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Life History and Taxonomy of *Aglaothamnion oosumiense* Itono (Ceramiaceae, Rhodophyta)

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Life history and post-fertilization process of *Aglaothamnion oosumiense* from Korea were studied in culture. This species showed a *Polysiphonia*-type life history with dioecious gametophyte as well as asexual reproduction via parasporangium on male plants. The occurrence of parasporangiate plants was not affected by environmental factors nor inherited strictly to the next generation. Most (>95%) of the paraspores developed into male plants, while less than 5% of paraspores became parasporangiate male plants again. Bisexual plants were also observed. Each carpogonial branch had two auxiliary cells, which divided distally to produce the primary gonimoblast initials, respectively, before the foot cells were cut off proximately from it by intercalary divisions. Two carposporophytes resulted from a successful fertilization. Morphologically, *Aglaothamnion oosumiense* resembled *Aglaothamnion callophyllidicola* (Yamada) Boo, Lee, Rueness et Yoshida, and the taxonomic characters separating them were found to be unstable. The taxonomic relationship between the two species, therefore, should be critically reassessed with a thorough re-examination including their type specimens.

Key Words: *Aglaothamnion oosumiense*, Ceramiaceae, life history, post-fertilization, Rhodophyta

INTRODUCTION

The genus *Aglaothamnion* was established by Feldmann-Mazoyer (1941) based on *A. furcellariae* known as a member of *Callithamnion*. The genus was distinguished by following three criteria; 1) uninucleate vegetative cells 2) 'zig-zag' or U-shaped carpogonial branches, and 3) 'lobed', unspherical gonimolobes. Many phycologists accepted the genus *Aglaothamnion* (e.g. Kylin 1956; Dawson 1962; L'Hardy-Halos 1970; Abbott and Hollenberg 1976; Itono 1977), while some insisted on including *Aglaothamnion* in *Callithamnion* (e.g. Boddeke 1958; Harris 1962; Dixon and Price 1981). Recently, L'Hardy-Halos and Rueness (1990) proposed reinstatement of *Aglaothamnion* for the species of *Callithamnion* complex on the basis of uninucleate vegetative cells, and moved some European callithamnioid species to *Aglaothamnion*. This new reinstatement has been broadly accepted by many phycologists (e.g. Boo *et al.* 1991; Maggs *et al.* 1991).

Three *Aglaothamnion* and nine *Callithamnion* species have been reported in Korea and Japan(Lee and Kang 1986; Yoshida *et al.* 1990). However, it is very difficult to make a delimitation of some related species, *A. oosumiense*, *C. callophyllidicola* and *C. minutissima* due to the diverse ranges of the forms in the species (Boo *et al.* 1989). From the thorough examination of the type specimen, however, Boo *et al.* (1991) proposed a new binomial *A. callophyllidicola* and treated *C. minutissima* as a later synonym of the species.

Aglaothamnion oosumiense was recorded by Itono (1971) on the basis of the plants collected from Tajiri, Oosumi peninsula, Japan. He reported that this species was similar to *Callithamnion paschale* in vegetative morphology but was different in branching pattern. The relationship between the two species was clearly denied by Boo *et al.* (1991). They reported that *C. paschale* was different from *A. oosumiense* in having a multinucleate vegetative cells, while the other having unicleate vegetative cells. There are still some questions remained on the relationship between *A. oosumiense* and *A. callophyllidicola*. Although these two species may be distinguished by some morphological characters as proposed by Itono (1977), we can not ascertain the species, delimitation considering the wide ranges of their morphological variation.

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In this study, we re-evaluated taxonomic characters of *A. oosumiense* by investigating the development of vegetative and reproductive structures as well as post-fertilization processes. We cultured the plants under various environmental conditions to examine their life history and conducted the crossing experiment with Japanese isolates collected from Shimoda.

MATERIALS AND METHODS

Both cystocarpic and tetrasporic plants of *Aglaothamnion oosumiense* were collected using SCUBA diving at shady rock recesses of the lower tidal zone in Eochungdo, the western coast of Korea (125°E, 35°N), on 23 June 1994. Morphological observations were made on material preserved in the buffered 3% formalin solution and re-examined with cultured plants.

Two isolates of *A. oosumiense*, one (#0623) from Eochungdo and the other (#0517) from Shimoda, Japan (136°E, 37°N) on 17 May 1995, were used for the laboratory culture. Cultures for life history and cross experiments were established from their excised apices. The plants were grown in the modified IMR enriched seawater at 15°C in a 16:8 h light-dark (LD) cycle under 10 μmol $cm^{-2}s^{-1}$ cool-white fluorescent light. To observe the effects of environmental factors on the morphology and reproduction of the species, some isolates were maintained under the following combinations of temperature, LD cycle and photofluence rate: 15°C + 8:16 h LD, 15°C + 12:12 h LD, 15°C + 16:8 h LD at 5-10 μmol $cm^{-2}s^{-1}$, 20°C + 8:16 h LD, 20°C + 16:8 h LD at 10-30 μmol $cm^{-2}s^{-1}$, and 25°C + 8:16 h LD at 25 μmol $cm^{-2}s^{-1}$ (Kim 1990). Further cultivation techniques followed Lee and West (1979). Procedures for crossing experiments were the same as described Kim *et al.* (1996).

To observe the nucleus in the cell, we transferred plants into a solution containing DAPI (20 μg/mL). The fixation was conducted by the use of microwave for 20-30 sec, which reduced autofluorescence and enhanced DAPI staining (Kim and Fritz 1993a).

RESULTS

Vegetative structure: The thallus grew in length by obliquely dividing apical cells of the indeterminate axis. Lateral branches developed alternately from the upper side of axial cells, 2-3 times ordered and curved slightly towards main axis. The oblique division of apical cell occurred to the right and left sides, alternately producing a single lateral branch for each axial cell. The plants were 0.3-2 cm in length and produced rhizoids at the basal portion attaching to other algae or sponges on the rock. The descending rhizoids branched sparsely, and developed terminal digitate holdfast on contact with the substratum.

The indeterminate branches were frequently produced at irregular intervals on axial segments (Fig. 1). They replaced the lateral determinate branches and grew in the same manner as the main axis. The lateral branches produced branchlets two to three times but did not overgrow the main axis. Adventitious branches were not produced. All the branches and branchlets were curved slightly towards the main axis (Fig. 1).

The cells of the main axes are 55-73 μm wide and 250-260 μm long. L/B ratio was 3.4-4.7:1 in axial cells of a median portion. Every vegetative and reproductive cell had only one nucleus except for carpogonial cells, which had two nuclei (Fig. 2C). The nucleus always had the same size regardless of the cell volume (Fig. 2A).

Tetrasporangial and spermatangial structures: Tetrasporangia were sessile, solitary or rather frequently in successive pairs on lower cells of the branches, divided tetrahedrally and became 50-52 μm $\times$ 70-73 μm after maturation (Figs 1C, 3C). Male plants were 0.3-1 cm in length and usually smaller than female plants. Main axes of mature male plants were 35-38 μm wide and 160-180 μm long. L/B ratio was 4-5:1 in axial cells of a median portion. When mature, the branches of male plants were curved slightly towards the base of main axis (Fig. 1B). Spermatangia were developed at each segment of the lateral branch (Fig. 1B). Each fertile segment of the determinate branch in the upper parts of the thallus cut off two or three initials of spermatangial mother cells by oblique divisions on the abaxial side, and each spermatangial mother cell produced one or two spermatangia, which extended through the outer pectic wall of the mother cells. Mature spermatangia were colorless and 3-4 μm in diameter.

Procarps and post-fertilization: Procarps were commonly borne on apical portion of the thallus, being formed singly on each of 2-3 segments of main and lateral axes (Figs 1A, 3A). The fertile segment first cut off two pericentral cells on the same plane as the lateral branches. Only one of the fertile pericentral cell produced an initial of the carpogonial branch. The carpogonial branch grew towards the other pericentral cell in the same segment. The carpogonial branch initial first divided into three-celled carpogonial branches. The terminal cell then

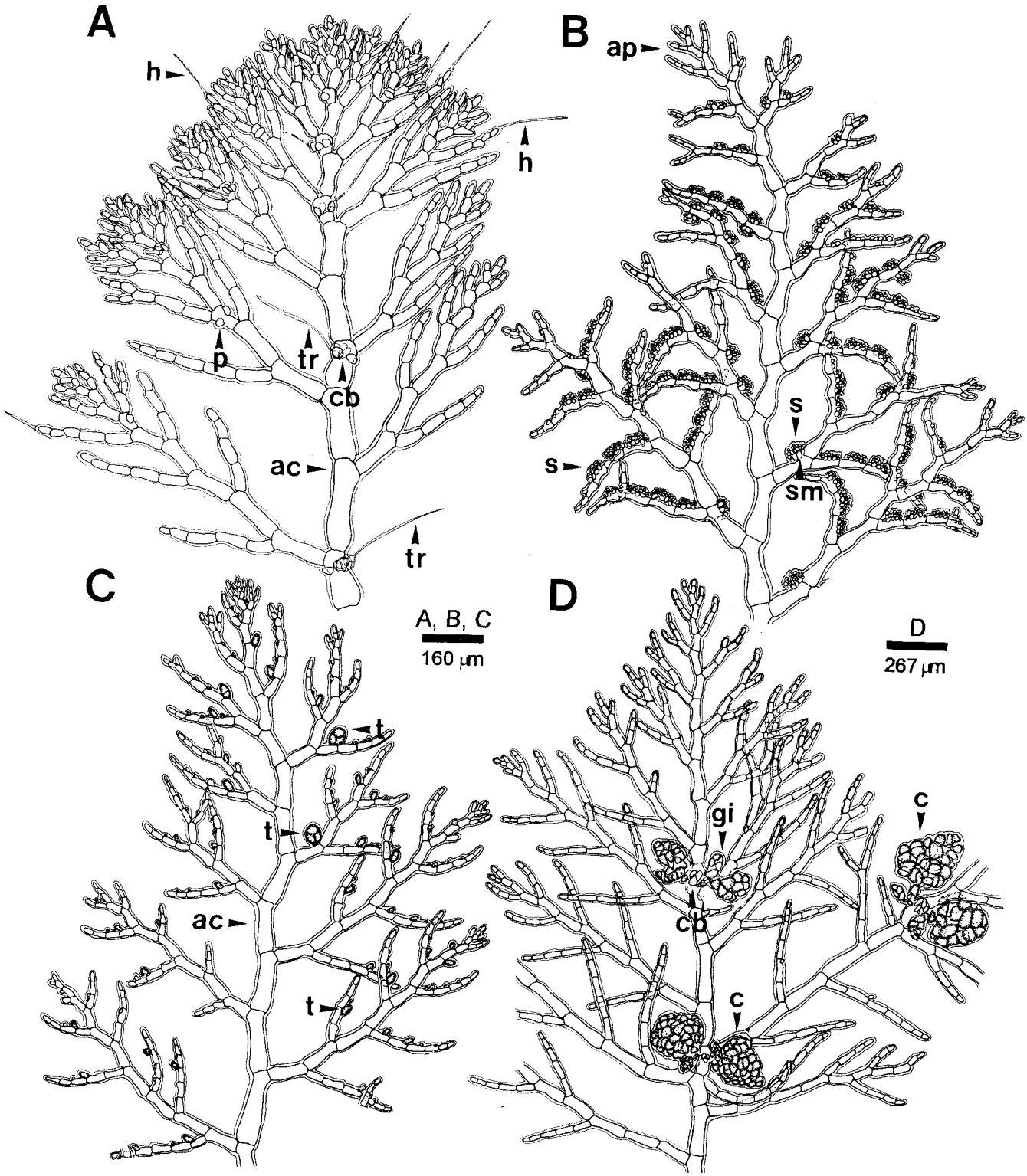

Fig. 1. *Aglaothamnion oosumiense* Itono.
A; Female thallus with hair cells and carpogonial branches, B; Male thallus with spermatangial clusters, C; Part of tetrasporophyte, D; Female plant with cystocarps. (ac; axial cell, ap; apical cell, c; cystocarp, cb; carpogonial branch, gi; gonimoblast initial, h; hair cell, p; pericentral cell, s; spermatangium, sm; spematangial mother cell, t; tetrasporangium, tr; trichogyne).

cut off distally a carpogonium with trichogyne (Fig. 4A). All carpogonial cells and pericentral cells were embedded in a common sheath (Fig. 2C).

After fertilization, the trichogyne withered and fertilized carpogonium divided into two cells (Fig. 4B). Sometimes trichogyne persisted for several days after

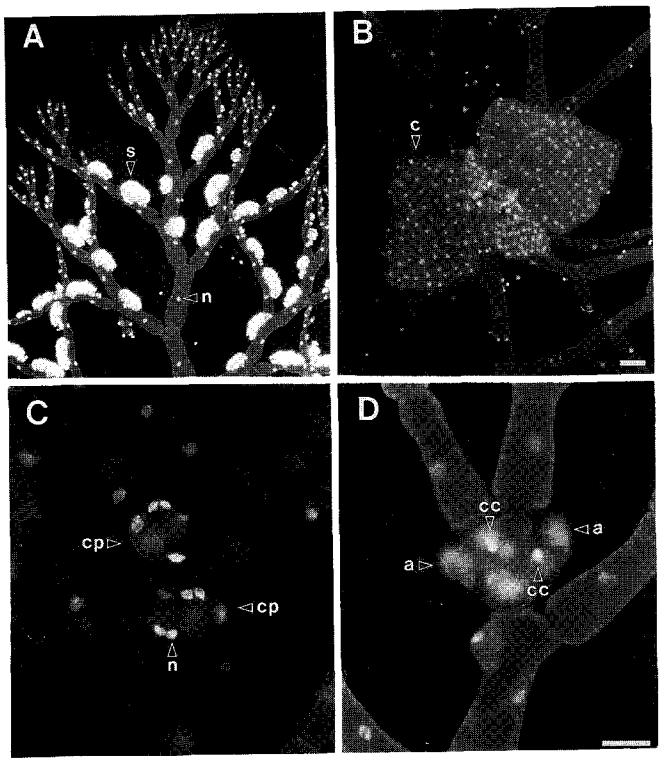

Fig. 2. Fluorescent micrograph with DAPI-staining of *Aglaothamnion oosumiense* Itono. A; Male plant, B; Carposporophyte after fertilization, C; Carpogonial branches, D; Female plant with connecting cell and auxiliary cell. (Scale bar; A, B=160 μm, C, D=67 μm, a: auxiliary cell, ac; axial cell, c; cystocarp, cb; carpogonial branch, cc; connecting cell, n; nucleus, s; spermatangium).

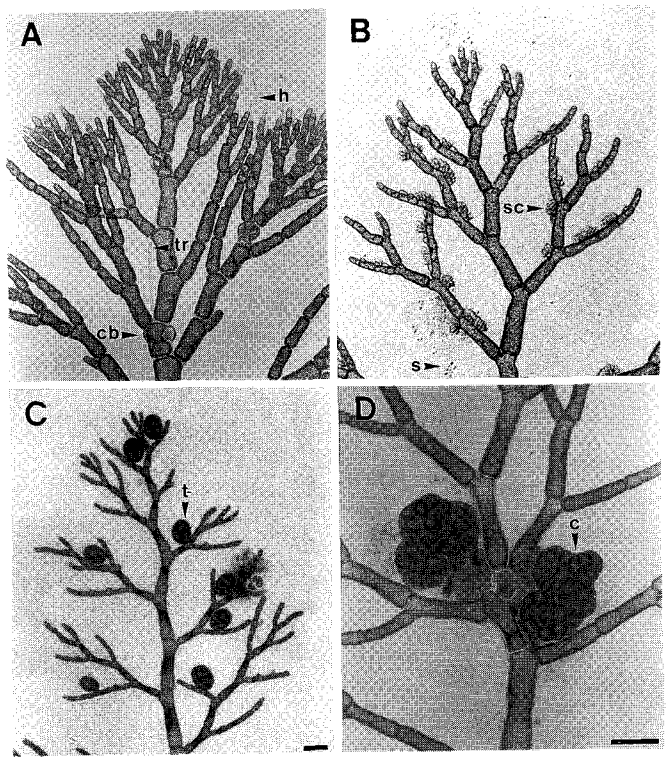

Fig. 3. Differential interference micrograph of *Aglaothamnion oosumiense* Itono.
A; Female plant with hair cells and carpogonial branches, B; Male plant developing spermatangial cluster, C; Tetrasporophyte, D; Carposporophyte. (scale bar; A, B, D=130 μm, C=260 μm, c; cystocarp, cb; carpogonial branch, h; hair cell, s; spermatangium. sc; spermatangial cluster, t; tetrasporangium, tr; trichogyne).

fertilization. Both pericentral cells cut off an auxiliary cell and a supporting cell, respectively, in one or two days after spermatial binding to the trichogyne (Fig. 4B). Each daughter cell of the fertilized carpogonium (fc in Fig. 4C) enlarged towards the auxiliary cell and cut off connecting cell (Fig. 4D). The diploid nuclei of each zygotic cell transferred to auxiliary cells via connecting cells (Fig. 2D).

The auxiliary cell enlarged and divided approximately into half to form a foot cell and the gonimoblast initial (Fig. 5A). The gonimoblast initial cut off the first gonimolobe initial from its distal end and so on (Fig. 5B). The gonimolobe filaments were dichotomously branched and formed a compact lobed mass of cells, most of which developed into carposporangia when mature (Fig. 5C). One successful fertilization, therefore, could produce two carposporophytes formed oppositely side by side. No sterile group of cells was formed in a fertile segment during the post-fertilization processes, and the growth of indeterminate axis did not stop during the maturation of carposporophyte (Figs 1D, 2B, 3D, 5C).

Culture Experiments: From excised vegetative apices of field-collected *Aglaothamnion oosumiense*, a tetrasporophyte (#0623) produced new sporangia after two months. Tetraspores grew into gametophytes; a male plant (#0624) produced spermatangia after two weeks and a female plant (#0625) produced procarps after one month. Hair cells were developed at the tip of lateral branches of a female plant (Fig. 1A). The spermatia bound to hair cells as well as trichogynes. The spermatial binding to hair cells and trichogynes was highly selective in this species. More than 95% of spermatia attached on surfaces of hair cells or trichogynes of the female thalli. After fertilization, two carposporophytes developed at a fertile segment. Carposporophytes released carpospores one month after fertilization. Carpospores germinated to form mature tetrasporophytes in two months.

The Eochungdo isolate of *Aglaothamnion oosumiense* showed a *Polysiphonia*-type of life history with isomorphic generations of tetrasporic and gametophytic phases.

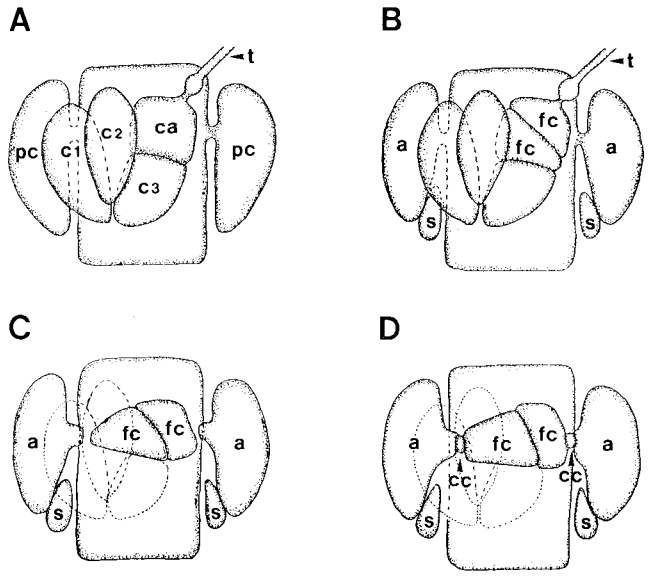

Fig. 4. Diagram of post-fertilization process of *Aglaothamnion oosumiense* Itono.
A; Carpogonial branch and pericentral cell, B; Carpogonium divided after fertilization. Auxiliary cells were divided at this time, C; Elongation of fertilized carpogonium to auxiliary cell, D; Fusion between connecting cell and auxiliary cell. (a; auxiliary cell, c; carpogonial branch 1, 2, 3, cc; connecting cell, fc; fertilized carpogonium, pc; pericentral cell, s; supporting cell).

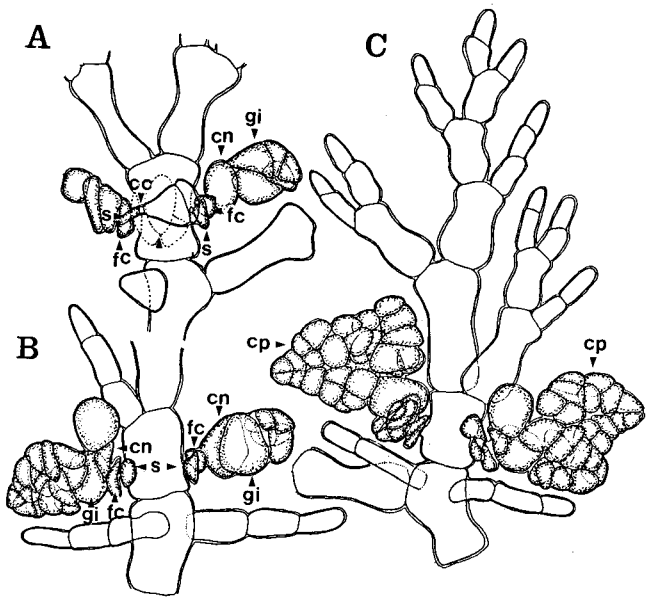

Fig. 5. The development of female reproductive structures of *Aglaothamnion oosumiense* Itono. A, B; Development of gonimoblast in young carposporophyte after fertilization, C; Mature carposporophyte (cc; connecting cell, cp; cystocarp, cn; central cell, fc; foot cell, gi; gonimoblast initial, sp; supporting cell).

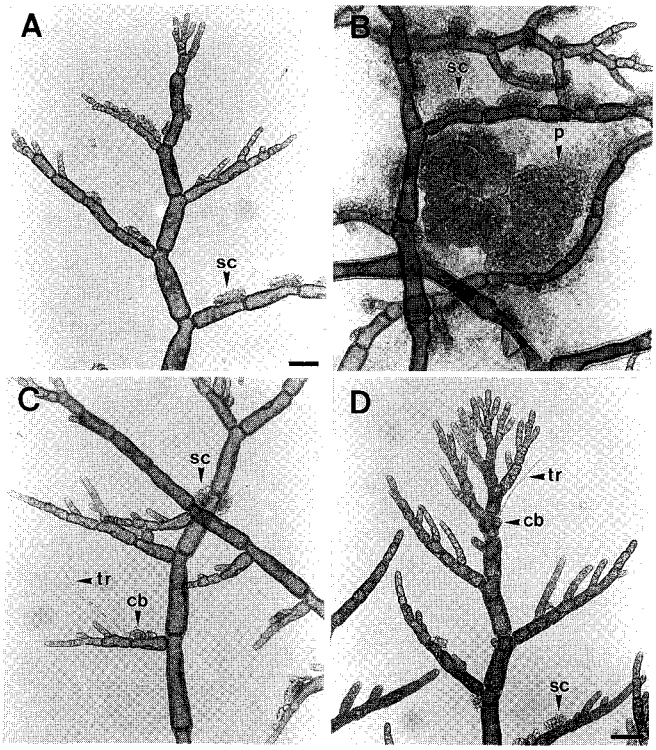

Fig. 6. Differential interference micrograph of *Aglaothamnion oosumiense* Itono.
A; Male plant of Shimoda isolate. B; Plant with Parasporangium from Eochugdo isolate. C; Bisexual plant of Shimoda isolate. D; The same of Eochungdo isolate. (scale bar; A, B, C, D=200 μm, cb; carpogonial branch, p; parasporangium, sc; spermatangial cluster, tr; trichogyne).

Some unusual reproductions, however, were observed (Fig. 6). About 2% of male plants developed parasporangia in addition to spermatangia (Fig. 6B). The paraspores released and developed into male plants (95.2%) or parasporangiate male plants (4.8%) again. Although the percentage of parasporangiate male plants increased a little (5-10%) at the successive generation, only a few paraspores developed into parasporangiate plants again. There was no significant differences in the percentage of parasporangiate plants according to the environmental conditions attempted.

Bisexual plants were also observed from the Eochungdo and Shimoda isolates (Fig. 6C, D). Less than 1% of the tetraspore germlings developed into bisexual plants. The position of carpogonial branch was different in the bisexual plants originated from Eochungdo isolates and Shimoda isolates (Fig. 6C, D). The difference between the bisexual plants and the parasporagiate plants was irreversibility of the former. Bisexual plants never became unisexual plants again, but parasporangiate plants often did not produce parasporangia any

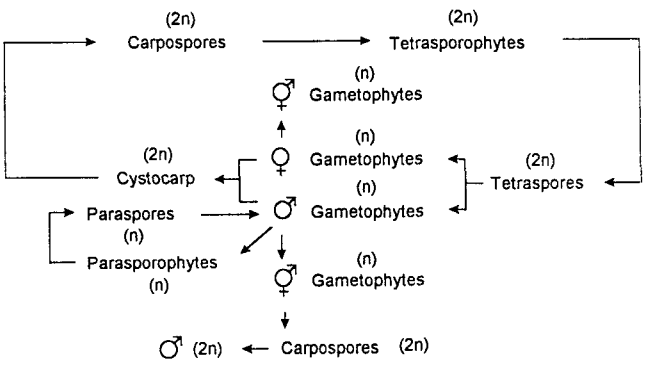

Fig. 7. Summarized life history of *Aglaothamnion oosumiense* Itono.

more regardless of environmental conditions. The life history of *Aglaothamnion oosumiense* is shown in Fig. 7.

Plants in culture showed the same branching pattern as in the field. During three years of cultivation under various environmental conditions, only female plants developed hair cells. Field collected female plants often had hair cells too. Male plant and tetrasporic plant never had hair cells both in field and culture condition. The sizes of axial cell and the curved lateral branch changed according to environmental conditions. Generally the high temperature (20-25°C) and high light intensity (20-30 μmol $cm^{-2}s^{-1}$) induced rotated branching system, small axial cells and short lateral branches. A flat form of thallus was more common in the low temperature (15°C) and low light intensity (5-10 μmol $cm^{-2}s^{-1}$). The sizes of axial cell and lateral branch were longer in this condition.

Cross experiment attempted with reciprocal crosses between Eochungdo isolates and Shimoda isolates successfully produced the carposporophytes which released carpospores in four weeks.

DISCUSSION

The Korean plants of *Aglaothamnion oosumiense* agreed well with the species originally described by Itono (1971) in branching pattern, height, and shape of apical cells. Although some processes are described for the first time in this study, the developments of reproductive structures and post-fertilization process were also basically similar to the original description (Itono 1971, 1977). Korean plants, however, were different from Itono's by having hair cells in female plants.

The occurrence of hair cells has been reported in several genera of Ceramiaceae especially in the genus *Antithamnion* (e.g. Cormaci and Furnari 1989), *Callithamnion* and *Aglaothamnion* (Magruder 1984). The hair cells in *Callithamnion* and *Aglaothamnion* have been generally interpreted as a result of some culture condition or as a character on population level which can be reversed by a long-term culture (Sundene 1964a, 1964b; Itono 1977). The presence of hair cells in *Callithamnion* (Price 1978) and *Acrochaetium* was supposed due to high light intensities for some culture conditions (Kim *et al.* 1996).

Magruder (1984), however, reported selective spermatial binding to hair cells as well as trichogynes in *Aglaothamnion neglectum*, and suggested that spermatia of this species might first attach to hair cells and later bind to a nearby trichogyne. Recently, Kim and Fritz (1993a, 1993b) also observed selective spermatial binding to hair cells in *Antithamnion nipponicum*, *A. aglandum*, and *A. sparsum*. They suggested that the hair cells might play a role as an additional collecting device for spermatia (Kim *et al.* 1996). The spermatial binding to hair cells as well as trichogynes of *Aglaothamnion oosumiense* is highly selective supporting Kim and Fritz's (1993a) hypothesis. As the hair cells do some important role during fertilization and they are produced on female plants regardless of environmental condition, the presence or absence and the shape of hair cells should be accepted as a new character in the genus *Aglaothamnion*.

The life history of *A. oosumiense* was described for the first time in this study. The occurrence of parasporangiate plants during the culture is of interest. This unusual reproduction is relatively common in the Tribe Callithamnieae including the genera *Aglaothamnion*, *Callithamnion*, and *Seirospora* (L'Hardy-Halos and Maggs 1991). In the study of life history of *Callithamnion hookeri*, Rueness and Rueness (1978) reported that parasporangiate plants mainly distributed northern limit of the species and suggested that they might have evolved to overcome unfavorable condition for sexual reproduction. The occurrence of parasporangiate plants in *A. oosumiense*, however, did not have any relations with environmental conditions. The percentage of parasporangiate plants was almost same regardless of environmental conditions, and most of the paraspores developed into normal male plants again. Parasporangiate plants, therefore, does not appear due to mutations or irreversible genetic changes.

The taxonomic position of *A. oosumiense* comes into question now because of the morphological similarity to *Aglaothamnion callophyllidicola* (Yamada) Boo, Lee, Rueness et Yoshida (= *Callithamnion callophyllidicola*). In

Table 1. A comparison of some taxonomic characters among *Aglaothamnion oosumiense* Itono and its related species

Characters	*C. pashale*	*C. minutissima*	*A. callophyllidicola*	*A. oosumiense*	*A. oosumiense*
Type locality	Easter Island, Chile	Hayama, Sagami, Provice, Japan	–	Tajiri, Oosumi Peninsula, Japan	–
Thallus	erect (2.5 cm)	erect (0.2-2.5 cm)	erect (0.5-2 cm)	erect (2.5 cm)	erect (2.5 cm)
Axis	naked	naked	naked	naked	naked
Lower axial cell	1.5-2.5:1 L/B	70-100 μm 1.5:1 L/B	70-90 μm X 200 μm 2.4-2.8:1 L/B	45 μm 2.5:1 L/B	80 mm X 200 μm 2.5-4.5:1 L/B
Branching pattern	alternate distichous multifarious in part	dichotomous in general	alternate to subdichotomous,	alternate to pinnate, distichous	alternate to dichotomous, brachiate
Lateral	4-5 order	–	3-4 order	3 order	3-4 order
Apex	–	obtuse	blunt	blunt	blunt
Grand cell	absent	absent	absent	absent	absent
Spermatangia	seriate	seriate	seriate	seriate	seriate
Cystocarp	nearly spherical	lobed	lobed	lobed irregular	lobed to subspherical
Tetrasporangia	45-55 μm in diam. solitary sessile	70 μm X 45 μm tetrahedral sessile	40-55 μm X 60-70 μm tetrahedral sessile	70 μm X 27 μm tetrahedral sessile	70 μm X 50 μm tetrahedral sessile, seriate
References	Børgesen (1924)	Yamada (1944)	Boo *et al.* (1991)	Itono (1971)	This study

the original description of *A. oosumiense*, Itono (1971) reported that this species was distinguished from *Callithamnion callophyllidicola* in having uninucleate vegetative cells, lobed gonimolobes, blunt apex and the absence of gland cells which was reported by Yamada (1932) in original description of the latter. Recent studies by Boo *et al.* (1989, 1991) on the type specimen of *Callithamnion callophyllidicola*, however, showed that there was almost no difference between the two species (Table 1). They stained part of *A. callophyllidicola* with DAPI and found that this species had a uninucleus (Boo *et al.* 1991). The carposporophyte in the type specimen had a lobed form like *Aglaothamnion* species. The gland cells were not observed from the thorough examination of the type specimen by Boo *et al.* (1991). Yamada's (1932) descriptions on the gland cells of *Callithamnion callophyllidicola*, therefore, were wrong.

Transferring *C. callophyllidicola* to the genus *Aglaothamnion*, Boo *et al.* (1991) treated *Callithamnion minutissima* Yamada (1944) as a later synonym. They suggested that *Aglaothamnion oosumiense* may also be a synonym of *Aglaothamnion callophyllidicola*. The taxonomic characters of *Aglaothamnion oosumiense* and its related species are summarized in Table 1.

In conclusion, *A. oosumiense* shows a rather moderate morphological differentiation from its closest relative species, *A. callophyllidicola*, and the remaining characters which distinguish the two species, such as the shape of apex and the size of axial cells, are found to be unstable according to environmental conditions. Although we have to consider the narrow species concept in the Ceramiaceae (Kim *et al.* 1996), *A. oosumiense* should be treated as a later synonym of *A. callophyllidicola*. The studies on type specimen, however, are essential to do this.

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