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The life history of *Leathesia japonica* INAGAKI (Phaeophyta, Chordariales) in culture

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A species in the Chordariales was linked through elucidation of its life history with a very simple member of the Ectocalpales. The heteromorphic and haplo- or diplo-biontic life history of *Leathesia japonica* from Wakasa Bay, Honshu, Japan was achieved in culture. Under cooler conditions, zoospore germlings from the unilocular sporangium gave rise the characteristic erect filaments, which were consistent with *Polytretus reinboldii* (REINKE) SAUVAGEAU (Ectocarpales). Unfused swarmers derived from the plurilocular sporangium on the *Polytretus*-like filaments developed into haploid and/or diploid *Leathesia* sporophytes, formerly identified as *L. japonica*. Under cooler conditions, the *Polytretus*-like filaments projected on the *Leathesia* sporophytes, as well. Karyological and morphological chimeras were observed in the same entity, a *Leathesia* sporophyte. The life history of *L. japonica* might support the FRITSCH's (1945) classification: the Chordariales should be merged in the Ectocarpales.

Key Index words: *Chordariales*; *Ectocarpales*; Leathesia; *life history*; Leathesia japonica; *Phaeophyta*; Polytretus; Polytretus reinboldii.

Leathesia japonica INAGAKI taxonomically belongs to the family Leathesiaceae in the Chordariales. The collections of the species were reported from the northern Pacific part of Japan (Rikuzen and Mutsu) and the middle part of Honshu facing the Japan Sea (Wakasa Bay) (INAGAKI 1958). In the genus *Leathesia*, 11 species have been reported as occurring in Japan and its vicinity by INAGAKI (1958). This author divided the genus *Leathesia* in two sections, section *Leathesia* containing three species, and section *Primariae* containing eight species. In the former section, the frond is hollow and its medullary layer is reticulated and composes of irregular polygonal cells. In the latter section, the frond is very small and solid, and its medullary cells are cylindrical or ellipsoid. *L. japonica* was placed in the latter section by INAGAKI.

Among three species in the former section, the life histories of *Leathesia difformis* (DANGEARD 1965) and *Leathesia saxicola* (AJISAKA unpublished), have been studied. However, until the present no life history study has been done for eight species belonging to the latter section. The following paper presents the life history of *L. japonica* in culture and its karyological and morphological observations. From this study, it has been found that *Polytretus*-like filaments projected on zoospore germlings of the so-called *L. japonica*.

Material and Methods

Sporophytes of *L. japonica* were collected at Obama in Wakasa Bay of Honshu Island facing the Japan Sea on May 6, 1979. Thalli were found growing epiphytically on *Sargassum hemiphyllum* (TURNER) C. AGARDH (Fig. 3 A), which grew on rocks one or two

meters below the low tide mark.

The mature sporophytes collected at low tide, were carried to the laboratory in a cool condition (ca. 5°C). For the culture study, the fertile fronds were rinsed throughly with several changes of autoclaved seawater and were dried for about one hour. And they were placed in the petri dishes containing the sterilized seawater until zoospores were obtained. The zoospores showing a negative phototaxis were washed 3-4 times in petri dishes containing the sterilized seawater by the micropipette method under a microscope. Then a little suspension of zoospores was poured over glass slides and left for half an hour for settlement. After the settlement, these slides were washed with a jet of the sterilized seawater and placed into glass vessels (6.5 cm×8.0 cm) containing 180 m*l* of medium.

For the investigation of the sexual reproduction, the mixing of swarmers liberated from the different individuals were done under a microscope.

For the single algal culture, each germling adhered to the glass slide was isolated with a micropipette and transferred to a culture test tube (2 cm×13 cm) containing 10 m*l* of medium. And the unilocular sporangia of the field and the culture plants, and also the plurilocular sporangia of the culture plants were cut off by needles under a microscope. Each of them was also transferred to a test tube with the micropipette method.

The culture medium used in this study was PROVASOLI's ES medium. The cultures were incubated in the freezer-incubators illuminated with the cool-white flourescent lamps (1500-3000 lux) under the following temperature-photoperiod regimes: 20°C: 16-$\overline{8}$ hr (Set 1); 20°C: 10-$\overline{14}$ hr (Set 2); 15°C: 14-$\overline{10}$ hr (Set 3); 15°C: 10-$\overline{14}$ hr (Set 4); 10°C: 14-$\overline{10}$ hr (Set 5); 10°C: 10-$\overline{14}$ hr (Set 6); 5°C: 10-$\overline{14}$ hr (Set 7); 25°C: 16-$\overline{8}$ hr (Set 8).

For the karyological observations, the germlings in the culture were fixed in alcohol: acetic acid (3 : 1), and the aceto-iron-haematoxylin-chloral hydrate staining method of WITTMANN (1965) was used.

Results

The culture of zoospores from the sporophytic frond (Fig. 3 A) taken from the field were started on May 8 and 9, 1979. The fertile fronds of the field material had only unilocular sporangia on the basal cells of the assimilating filaments (Fig. 3 B). The mature unilocular sporangium was usually obovoid or ellipsoid, measuring 69-88 μm×27-37 μm in size.

1) Development of zoospore germlings

The zoospore from the unilocular sporangium was measured 6.0-8.0 μm×4.0-5.0 μm in size. It was pear-shaped with a single chromatophore and an eyespot, and was laterally biflagellated (Fig. 1 A). The settled zoospore became spherical, measuring 4.0-5.0 μm in diameter (Fig. 1 B).

Within 1-2 days, the settled zoospore germinated by pushing out a protuberance, whose diameter was 1/2-2/3 times as large as that of the settled zoospore (Fig. 1 C). And then, the protuberance transversally divided into two cells (Fig. 1D). Occasionally, all contents of the zoospore moved into the protuberance.

The germling developed by the successively transversal divisions into a creeping uniseriate filament consisting of 3-6 cells and 40-100 μm in length (Fig. 1 E). The cells near the initial zoospore rounded with a diameter of 6-8 μm, colored dark brown, and produced primary branches (Fig. 1 F). Secondary branches projected on the basal cells of the primary branches and were 8-12 μm in diameter (Fig. 1 G).

Within 2 weeks in Sets 1-4 and 8, as a result of the extensive branching, the zoospore germling developed into a profusely branched filamentous microthallus, measuring 500-800 μm in diameter (Fig. 3 C). It consisted of a large prostrate basal layer and a profusely branched erect portion. Within one month, it grew into a large hemispherical microthallus, measuring 2.0-3.0 mm in diam., but did not project hairs.

In Set 1, multi-seriate plurilocular sporangia were formed on the basal cells of the upright

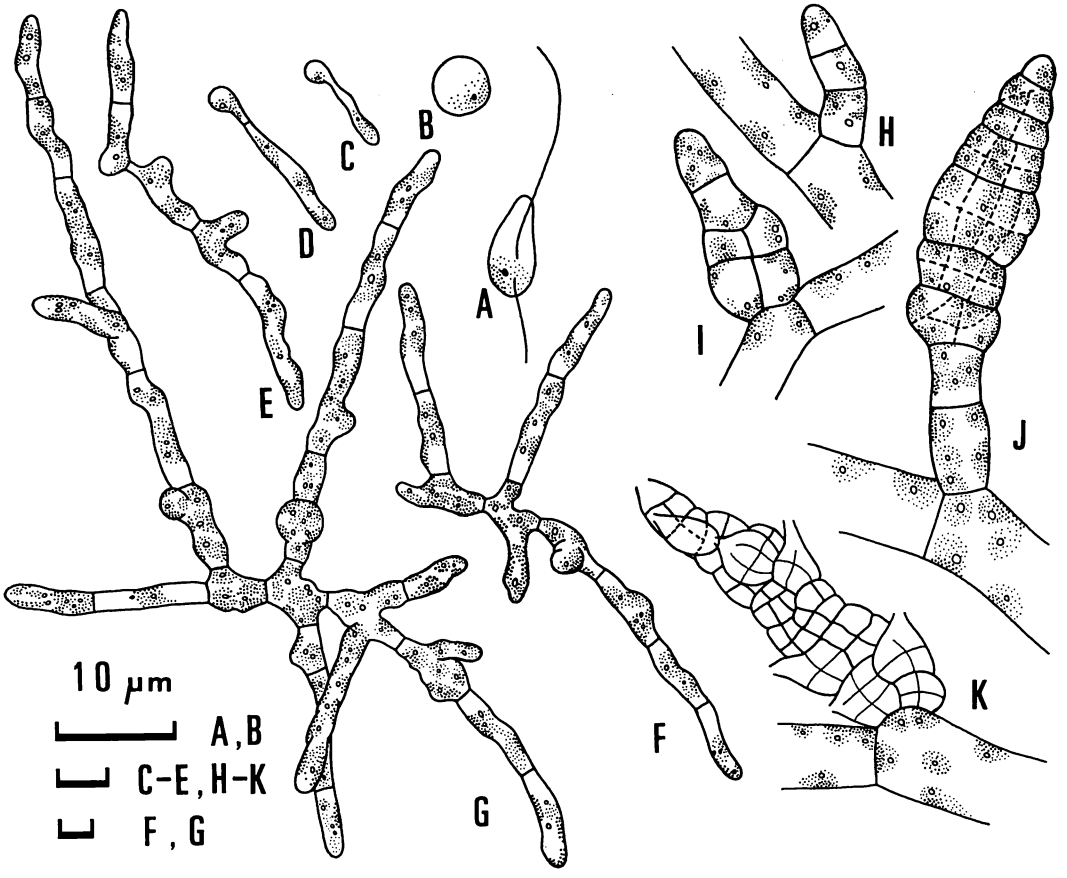

Fig. 1. *Leathesia japonica*. Developmental stages of zoospores released from unilocular sporangia. A. Zoospore; B. Settled zoospore; C-G. 3(C)-, 5(D)-, 8(E)-, 10(F)- and 12(G)-day-old germlings in Set 5; H-K. Plurilocular sporangia on the ectocarpoid erect filaments in Set 5. Immature sporangia (H, I, J) and empty sporangium (K), from which all swarmers just released.

filaments. These sporangia were superficially similar to those produced under cooler conditions as mentioned below. In Set 8, the microthalli grew to 1.8-2.0 cm in diam., not producing any reproductive organs for 4-6 months.

On the other hand, within 2 weeks in Sets 5 and 6 the germling developed into a small filamentous microthallus, measuring 400-500 μm in diameter. Several characteristic erect filaments projected on the initial uniseriate filaments. These were consistent with the erect filaments of some Ectocarpaceae species (Fig. 3 D-F). The erect filaments usually projected in Sets 5, 6 and 7, sometimes in Sets 3 and 4, and occasionally in Sets 1 and 2. However, they never projected in Set 8. When the hemispherical filamentous microthallus growing under warmer conditions (Sets 1, 2 and 8) were transferred into cooler conditions (Sets 5, 6 and 7), it produced the ectocarpoid erect filaments.

The zoospore germlings, either the prostrate filamentous microthalli or the ectocarpoid erect filaments, had 12-14 chromosomes (Fig. 3 K).

2) Morphology of the erect filaments

Within 4-5 months, the erect filaments developed into tuft-like erect filaments, measuring 3-5 cm in height. The chromatophores of the erect filament were discoid, dispersed irregularly within the cell, each with one pyrenoid (Fig. 1 H-K, 3 G). Apical hyaline hairs projected on the branches of

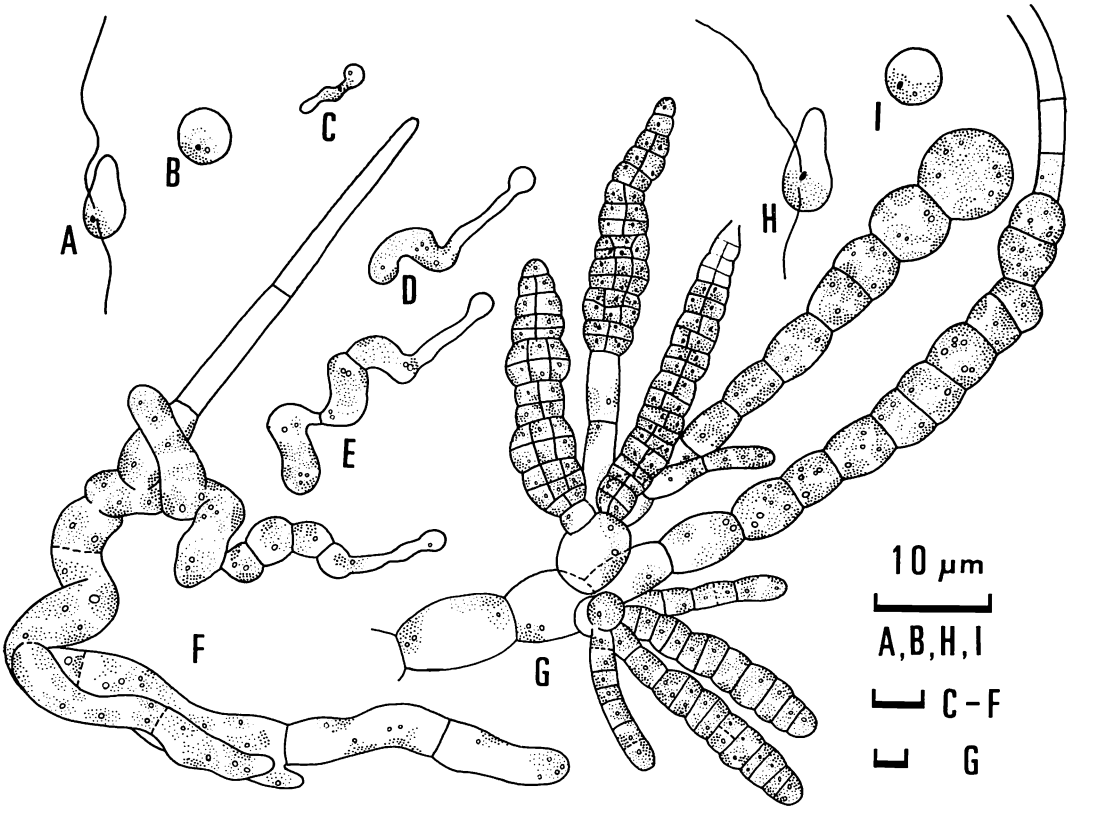

Fig. 2. *Leathesia japonica*. Developmental stages of swarmers released from broader fusiform plurilocular sporangia on the ectocarpoid erect filaments, and slender ones on the sporophytic macrothalli. A. Swarmer; B. Settled swarmer; C-F. 3(C)-, 7(D)-, 10(E)- and 13(F)-day-old germlings in Set 3; G. Slender fusiform plurilocular sporangia in Set 5; H, I. Swarmer (H), and settled swarmer (I) from slender plurilocular sporangia.

the erect filaments (Fig. 3 D-F). The prostrate basal system consisted of the scarcely branched rhizoidal filaments, and did not develop into the discoid microthallus (Fig. 3 D, F). The meristems scattered on the upper portion of the erect filaments (Fig. 3E).

Plurilocular sporangia were laterally or terminally formed on the branches or branchlets of the erect filaments, and were sessile or pedicellate with several cells (Fig. 3 G). The immature sporangia were initially cylindrical or conical (Fig. 1 H, I), but matured ones became fusiform and undulated at their margin (Fig. 1 J, K; 3 G). Each sporangium was partitioned into a number of compartments. Sometimes they grouped closely in two or three together. Swarmers were discharged through an opening formed in each compartment of the sporangium. An opening was formed either in each loculus or at an apex in the sporangium. (Fig. 1 K).

3) Development of swarmer germlings

The swarmer derived from the plurilocular sporangium measured 4.9-6.1 μm×2.9-4.0 μm in size, and was slightly smaller than the zoospore. It had an eyespot and one chromatophore and was laterally biflagellated (Fig. 2 A). Conjugation was not observed. As soon as the unfused swarmer settled on the substratum, it became spherical, measuring 2.9-5.5 μm in diameter with an average of 5.0 μm (Fig. 2 B).

Two types of swarmer development were observed.

a) Under warmer conditions (Sets 1, 2 and 8), most of the swarmers derived from the

sporangia on the basal system and some derived from the sporangia on the ectocarpoid filaments, both developed into germlings similar to those from the zoospores.

b) Under cooler conditions (Sets 3-7), most of the swarmers derived from the sporangia on the ectocarpoid filaments developed into the sporophytic thalli.

Within 1-2 days the swarmer germinated by pushing out a protuberance, whose diameter was 1/2-2/3 times as large as the settled swarmer (Fig. 2 C). Occasionally, all contents of the swarmer moved into the protuberance (Fig. 2 D). And then two cells-stage germling was produced by a transversal divison (Fig. 2 E).

The germling developed initially into an irregularly curved, creeping uniseriate filament consisting of about 10 cells and 100-150 μm in length (Fig. 2 F). The apex of the protuberance enlarged to 12-13 μm in diam. and produced the primary branch. At this stage, one hyaline hair projected on the initial swarmer cell or on the apical cell of the primary branch. The germling developed into a filamentous prostrate microthallus with 8-10 primary branches. However, the primary branching of the swarmer germling started later than that of the zoospore germling.

The cells of the initial uniseriate filament enlarged to 15-20 μm in diam., became dark brown and developed into a single row of cells. Soon, these cell-rows were transformed into the primary assimilating filaments which were superficially consistent with those of sporophytes in field. Some of these assimilating filaments had apical hairs under cooler conditions (Fig. 2G). Basal prostrate filaments transformed into the rhizoidal filaments, producing a basal system. The primary assimilating filaments aggulutinated together to form a bundle. Within one month in Set 3, the assimilating filament became 10-12 cells and 100-140 μm in length. The apical cell enlarged to a globular form, measuring 25-28 μm in diameter. And it became gradually tapering toward the lower portion, where the diameter was 10 μm (Fig. 2 G). The basal cells of the assimilating filament enlarged to 30-40 μm$\times$20 μm in size and developed into the medullary cells. The sporophyte grew to very small (1.0-3.0 mm in diam.), solid, cushion-like or hemispherical thallus (Fig. 3 H) with an irregular surface, but never developed into a lubricous spherical thallus.

Within 44 days in Sets 4-6 and 7, bi- or tri-seriate plurilocular sporangia were formed on the basal cells of the assimilating filament (Fig. 2 G). They were slender, fusiform or conical, measuring 74-123 μm$\times$7-20 μm in size, and became gradually tapering toward the apex. The sporangium was sessile or pedicellate with 1-2 cells, solitary or gregarious (Fig. 2 G). The swarmers, measuring 7.4-8.0 μm$\times$4.4-5.0 μm in size, were released through an apical opening of the sporangium (Fig. 2 H). Conjugation was not observed. As soon as the swarmer settled on the substratum, it became spherical, measuring 4.5-6.0 μm in diameter (Fig. 2 I). The developmental manner of the swarmer was consistent with that from the ectocarpoid erect filaments under cooler conditions.

When the sporophytic thalli were transferred under warmer conditions (e. g. within 38 days in Set 1), the hemispherical thallus formed unilocular sporangia with a size of 73-98 μm$\times$25-32 μm and released zoospores. The zoosproe germling developed into the haploid microthallus under all conditions, as did the zoospsore germling derived from the sporophyte in field.

Under comparatively cooler coonditions (Sets 3 and 5), some ectocarpoid filaments projected from the hemispherical sporophyte (Fig. 3 I). Each erect filament had an apical hair. Some primary assimilating filaments with an apical hair transformed into ectocarpoid filaments, and some branchlets of the ectocarpoid filaments transformed into assimilating filaments (Fig. 3 I, J). The broader fusiform plurilocular sporangia were formed on the ectocarpoid filaments, while the slender fusiform ones were on the basal sporophytic thallus.

n=12-14 and 2n=20-26 chromosomes were

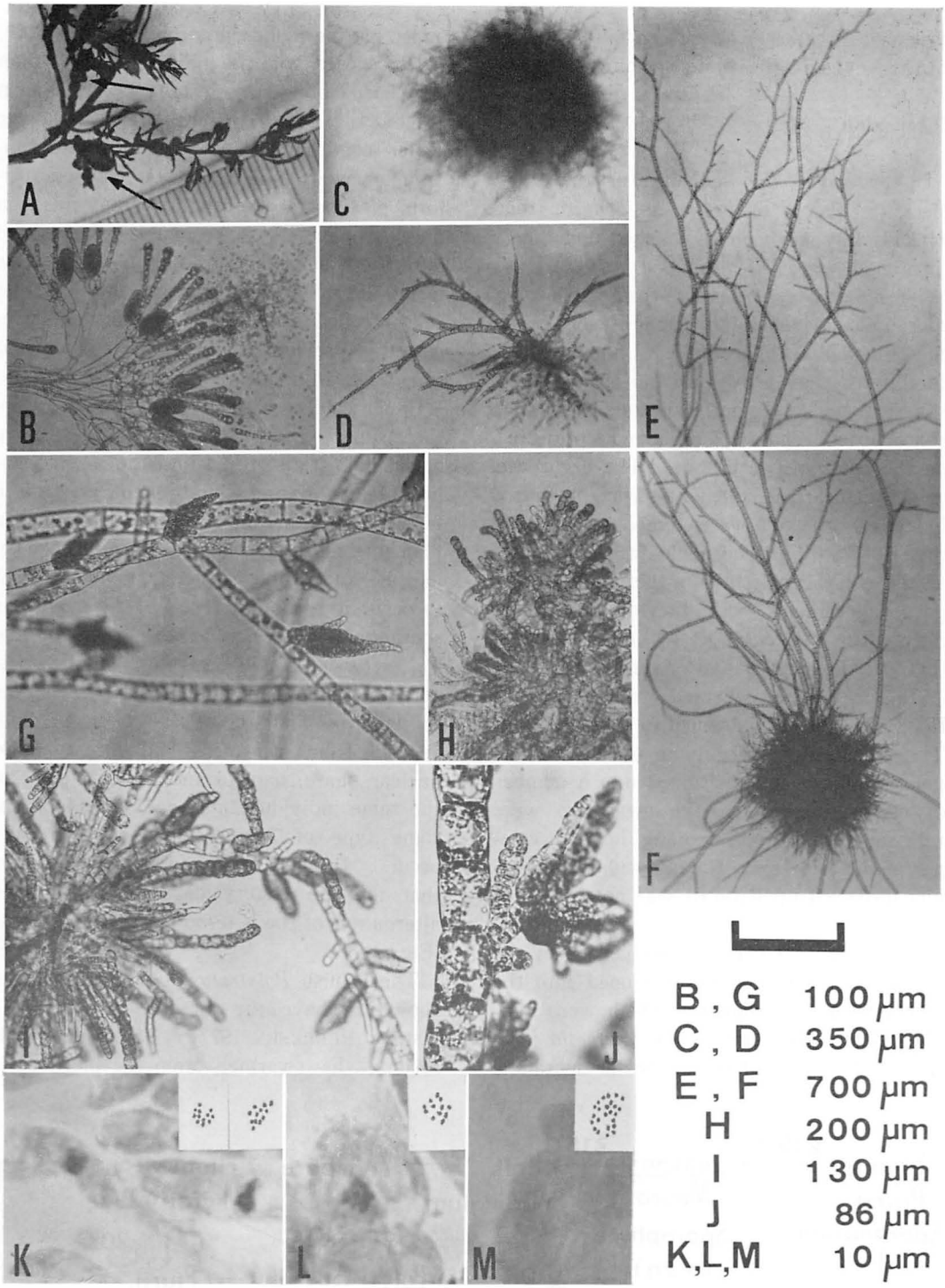

Fig. 3. *Leathesia japonica*. Developmental stages from sporophytes taken from the field, through the *Polytretus*-like stage to the *Leathesia* stage. A. Sporophytic thalli (arrows) growing epiphytically on *Sargassum hemiphyllum*; B. Unilocular sporangia releasing zoospores; C. A profusely branched filamentous microthallus in Set 3; D-F. Erect filaments developed from the small filamentous microthallus. 15(D)- and 30(E, F)-day-old germlings in Set 5. (E: apical portion, F: basal portion); G. Plurilocular sporangia on the erect filaments in Set 5; H. A sporophytic macrothallus in Set 3; I. An erect filament arising from the sporophytic macrothallus in Set 5; J. An assimilating filament developed directly on the erect filament in Set 3; K-M. Chromosomes in the zoospore germling (K: n=12) and the sporophytic macrothalli (L: n=12, M: 2n=24).

observed in the swarmer germlings (Fig. 3 L, M), even in the same germling.

Discussion

In this study, the sequence of the complete life history of *Leathesia japanica* from Wakasa Bay has been established under culture conditions.

The zoospores released from unilocular sporangia developed into the profusely branched filamentous microthalli. Under warmer conditions, they grew into the larger hemispherical ones. Under cool conditions, the characteristic ectocarpoid filaments projected on the zoospore germlings. The occurence of the ectocarpoid filaments was obviously induced by the cool water temperature (lower than 10°C). The morphological characters of the ectocarpoid thalli in this study are in good agreement with the description of *Polytretus reinboldii* (REINKE) SAUVAGEAU (Ectocarpales) in Japan given by KUROGI (1978). And he collected this species in Hokkaido and at Maizuru in Wakasa Bay. The plurilocular sporangium on the ectocarpoid thallus was partitioned into a number of compartments and the swarmers were released through an opening in each compartment. However, the unilocular sporangium observed by KUROGI was not formed in this study.

The unfused swarmers derived from the plurilocular sporangium developed into the hemispherical sporophytes which were morphologically consistent with *Leathesia japonica*. They formed the unilocular sporangia under warmer conditions (higher than 15°C). All zoospores from the unilocular sporangium developed into the microthalli, which soon erected the *Polytretus*-like filaments under cooler conditions. Also, under cooler conditions (lower than 15°C), the slender fusiform plurilocular sporangia were formed on the sporophytes. Their swarmers developed into the hemispherical sporophytes. The formation of the reproductive organs must be controlled by water temperature, as reported in previous studies (e. g. in *Ectocarpus siliculosus*, MÜLLER 1963).

Under cold conditions (lower than 10°C), the primary assimilating filaments with an apical hair transformed into the *Polytretus*-like filaments, and the branchlets of these filaments transformed into the assimilating filaments here and there. From the karyological study, the reduction division ought to occur in the mother cell of the unilocular sporangium of the *Leathesia* sporophyte. The *Polytretus*-like thalli derived from the zoospores were the haploid phase. However, the sporophytes and the *Polytretus*-like thalli derived from swarmers had both types of nuclear phase, haploid and diploid, even in the same individual. So we consider that some type of chromosomal chimera may occur. From these results, we conclude that the life history of *L. japonica* is an alternation of the heteromorphic generations (Fig. 4).

The Danish *Polytretus reinboldii* has been shown to have the direct type of the life history (PEDERSEN 1977). According to his results, the swarmer from the plurilocular

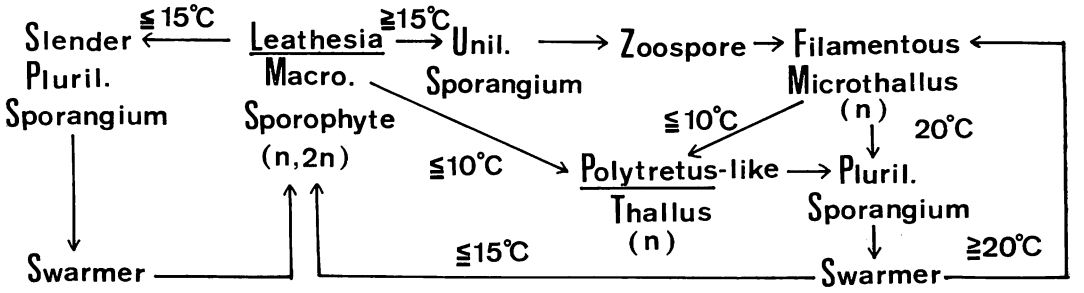

Fig. 4. A diagram of the life history of *Leathesia japonica* INAGAKI in culture.

sporangium develops into a prostrate uniseriate branched system, from which the erect filaments with an apical hair project. Its developmental process is consistent with that of the zoospores of *Leathesia japonica* described in this study. However, the developmental process of the swarmer in the Danish *Polytretus* is different from that of the swarmers of the *Polytretus*-like thalli in this study. The former directly develops into the *Polytretus* thalli. On the other hand, the latter developed into the *Leathesia* thalli. And in the Danish culture, the formation of the erect filaments is strongly inhibited by the comparatively high temperature (15°C). In the present study, the *Polytretus*-like filaments did not project from the microthalli under warmer conditions (20-25°C). PEDERSEN did not study karyologically in his material.

In the previous study, the macroscopic erect filaments arising from the filamentous microthallus were observed in the zoospore germlings (gametophyte stage) of *Acrothrix pacifica* OKAMURA et YAMADA (Acrotrichaceae) (AJISAKA 1979). In addition, the zoospore germlings of *Petrospongium rugosum* S. et G. (Leathesiaceae) (ARASAKI 1948) forms the larger fusiform or conical multiseriate plurilocular sporangia, which are consistent with those of the ectocarpacean species. Consequently, some microthallus (gametophyte stage) in the member of Chordariales may be actually identified or described as the member of Ectocarpales.

WYNNE and LOISEAUX (1977) reported that four phaeophycean orders, the Ectocarpales, Chordariales, Dictyosiphonales and Scytosiphonales, were closely related. Much earlier FRITSCH (1945) proposed to merge the member of those four orders into one large orders, the "Ectocarpales" and this proposal have been supported by RUSSELL (1964).

RUSSELL (1973) recently said, "It will be difficult to avoid confusion between the status of ectocarpoid microthalli and that of very similar plants in the Ectocarpales which has been shown to have autonomous life histories". For instance, swarmers from the plurilocular sporangia of *Hecatonema maculans* (COLL.) SAUV. give rise to the filamentous plethysmothalli which project the macroscopic plants belonging to the genus *Myriotrichia* (Striariaceae, Dictyosiphonales) (LOISEAUX 1969). Zoospores from the unilocular sporangia of *Streblonema anomalum* S. et G. (Ectocarpales) from California give rise the plants identifies as a small *Scytosiphon*, closly resembling *S. pygmacus* REINKE (Scytosiphonales) (LOISEAUX 1970). Swarmers from the plurilocular sporangia of *Hecatonema maculans* (COLL.) SAUV. (Ectocarpales) develop into *Punctaria latifolia* GREVILLE or *Desmotrichum undulatum* REINKE (Dictyosiphonales) (CLAYTON 1974). And also, FIORE (1977) reported that *Stictyosiphon subsimplex* HOLDEN (Dictyosiphonales) and *Farlowiella onusta* (KÜTZING) KUCKUCK in KORNMANN (Ectocarpales) were the sporophytic and gametophytic generations, respectively.

In this study, the small frond of *Leathesia japonica* (Chordariales) and the rather large filamentous thalli of *Polytretus reinboldii* (*Polytretus*-like thalli) (Ectocarpales) alternated with each other. These results support FRITSCH's early proposal to merge the four orders into the "Ectocarpales". The proposal should be re-examined with the aim of reconstructing the phaeophycean taxonomy, and the further researches may be elucidate the whole life history of the diverse genera in the "Ectocarpales".

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鰺坂哲朗: 培養によるコゴメネバリモ（褐藻類ナガマツモ目）の生活史

若狭湾のイソモク体上に生育するネバリモ科のコゴメネバリモ (*Leathesia japonica* INAGAKI) の生活史を室内培養条件下で研究した。コゴメネバリモ体上の単子嚢からの遊走子は高温条件で単相の微小体となるが，低温条件では単相で，シオミドロ目の *Polytretus reinboldii* (REINKE) SAUVAGEAU に非常に似た直立糸状体になる。この糸状体は幅広く，多列の複子嚢を形成する。これからの遊走細胞は接合しなくて，低温条件で再び単相か，または複相のコゴメネバリモ体（胞子体）になる。この胞子体は高温で単子嚢を，低温で細長い多列の複子嚢を形成する。また，胞子体上に *Polytretus* 状の直立糸状体が生じたり，その上に胞子体の同化糸が形成されるという形態的キメラが観察された。本種の生活史は異型世代交代といえる。また，この研究から FRITSCH (1945) のナガマツモ目をも含めた広いシオミドロ目の分類を支持する有効なる証明ともなる。(606 京都市左京区北白川追分町　京都大学農学研究科熱帯農学専攻水産資源学研究室)