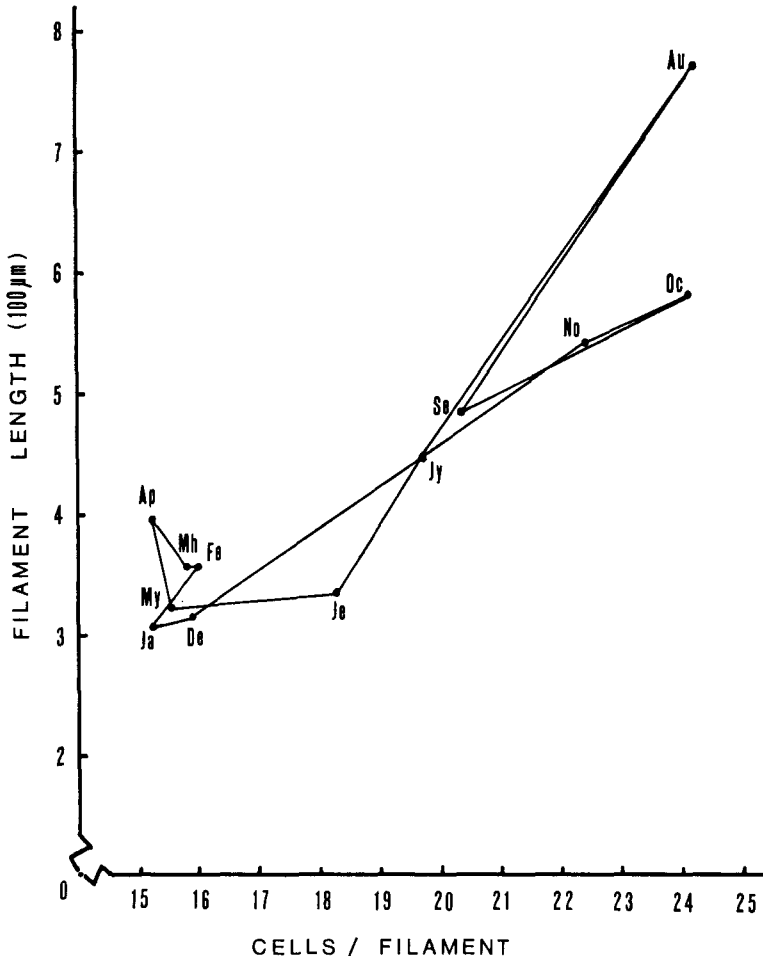
Phenological observations were carried out on materials collected at an established site in the lower intertidal zone at Muroran, Hokkaido, from August 1977 to July 1978. The statistical data on the growth and reproduction of gametophytes shown in Figs. 6 and 7 were obtained from observations of 100 plants each month, and those on the growth and reproduction of tetrasporophytes in Fig. 8 were from 10–20 plants.

Gametophytes occur throughout the year exclusively on *Alaria crassifolia*. However, the life expectancy of an individual gametophyte was hard to determine because of the continuous production and germination of monospores and the resulting heterogeneous population. The first erect filament\* of summer plants appears to be longer and composed of more cells than that of winter ones (Fig. 6). More than 90% of the plants have 2–3 erect filaments on a single basal cell every month except September when about 30% of the plants have a single erect filament. Hairs are rather rich in August, September, October, April and July, while poor in December and June. The production of monosporangia reaches a maximum in July and a minimum in December (Fig. 7). The dimensions (especially width) of the monosporangia vary little from month to month. Sexual reproductive structures are seen during October to February and show their maximum development in December (Fig. 7).

The occurrence of carposporophytes reaches its maximum in January, this is following the period of maximal abundance of sexual reproductive structures (Fig. 7).

Tetrasporophytes begin to appear as germlings among the gametophytes on the blades of *Alaria crassifolia* in December when production of carposporangia is high. However, mature tetrasporophytes were also observed on other hosts, *Sargassum thunbergii*, *Chondrus yendoii* and *Laurencia* sp.

\* The term "first erect filament" is used in this paper to indicate the most developed one among the erect filaments arising from a single basal cell.



**Fig. 6.** *Audouinella alariae*, monthly growth-graph of the gametophyte represented by the length of first erect filament (mean value; standard deviation =  $\pm 5.74 - \pm 17.33$ ) compared to the number of its component cells (mean value; standard deviation =  $\pm 1.98 - \pm 4.67$ ).

Ja. January; Fe. February; Mh. March; Ap. April; My. May; Je. June; Jy. July; Au. August; Se. September; Oc. October; No. November; De. December.

The tetrasporophytes are senescent in May and disappear in June at Muro-ran. The tetrasporophytes produce only monosporangia from December to February when most plants are still young, and tetrasporangia predominate from March to May (Fig. 8).

Fig. 9 shows environmental factors, surface seawater temperature, nitrate concentration and day length, during the growth periods of gametophyte

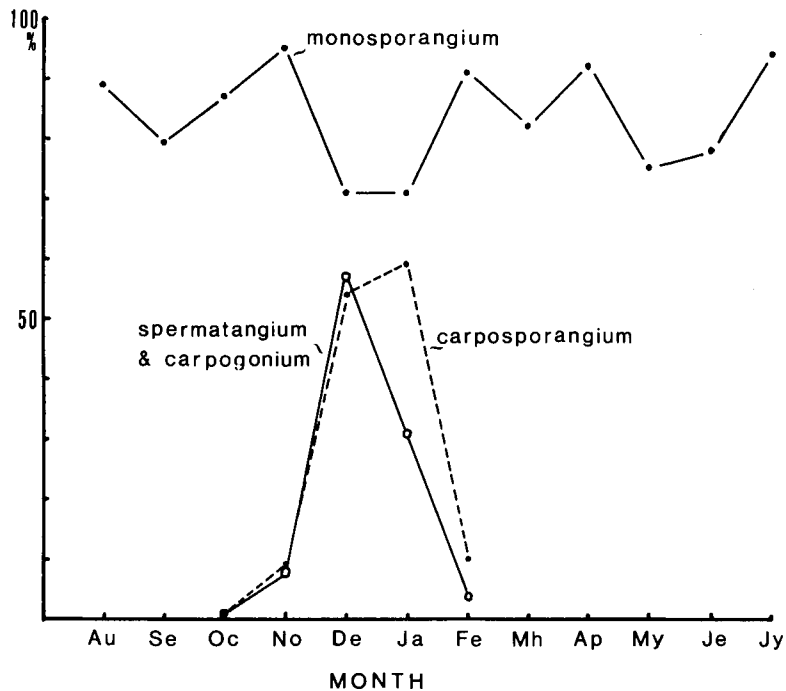


Fig. 7. *Audouinella alariae*, seasonal occurrence in percentage of erect filaments bearing monosporangia and sexual reproductive structures on gametophytes.

and tetrasporophyte. From October to February, when sexual reproductive structures are formed in gametophytes, the temperature is from 14 to 2°C, nitrate rich and daylength short. On the other hand, in March to May, when tetrasporangia are formed, the temperature is from 2 to 9°C, nitrate poor and daylength long.

## Discussion

### *Life history*

The field-collected gametophytes are identified as *Audouinella alariae* (JÓNSSON) WOELKERLING, and the tetrasporophytes are identical with *Rhodochorton repens* JÓNSSON (= *Acrochaetium jonssonii* PAPENFUSS). The interpretation of the life history of this taxon is based on the following results obtained from culture experiments and phenological observations on both the gametophytic and tetrasporophytic generations.

1) In culture, the plants derived from both the tetraspores of *R. repens* and the monospores of *A. alariae* have a unicellular base and produce male

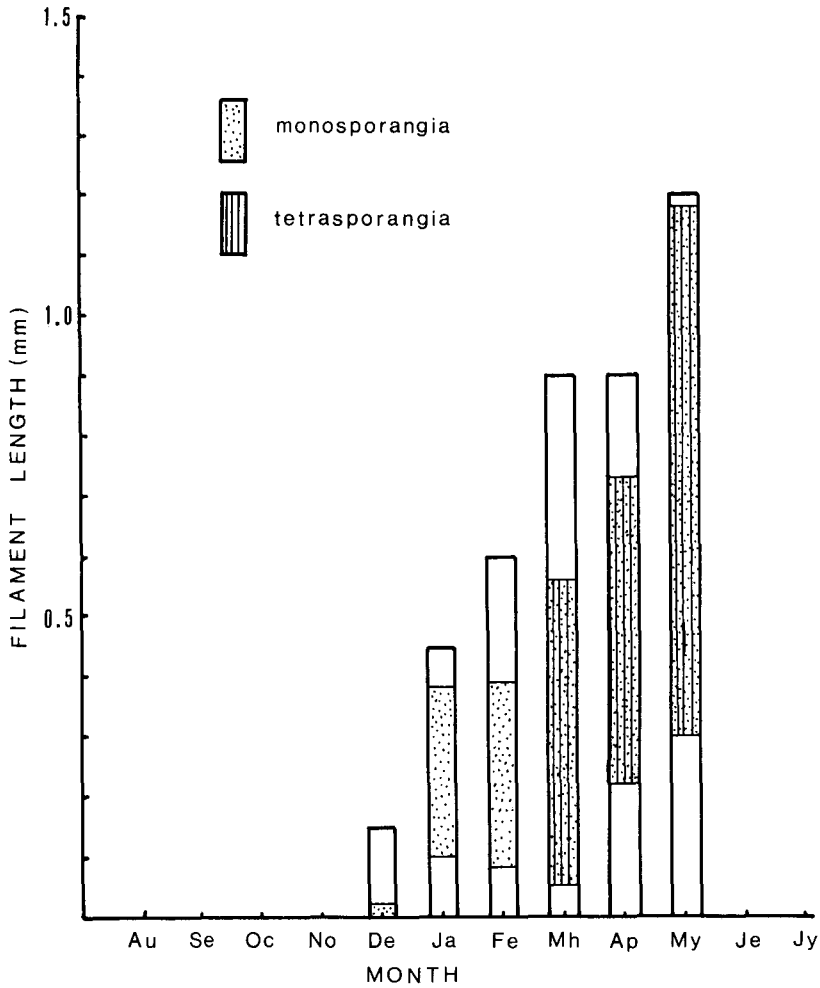


Fig. 8. *Audouinella alariae*, monthly length of erect filament of tetrasporophyte and the region bearing monosporangia and tetrasporangia.

and female reproductive structures as well as monosporangia. The unicellular base and the morphology of male and female reproductive structures of the plants in culture are similar to field-collected materials of *A. alariae*.

2) The simple development of the carposporophyte in cultured plants is the same as in field-collected *A. alariae*.

3) Monospores of *R. repens* germinate in a septate fashion and develop into plants having a multicellular base similar to carposporelings from the

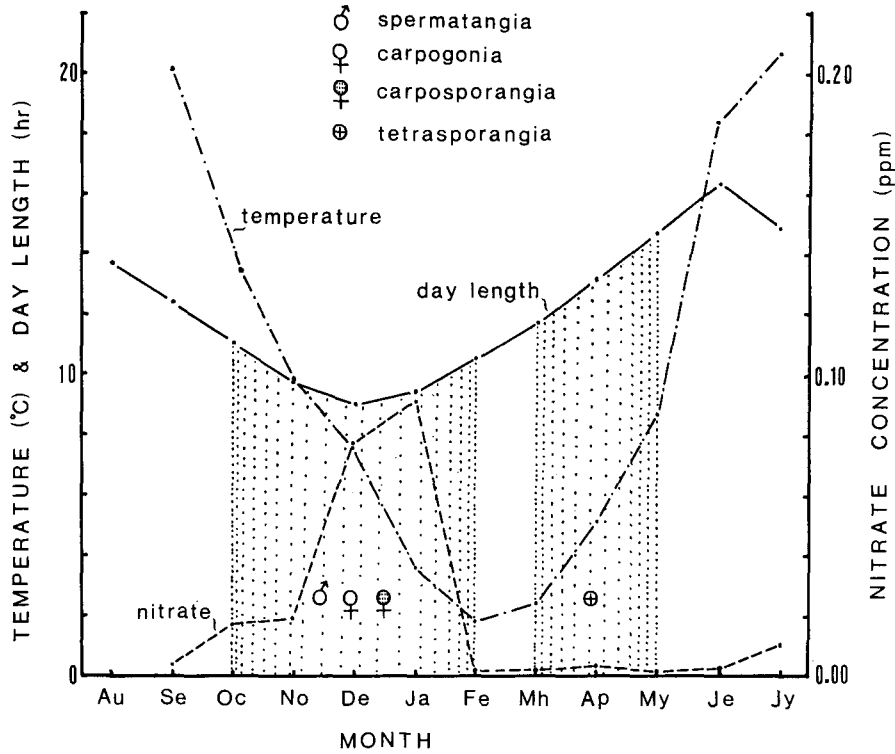


Fig. 9. *Audouinella alariae*, seasonal occurrence of sexual reproductive structures and asexual ones, compared with environmental factors, day-length, surface seawater temperature and nitrate concentration (from data of the Institute of Algological Research, Hokkaido University).

carposporophyte on the thallus of *A. alariae*.

4) Plants of *R. repens* begin to appear when carposporangia are first produced in large quantities by the carposporophyte of *A. alariae*.

The life history of this taxon involves three generations: gametophyte, carposporophyte and tetrasporophyte. The gametophyte is composed of a unicellular base and 1-3(-4) erect filaments with hairs. It occurs throughout the year, and produces spermatangia, carpogonia and monosporangia on the same thallus. Spermatangia and carpogonia are produced during the 5-month period from October to February while monosporangia are produced during the entire year. The carposporophyte usually consists of 4-5 or rarely 9 cells (including the carposporangia), occurs during the 5-month period from October to February, and produces only carposporangia. The tetrasporophyte is composed of a multicellular base and erect filaments without hairs. It occurs during the 6-month period from December to May, and produces

tetrasporangia and monosporangia on the same thallus. Tetrasporangia occur from March to May.

The morphologies of the three generations in the life history of *A. alariae* show similarities to other taxa which have been investigated recently, e. g., *Acrochaetium densum* (STEGENGA and VROMAN 1976) and the *Chromastrum reductum* — *C. kylinoides* complex (STEGENGA and VAN WISSEN 1979).

The carposporophyte structure in *A. alariae* is rather simple and morphologically similar to those in *Chromastrum kylinoides* (FELDMANN) STEGENGA et VAN WISSEN (1979) and *Audouinella kurogii* Y. P. LEE et LINDSTROM (1979) but not as simple as in *Acrochaetium hummii* AZIZ (1965).

Carposporangia are nearly equal in size to the monosporangia of the tetrasporophyte, while the monosporangia of the gametophyte are smaller than both carposporangia and monosporangia of tetrasporophyte. Carpospores also germinate in the same fashion as the monospores of the tetrasporophyte. These two characteristics may help to confirm the relationship between the gametophytic and tetrasporophytic phases of *Audouinella* taxa.

#### *Environmental factors*

As for the environmental factors in sporulation and gametogenesis in life history, KNAGGS (1966, 1967) discussed the effect of light intensity on tetrasporangia formation of *Rhodochorton purpureum* (LIGHTFOOT) ROSENVINGE, and the relationship between nutrients (nitrate and phosphate) concentration and light intensity for tetrasporangia formation of *Rhodochorton floridulum* (DILLWYN) NÄGELI. WEST (1972) described on the effects of daylength, temperature and other factors on the formation of tetrasporangia and male and female gametangia of *Rhodochorton purpureum*. STEGENGA and VROMAN (1976) and STEGENGA and BORSJE (1977) also discussed the optimal temperatures and light intensities for tetrasporangia and gametangia formation in *Acrochaetium densum* (DREW) PAPENFUSS and *A. polyblastum* (ROSENV.) BØRGESEN-*A. hallandicum* (KYLIN) HAMEL.

In this study of *A. alariae*, daylength appears to be one of the critical factors in the formation of sexual reproductive structures, carposporangia and tetrasporangia in both nature and culture. However, seawater temperature does not appear to have an effect on the gametogenesis and sporulation. A peak in the concentration of nitrate in seawater coincides with the formation of both sexual reproductive structures and carposporangia in nature, however the concentration is not rich during the period of tetrasporangia formation in nature.

### Nomenclature

JÓNSSON (1901) described simultaneously two species of acrochaetioid algae from Iceland, *Chantransia alariae* JÓNSSON (p. 132) and *Rhodochorton repens* JÓNSSON (p. 147). *C. alariae* was variously combined with the acrochaetioid genera, *Acrochaetium*, *Rhodochorton*, *Kylinia*, *Chromastrum* and *Audouinella* according to different generic concepts of the authors mentioned in the introduction of this paper. We have used the name of *Audouinella alariae* (JÓNSSON) WOELKERLING (1973) as mentioned before. According to the generic concept of PAPENFUSS (1945), *R. repens* was renamed as *Acrochaetium jonssonii* PAPENFUSS because of the presence of *A. repens* BØRGESEN (1915). However, we have, following the original name, used the name *R. repens* in this paper.

In this study, the two species have been shown to represent the alternate phases in the life history of the same species. The former is gametophyte and the latter tetrasporophyte. From this, we must choose one of the two names. According to the Art 57 in the International Code of Botanical Nomenclature (1978), we chose the name, *Audouinella alariae* (JÓNSSON) WOELKERLING, for this taxon. The name of *Audouinella alariae* also seems more appropriate for the taxon involved because it has been applied originally to the gametophyte which presents a taxonomically important feature of postfertilization in Florideophyceae.

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