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# The life history of *Ahnfeltia concinna* J. AGARDH (Rhodophyta, Gigartinales) from Japan[1),2)]

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The life history of the red alga *Ahnfeltia concinna* J. AGARDH from Japan was completed in laboratory culture. Carpospores from field plants germinated to form crustose thalli. The crustose thalli bore 2-8 tetrasporangial nemathecia which bulged from the thallus surface. Intercalary tetrasporangia were formed in 2-3 successive cells of a single filament of the nemathecia. Tetrasporelings gave rise to basal discs from which upright axes developed. The upright axes became fertile before producing branches and formed spermatangia and procarps on separate plants. They continued to grow into dichotomously divided thalli similar in morphology to field plants. Spermatangia were formed in a sorus and released cylindrical spermatia. Procarps were formed in groups and each consisted of a large supporting cell, a three-celled carpogonial branch and a sterile cell. Excised vegetative apices from single field male and female plants grew well and formed reproductive structures in a manner similar to that of plants derived from tetraspores. Female plants bore cystocarps only when crossed with male plants and discharged viable carpospores through carpostomes.

*Key Index Words*: Ahnfeltia; A. concinna; *crustose tetrasporophyte*; *nemathecia*; *Gigartinales*; *life history*; *Phyllophoraceae*; *Rhodophyta*; *taxonomy*.

MAGRUDER (1977) described the life history of *Ahnfeltia concinna* J. AGARDH (Phyllophoraceae) from Hawaii. It involves the alternation of upright dioecious gametophytes with a crustose tetrasporophyte which forms intercalary catenate tetrasporangia in distinct sori. On west coast of the Pacific *A. concinna* has been recorded from various localities of middle to southern Japan (OKAMURA 1936). Female gametophytes with cystocarps were described by OKAMURA (1922) and MIKAMI (1965), but male gametophytes and tetrasporophytes have not been reported yet. INOH (1947) found that upright axis primordia were differentiated from carposporelings of Japanese *A. concinna*. This suggested that the alga has a direct-type of life history. The present study was conducted to clarify the life history of *A. concinna* growing in Japan and to compare it with that of the Hawaiian *A. concinna* as reported by MAGRUDER (1977).

## Materials and Methods

Female plants with mature cystocarps and male plants with spermatangia were collected at Susaki (34°39′N 138°58′E), Shimoda, Shizuoka Pref. on August 2, 1980 and on April 3, 1981 and at Jogashima (35°08′N 139°38′E), Kanagawa Pref. on February 20, 1982. Carpospores were isolated into unialgal

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culture using Susaki material collected on August 2, 1980 (culture nos. 653 and 654) according to methods reported for *Neodilsea crispata* (MASUDA 1973). Reproductively sterile apices of branches of female and male plants for Susaki material (nos. 666 male, 667 female, 841 male, 842 male, 843 female and 844 female) and Jogashima material (nos. 1183 female, 1184 male, 1185 male, 1186 male and 1187 female) were cleaned by Kimwipe tissues, excised about 200 $\mu$m long with a scalpel (Feather No. 15) and were introduced individually into screw cap tubes (18 mm×135 mm) containing 10 ml of PES medium. Two months after inoculation clean apices were transferred to culture vessels (65 mm×80 mm) containing 200 ml of medium.

The cultures were placed in plant growth chambers illuminated with cool-white fluorescent lamps (2500–3000 lux). The temperatures and photoperiods were regulated in the following combinations: 15°C, 16:8 LD (light and dark cycle); 15°C, 8:16 LD; 20°C, 16:8 LD and 20°C, 8:16 LD. Mixed cultures of mature female and male plants were placed on a Taiyo R-II Rotary Shaker at 90–100 rpm.

Microscopic examinations were done chiefly on living material and also sometimes on material preserved in 70% ethyl alcohol. Sections were made by hand using a straight-edge razor and pith stick and stained with 0.5% (w/v) cotton blue in a lactic acid/phenol/glycerol/water (1:1:1:1) solution. Voucher specimens are deposited in the Herbarium of Faculty of Science, Hokkaido University, Sapporo (SAP 032220–032225). Stock cultures of male (653, 666 and 1186) and female (653, 667 and 1187) are maintained in a plant growth chamber at the Center for Experimental Plants and Animals of Hokkaido University.

## Results

*Carpospore culture:* Liberated carpospores are globular, light red in color and measure 15–20 $\mu$m in diameter (Fig. 1, A). They were first cultured at 15°C, 16:8 LD and 20°C, 16:8 LD. They attached to the substrate and divided into two cells within 2 days (Fig. 1, B). The vast majority of these cells then divided successively and formed circular crusts (Fig. 1, D–E). However, some of these bore a filamentous outgrowth (Fig. 1, C) which eventually formed crusts. The crusts grew both concentrically by a marginal meristem and upward in the central portion. They reached 300–600 $\mu$m in diameter at 15°C, 16:8 LD and 680–1150 $\mu$m in diameter at 20°C, 16:8 LD 1 month after initiation. Most formed 10–18 colorless hairs from the superficial cells during this period. These hairs were 150–500 $\mu$m in length and 5–6 $\mu$m in diameter near the proximal portion. Each of one month old cultures grown at 15°C, 16:8 LD and 20°C, 16:8 LD was divided into two groups; one group was shifted to 15°C, 8:16 LD and 20°C, 8:16 LD and the other group was maintained at 15°C, 16:8 LD and 20°C, 16:8 LD. The crusts grew well under all the culture conditions attempted and the cuticular surface peeled off but was repeatedly regenerated as did cultured foliose thalli of *Gigartina johnstonii* DAWSON (WEST and GUIRY 1982).

The crusts reached reproductive maturity and formed tetrasporangial nemathecia at 20°C, 16:8 LD (Fig. 1, F) 4 months after initiation, at 15°C, 16:8 LD (Fig. 1, G) and 20°C, 8:16 LD for 5 months after initiation, and at 15°C, 8:16 LD 9 months after initiation. The fertile crusts were 7–19 mm in diameter and 80–110 $\mu$m in thickness in the center. They were composed of a monostromatic hypothallus, which consisted of radiating filaments, and a polystromatic perithallus, which consisted of coalescent erect filamets (Fig. 1, I-J; 2, A-B). The perithallus was composed of 11–14 cell-layers at the center of the crust. Erect filaments of the perithallus were dichotomously divided (Fig. 2, A-B) and the cells of adjacent filaments were frequently connected by secondary pit plugs (Fig. 2, A-B).

Two to eight nemathecia were formed

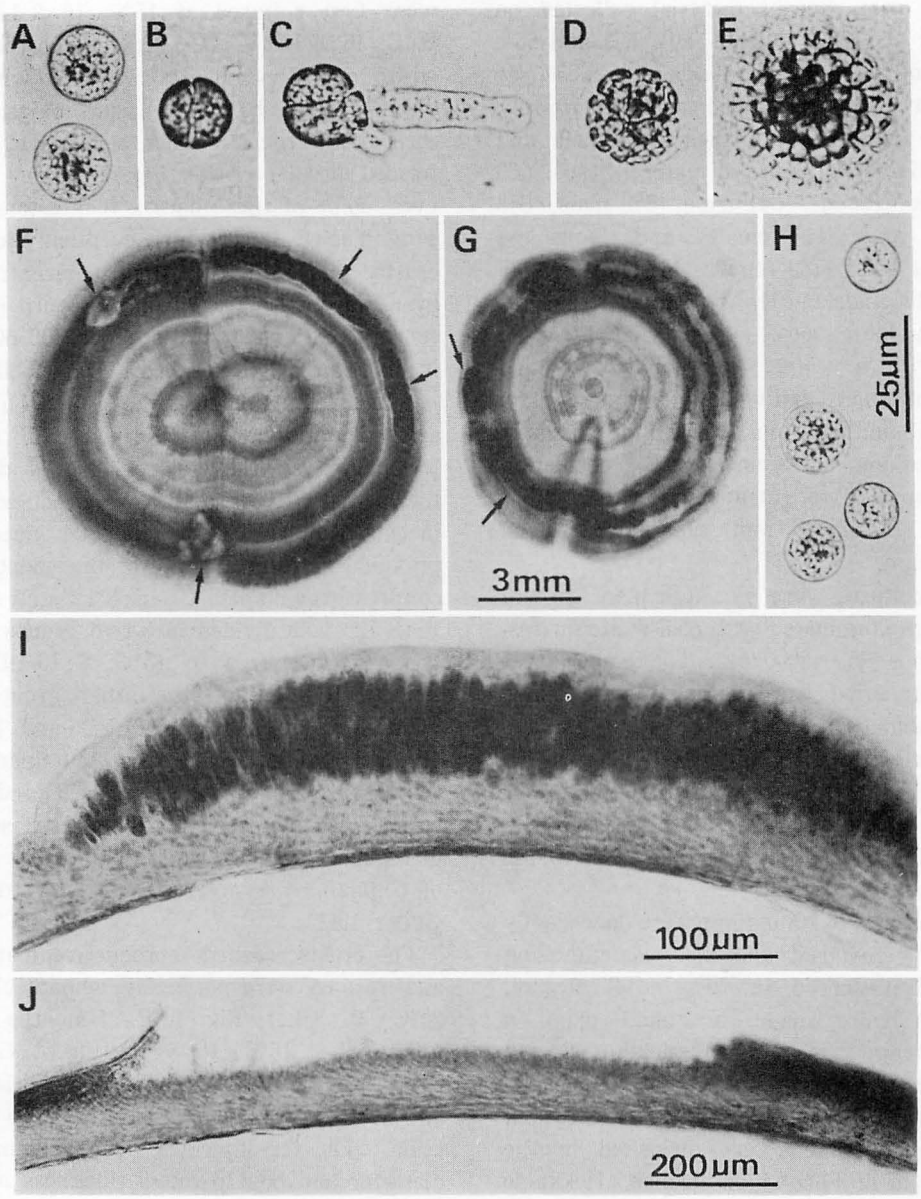



Fig. 1. Carpospores and cultured tetrasporophytes of *Ahnfeltia concinna*. A. Carpospores from a field-collected plant. B–E. Carposporelings grown at 20°C, 16 : 8 LD (culture no. 653) : B, two days old; C–D, five days old; E, ten days old. F–G. Fertile tetrasporangial crusts bearing nemathecia (arrows) : F, two coalescent crusts (4 months old) grown at 20°C, 16 : 8 LD (no. 653) ; G, five months old crust grown at 15°C, 16 : 8 LD (no. 654). H. Released tetraspores from crusts shown in F. I–J. Radial sections of crusts shown in F, indicating the nemathecium before spore release (I) and that after spore release (J). Scale in G applies also to F; scale in H applies also to A–E.

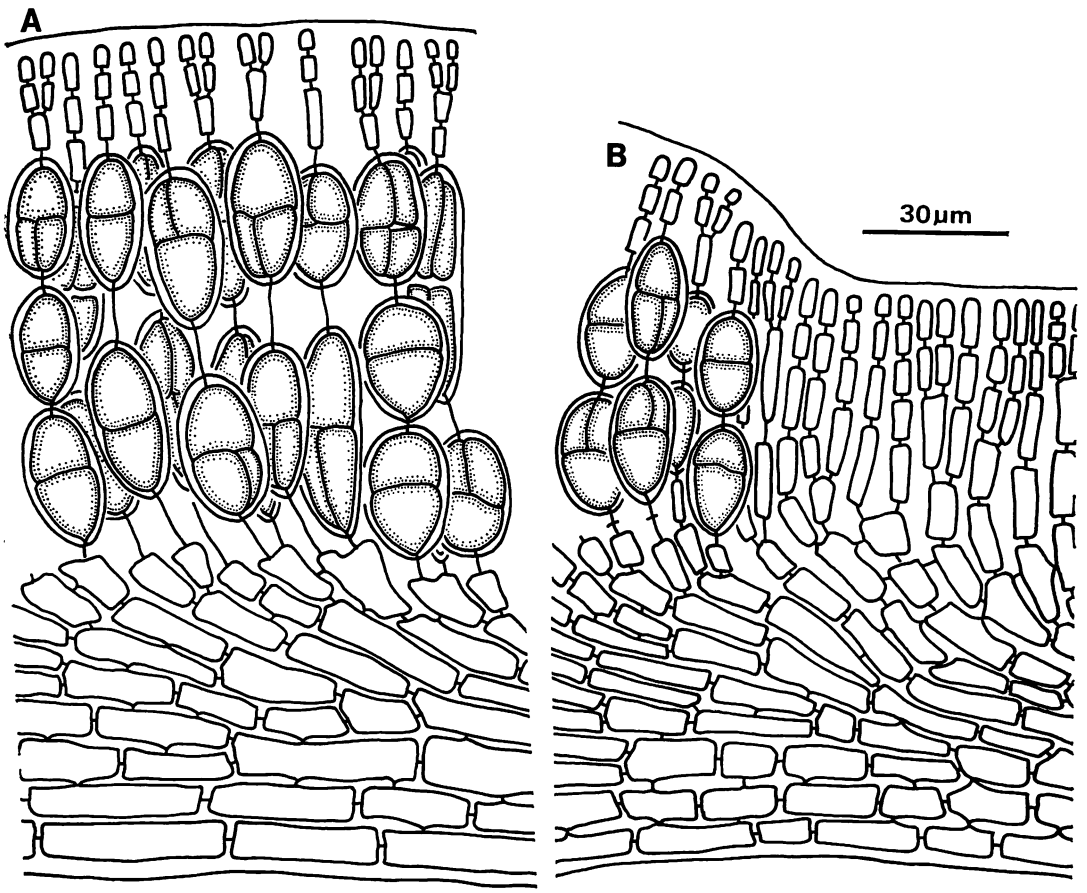



Fig. 2. Cultured tetrasporophyte of *Ahnfeltia concinna*. A-B. Radial section of a crust shown in Fig. 1, F through a nemathecium: A, central portion of the nemathecium; B, marginal portion of the nemathecium.

along a marginal concentric ring of eachcrust (Fig. 1, F-G). The majority of the nemathecia were almost circular to elliptical and 550-1400 μm in diameter. Some nemathecia were band-shaped and 5-15 mm long and 800-1400 μm wide. These band-shaped nemathecia were commonly formed on the crusts grown at 20°C, 16:8 LD (Fig. 1, F). The nemathecia were 130-200 μm thick in the center. Intercalary tetrasporangia were formed on the erect filaments of the nemathecia (Fig. 2, A-B). They were formed in 2-3 successive cells of a single filament. The terminal 2-4 cell-rows of fertile filaments remained sterile. Some of the cell-rows were branched dichotomously as were those of the Hawaiian alga (MAGRUDER 1977, Fig. 13). These sterile cells became paler in color as the tetrasporangia developed. Mature tetrasporangia were ellipsoid, 37.5-42.5 μm long and 17.5-22.5 μm wide, and divided cruciately. The tetrasporangia of each nemathecium released tetraspores almost synchronously. The tetraspores were slightly smaller than the parent carpospores at 12.5-16.3 μm in diameter (Fig. 1, H). After the spore release, the nemathecium disintegrated leaving the lower vegetative portion (Fig. 1, J).

*Tetraspore culture:* Tetraspores from cultured plants were grown at 15°C, 16:8 LD and 20°C, 16:8 LD. They germinated and grew into discoid thalli in a manner similar to that of carpospores described above (Fig. 3, A-C). After 3 months they

reached 4-6 mm in diameter and began to produce upright axes in a concentric ring (Fig. 3, D). The sructure of the basal discs was similar to that of the tetrasporophytic crusts. The upright axes became fertile before producing branches and formed spermatangia and procarps on separate plants 5 months after germination.

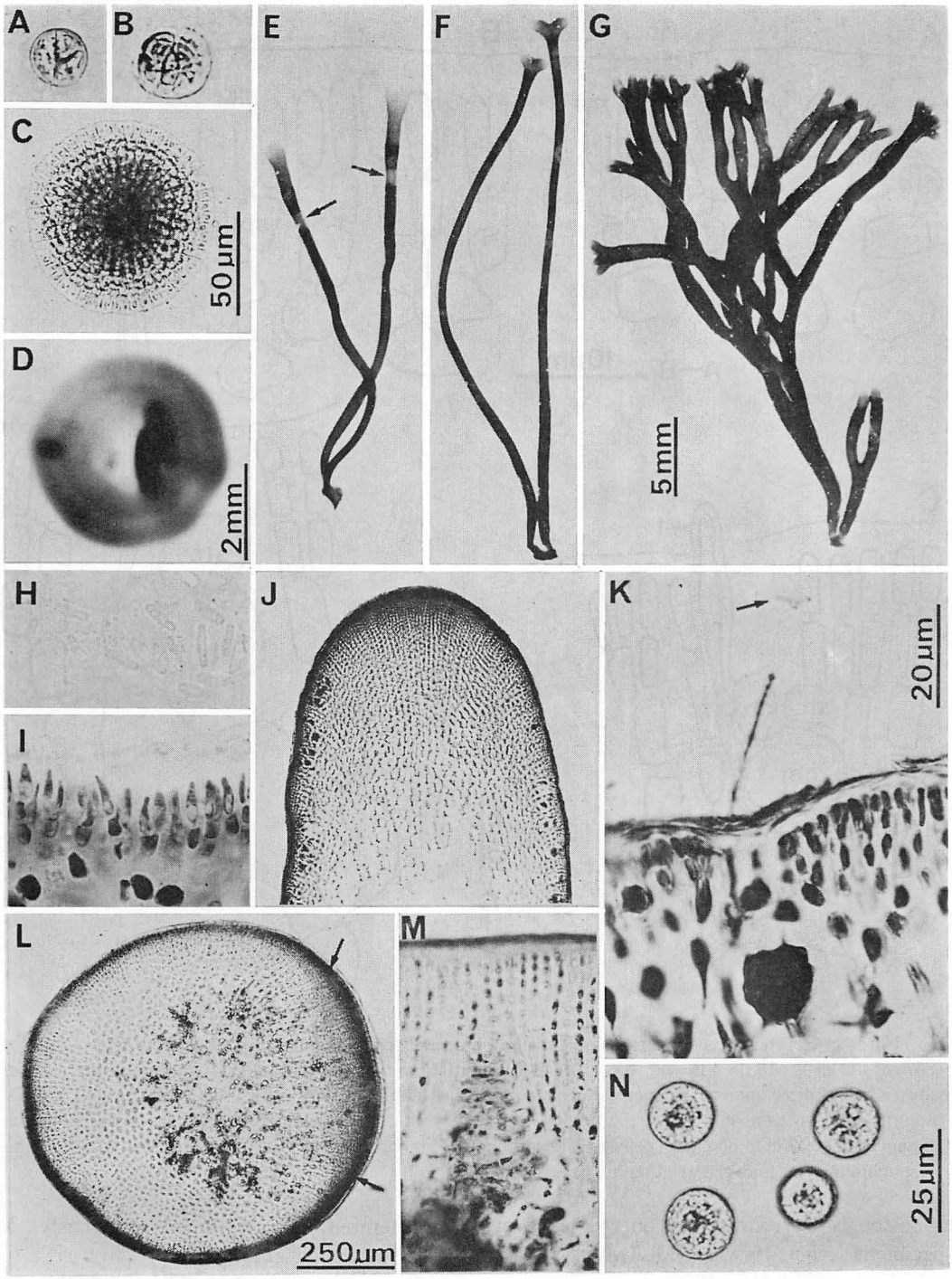
Some tetrasporelings grew into spherical masses of cells with a few rhizoidal filaments or without any rhizoidal filaments. None of these sporelings formed a marginal meristem. The sporelings attached loosely to the substrate and with the slightest mechanical disturbance they became free from the substrate. They developed single upright thalli. One month old upright thalli reached 300-500 $\mu$m in length and 190-220 $\mu$m in diameter (Fig. 5, A). They formed spermatangia and procarps on separate plants (Fig. 5, B-C) 3 months after germination. Both the detached and attached male and female thalli grew into dichotomously branched terete thalli, which were similar in morphology to those of field plants, while continuing to form reproductive structures on their upper portions. However, the upright thalli showed a somewhat different morphology according to temperature. The thalli grown at 15°C, 16: 8 LD (Fig. 3, G) were thicker and much more branched than those grown at 20°C, 16:8 LD (Fig. 3, E-F). Of 80 detached and attached plants cultured from single tetraspores, 38 were male and 42 were female.

Spermatangia were formed in a sorus near the branch apex of male thalli. One or two spermatangia were produced from a single spermatangial parent cell (Fig. 3, I; 4, A-B). Spermatia were released forming an opaque, white cloud around the sorus. The spermatia were cylindrical, 6.4-15.0 $\mu$m in length and 2.4-3.8 $\mu$m in diameter (Fig. 3, H). After release of spermatia, the sorus became paler in color than the vegetative parts and showed a banded appearance (Fig. 3, E).

Procarps were borne within the cortex near the branch apex of female thalli (Fig. 3, J). The procarps were formed in groups and each procarp consisted of a large supporting cell and a three-celled carpogonial branch. A single sterile cell was borne on the first cell of the carpogonial branch (Fig. 4, C-D) as in field plants of this species (MIKAMI 1965).

Isolated female plants did not produce cystocarps. After starting mixed cultures of female thalli with numerous procarps and male thalli with numerous spermatia on a shaker, the spermatium attached to the trichogyne (Fig. 3, K). After the trichogyne degenerated, many gonimoblast filaments issued from the supporting cell, which functioned as an auxiliary cell, and grew inward through the medulla (MAGRUDER 1977). The cortex around the fertilized procarp became thicker (Fig. 3, L). Mature cystocarps appeared on all the females after 1 month at 20°C, 16:8 LD and discharged viable carpospores (Fig. 3, N) which gave rise to crustose thalli. The cystocarps were provided with specialized pores (carpostomes) in the thickened cortex (Fig. 3, M) through which carpospores were discharged. The

Fig. 3. Cultured gametophytes of *Ahnfeltia concinna* (no. 653). A-D. Tetrasporelings grown at 20°C, 16: 8 LD: A, two days old; B, four days old; C, eighteen days old; D, three months old one issuring upright axes. E-G. Twelve months old fertile gametophytes: E, male plant grown at 20°C, 16: 8 LD (arrows indicate band-shaped spermatangial sori after release of spermatia); F, female plant grown at 20°C, 16: 8 LD; G, female plant grown at 15°C, 16: 8 LD. H. Released spermatia. I. Longitudinal section through a spermatangial sorus, showing a single layer of elongated spermatangia. J. Longitudinal section of a branch apex of a female plant, showing procarps stained with cotton blue. K. Longitudinal section of a procarpic branch, showing fertilization between a trichogyne and a spermatium (arrow). L. Cross section of a cystocarp (arrows indicate the thickened cortex). M. Carpostome formed in the thickened cortex. N. Released carpospores. Scale in C applies also to M; Scale in G applies also to E-F; scale in L applies also to J; scale in N applies also to A-B and H-I.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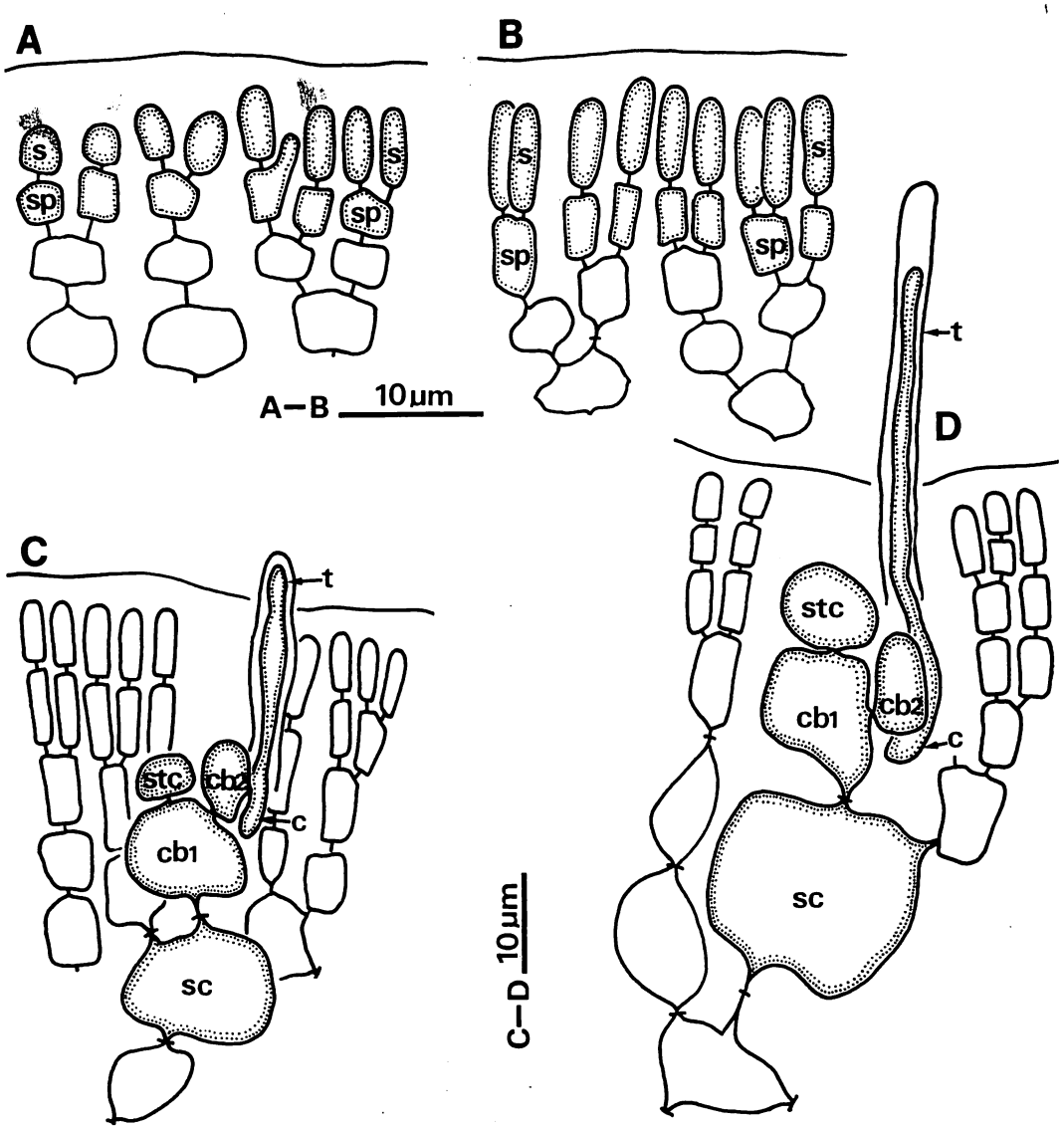


Fig. 4. Reproductive structures of cultured male and female gametophytes of *Ahnfeltia concinna* grown at 20°C, 16: 8 LD (no. 653). A-B. Longitudinal section through a spermatangial sorus, showing the development of spermatangia (sp, spermatangial parent cell; s, spermatangium). C-D. Longitudinal section of a procarpic branch, showing young (C) and mature (D) procarps; note the supporting cell (sc), the two cells of the carpogonial branch ($cb_1$ and $cb_2$), the sterile cell (stc), the carpogonium (c) and the trichogyne (t).

carpostomes were described on the basis of specimens from Hawaii (MCFADDEN 1911) and Japan (MIKAMI 1965). However, no cystocarp development was observed on the females mixed with males at 15°C, 16:8 LD for 2 months. On upright thalli and basal discs of all cultured plants the cuticular surface peeled off and it was repeatedly regenerated as mentioned previously for tetrasporangial crusts.

*Branch apex culture of gametophytes:* Excised vegetative apices of branches were first cultured at 15°C, 16:8 LD. Two-month-old cultures were divided into two groups and grown at 15°C, 16:8 LD and 20°C, 16:8 LD. One month later the

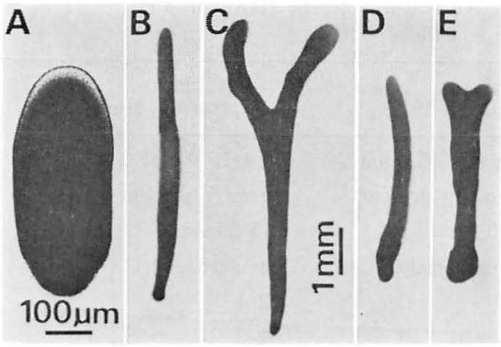


Fig. 5. Cultured gametophytes of *Ahnfeltia concinna*. A-C. Plants derived from spherical masses of cells, which originated from single tetraspores, and grown at 20°C, 16 : 8 LD (no. 653) : A, one month old tetrasporeling issuing a single upright axis; B, three and a half months old male thallus; C, three and a half months old female thallus. D-E. Three months old plants derived from excised apices of branches grown at 15°C, 16 : 8 LD : D, male thallus (no. 666) ; E, female thallus (no. 667). Scale in C applies also to B and D-E.

majority of the plants reached reproductive maturity under both regimes before producing branches and formed spermatangia and procarps on separate individuals (Fig. 5, D-E). They grew into dichotomously branched thalli in a manner similar to that of plants derived from tetraspores. All female isolates (Susaki 667, 843 and 844; Jogashima 1183 and 1187) did not produce cystocarps when they were separated from male isolates. These female isolates were crossed with male isolates derived from branch apices (Susaki 666, 841 and 842; Jogashima 1184, 1185 and 1186). Cystocarps were formed on all females of the 30 attempted crosses using these 5 female and 6 male isolates and viable carpospores were discharged within 1 month at 20°C, 16 : 8 LD.

## Discussion

The life history of *Ahnfeltia concinna* studied here involves the alternation of upright dioecious gametophytes with a crustose tetrasporophyte. INOH (1947) described upright axis primordia which were differentiated from 7-day-old carposporelings of *A. concinna* collected from Shikine Island situated about 45 km to the southeast of Susaki, Shimoda. This suggests that some local populations of this species may recycle directly without bearing crustose tetrasporophytes. Further life-history studies of *A. concinna* from other localities including Shikine Island are needed to elucidate this problem.

The observed life-history pattern is similar to that reported for the Hawaiian *A. concinna* (MAGRUDER 1977). However, the following two morphological features of the alga under study do not coincide with those of the Hawaiian *A. concinna*, although other quantitative features listed in Table 1 and gross morphological features of gametophytes are similar. The procarp of the Japanese alga always possesses a single sterile cell which was "not normally present" on the procarp of Hawaiian alga (MAGRUDER 1977, p. 199). The sterile cell has been found on the carpogonial branch of several species of the Phyllophoraceae : *Ahnfeltia gracilis* (YAMADA) YAMADA et MIKAMI (MIKAMI 1965), *A. yamadae* (SEGAWA) MIKAMI (MIKAMI 1965), *A. gigartinoides* J. AGARDH (DECEW, WEST and MASUDA, unpubl.), *A. paradoxa* (SURINGAR) OKAMURA (MASUDA unpubl.), *Gymnogongrus linearis* (C. AGARDH) J. AGARDH (DOUBT 1935), *G. flabelliformis* HARVEY (TOKIDA and MASAKI 1959, MIKAMI 1965, MASUDA 1981), *G. crustiforme* DAWSON (WEST, DECEW and MASUDA unpubl.), *Stenogramme interrupta* (C. AGARDH) MONTAGNE (KYLIN 1956) and *Phyllophora antarctica* A. et E. S. GEPP (MILLER pers. comm.). This seems to be a characteristic feature of the Phyllophoraceae or at least of the species group including *A. concinna*. Further investigation of the procarps of the Hawaiian *A. concinna* is needed. The tetrasporangia of the Japanese *A. concinna* are formed in nemathecia bulging from the thallus surface, whereas those of the Hawaiian alga are embedded in the thallus. Whether or not tetrasporangial sori are

Table 1. A comparison of some reproductive features of the Hawaiian and Japanese *Ahnfeltia concinna*.

| | Hawaii (MAGRUDER 1977) | Japan (present author) |
|---|---|---|
| Size of spermatia (length × diameter) | 8-14 μm × 3.5-5.0 μm | 6.4-15.0 μm × 2.4-3.8 μm |
| Sterile cell on carpogonial branch | not normally present | always present |
| Size of carpospores (diameter) | 9.5-18.0 μm | 15-20 μm |
| Tetrasporangial sorus | non-nemathecial | nemathecial |
| Number of sterile cap cell-rows | 2-4 | 2-4 |
| Number of tetrasporangia in series | 2-4 | 2-3 |
| Size of tetraspores (diameter) | 9.5-18.0 μm | 12.5-16.3 μm |

nemathecial is of considerable taxonomic significance at the species level (MASUDA *et al.* 1979). On the basis of this difference it may be reasonable to segregate the Japanese alga from *A. concinna* of which the type collection was made from the Hawaiian Islands (C. AGARDH 1822, J. AGARDH 1847). Of the *Ahnfeltia* species, *A. gigartinoides* seems to be most closely allied to *A. concinna*. YENDO (1916) stated that the type specimens of both species were hardly separable one from the other. *A. gigartinoides* from Mexico possesses a crustose tetrasporophyte which bears intercalary tetrasporangia in nemathecia (DECEW, WEST and MASUDA unpubl. cf. MASUDA *et al.* 1977, p. 71). The tetrasporangia of *A. gigartinoides* are fewer and smaller than those of *A. concinna*, 1-2 sporangia on each fertile filament and 18-39 μm long and 8-13 μm wide (cf. Table 1). The elucidation of the taxonomic relationship between the Hawaiian and Japanese *A. concinna* and the Mexican *A. gigartinoides* must await further detailed investigations, including hybridization experiments.

The tetrasporophytes of *Ahnfeltia concinna*, whether or not their tetrasporangial sori are nemathecial, are characterized by the production of catenate cruciate tetrasporangia which originate from intercalary cells of the erect filaments and distinguished from those of *A. plicata* (HUDSON) FRIES, the type species of the genus, which form single zonate tetrasporangia terminally on the erect filaments (FARNHAM and FLETCHER 1976, CHEN 1977). Upright thalli of *A. plicata* bear "monosporangia", which are probably equivalent to carposporangia, in external pustule-like nemathecia (ROSENVINGE 1931, GREGORY 1934, SCHOTTER 1968, FARNHAM and FLETCHER 1976). However, those of *A. concinna* produce internal cystocarps with carpostomes. These fundamental differences are of taxonomic significance at the generic level. Taxonomic revision of the genus *Ahnfeltia* is needed. The establishment of a new genus to accommodate *A. concinna* will be proposed by DECEW and SILVA (pers. comm.) at a later date (cf. SILVA 1979).

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**増田道夫：日本産サイミ（紅藻スギノリ目）の生活史**

サイミの果胞子と枝の先端部から培養を行い生活史を調査した。果胞子は発芽して殻状の四分胞子体になり，その表面に隆起したネマテシアを数個形成した。四分胞子嚢はネマテシア内の直立糸に 2-3 個連続して介生的に形成された。四分胞子の発芽体は雌雄異株の配偶体に生長し，精子嚢とプロカルプを生じた。プロカルプには1個の sterile cell が認められた。配偶体は生殖器官の形成を続けながら生長し，分枝した個体は天然産のそれによく似た形態を示した。枝の先端部の培養からも同様な生長を行う雌雄の配偶体が得られた。雌性配偶体は雄性配偶体と交配した時にのみ嚢果を形成し，果胞子を放出した。日本産のサイミはハワイ産のそれとはネマテシアを形成すること，及びプロカルプに sterile cell が存在することで異なり，今後両者の詳細な比較検討が必要である。(060 札幌市北区北10条西8丁目　北海道大学理学部植物学教室)