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The Specific Identity and the Life History of Japanese *Syringoderma* (Syringodermatales, Phaeophyceae)*

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Observations on Japanese *Syringoderma* from Rishiri Island, which had been previously identified as *S. australe*, were made based on newly collected fertile material. These results and comparisons with the type specimen of *Syringoderma abyssicola* (= *Chlanidophora abyssicola*) revealed that the Rishiri Island plants should be identified as *Syringoderma abyssicola*. *Syringoderma abyssicola* from Rishiri Island formed unilocular sporangia among the paraphyses on the fan-shaped blades in winter. The first products (uni-spores) in the unilocular sporangia form flagella, and soon after form cell walls before release. Then these reduced gametophytes divide into tetrads and form swarmers, each of which contains a chloroplast with a stigma. These swarmers germinate into branched filaments, from which thicker erect filaments of apical growth tissue. At 5-10 C these erect filaments formed fan-shaped blades under long-day conditions, and unilocular sporangia under short-day conditions corresponding respectively to spring and winter at Rishiri Island. Accordingly, the seasonal growth pattern of the species is considered to be controlled by responses to photoregime and temperature.

Key words: Life history — Phaeophyceae — *Syringoderma abyssicola* — Syringodermatales — Taxonomy

The systematic position of *Syringoderma* has been controversial since the establishment of the genus by Levring (1940). He based the genus on *Chlanidophora abyssicola* Setchell and Gardner (1924) and described a second species, *S. australe*. He placed *Syringoderma* in the Dictyotales, although the nature of the reproductive structures remained unclear. Delépine (1968) and Wynne (1972) suggested that *Syringoderma* might belong to the order Sphacelariales based on superficial morphological resemblance to *Halopteris*. Walker and Henry (1978) found that the unilocular sporangia of *S. abyssicola* contain many subunits, each surrounded by a distinct cell wall. These walled subunits were frequently subdivided into tetrads, and the presence of plastids and flagella within the tetrads was detectable. Henry and Müller (1983) described *Syringoderma phinneyi*, the third species in the genus, and reported a typical heteromorphic life history, with alternation between fan-shaped sporophytes and filamentous dioecious isogamous gametophytes. Henry (1984) described the fourth species, *Syrin-*

* Dedicated to the memory of the late Professor Munenao Kurogi.

goderma floridana, and reported a heteromorphic life history in which the zoospores from unilocular sporangia are scarcely motile and the gametophyte is reduced to a cell which divides into two, yielding two biflagellate isogametes. He supposed that *S. abyssicola* has a similar reduced gametophyte, which develops within the unilocular sporangium, dividing into four to release four biflagellate isogametes. Based on the heteromorphic life history in *Syringoderma* and some distinctive morphological characters, he established a new order Syringodermatales containing the new monogeneric family Syringodermataceae. Müller *et al.* (1982) reported a new sexual pheromone viridiene in *Syringoderma phinneyi*, which may support the independence of the new order.

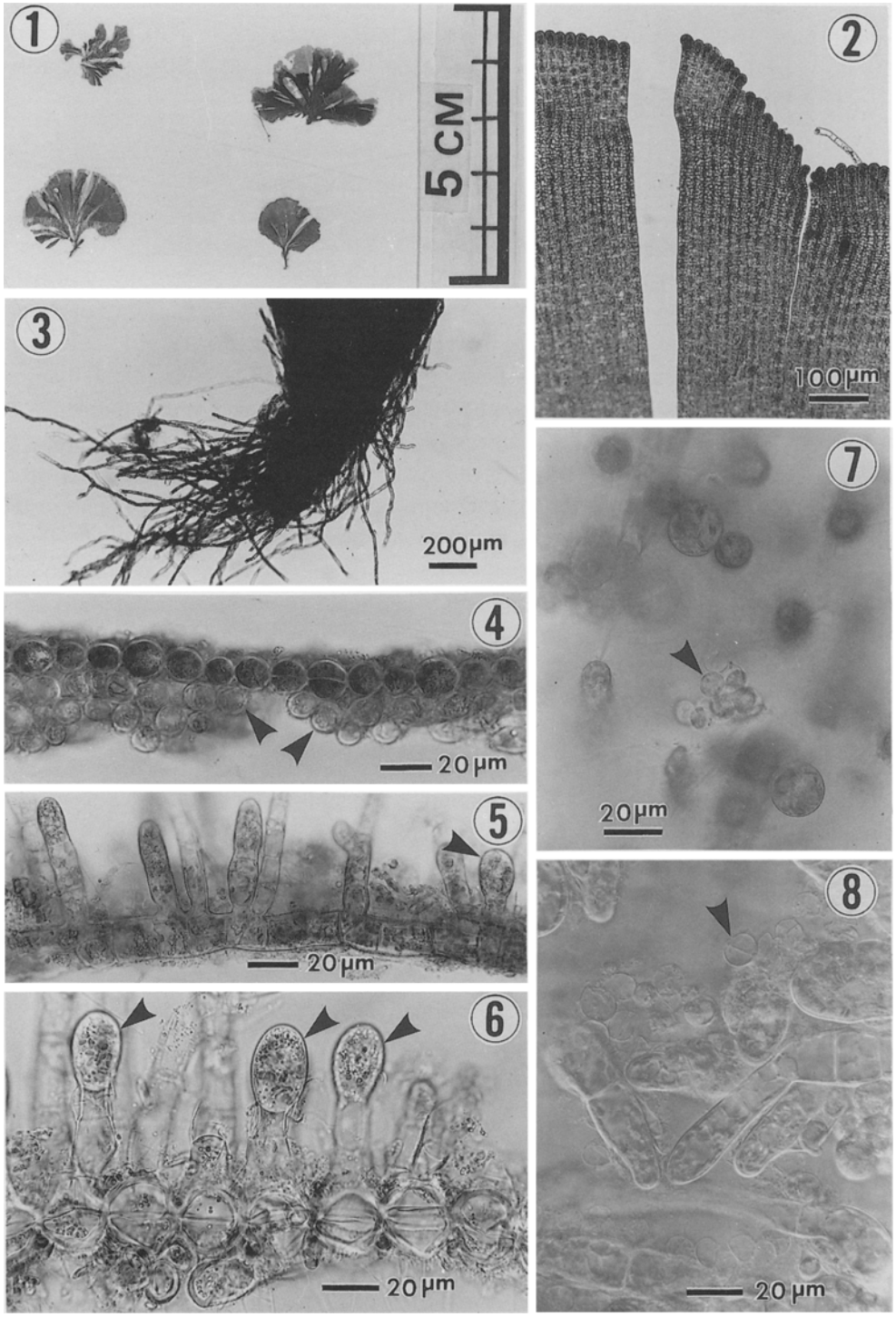
In Japan, Matsunaga and Yamada (1974) reported the occurrence of *Syringoderma* from Rishiri Island in the Sea of Japan and identified it as *S. australe*, which had been described from the Antarctic Sea. However, the specific assignment of this material was doubtful in the absence of fertile specimens and information on the life history. The aim of the research described here was to study the morphology of Japanese *Syringoderma* based on newly collected fertile material, to observe its life history and to reexamine its taxonomy.

Materials and Methods

Specimens were collected on 12 August and 8 December 1986 by SCUBA diving at Rishiri Island (45°22′N, 141°13′E), Hokkaido, Japan. Morphological observations by light microscopy were made on living materials and on specimens preserved in 5% formaldehyde-seawater. Type material of *Syringoderma abyssicola* (UC 229737) was examined for comparison with the Japanese material.

Unialgal cultures were established from apical segments of the sterile blade collected on 12 August 1986 and cultured in glass vessels containing 200 ml of PESI medium (Tatewaki 1966). Culture conditions were 5 C SD (short-day ; 8 : 16 hr Light : Dark), 5 C LD (long-day ; 16 : 8 hr Light : Dark), 10 C SD, 10 C LD, 15 C SD, 15 C LD, 20 C SD and 20 C LD, under white fluorescent light of about 30 $\mu E \cdot m^{-2} \cdot s^{-1}$ (5 C) or 50 $\mu E \cdot m^{-2} \cdot s^{-1}$ (10 C, 15 C, 20 C). For TEM observations, materials were prefixed in 3% glutaraldehyde in 0.1 M cacodylate buffer, postfixed in 2% OsO_4 in 0.1

Figs. 1–8. Field material of Japanese *Syringoderma abyssicola* collected at Rishiri Island.
Fig. 1. Habit of the plants collected on 12 August 1986.
Fig. 2. Marginal part of the fan-shaped thallus composed of cylindrical filaments with apical growth.
Fig. 3. Rhizoidal filaments in the basal part of the thallus.
Fig. 4. Transverse section of a vegetative thallus without paraphyses. Arrowheads show rhizoidal filaments.
Figs. 5, 6. Longitudinal (Fig. 5) and transverse (Fig. 6) sections of the mature thallus with paraphyses and unilocular sporangia (arrowheads) to the axis.
Figs. 7, 8. Surface view of the mature thallus showing the walled spores (Fig. 7, arrowhead) and emptied spore walls (Fig. 8, arrowhead) attached to the walls of unilocular sporangia and paraphyses.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M cacodylate buffer, dehydrated in an acetone series and embedded in Spurr's epoxy resin (Spurr, 1969), sectioned with a diamond knife, and stained with uranyl acetate and lead citrate. Observations were made using a Hitachi H-300 TEM at the Institute for Algological Research, Faculty of Science, Hokkaido University.

Results

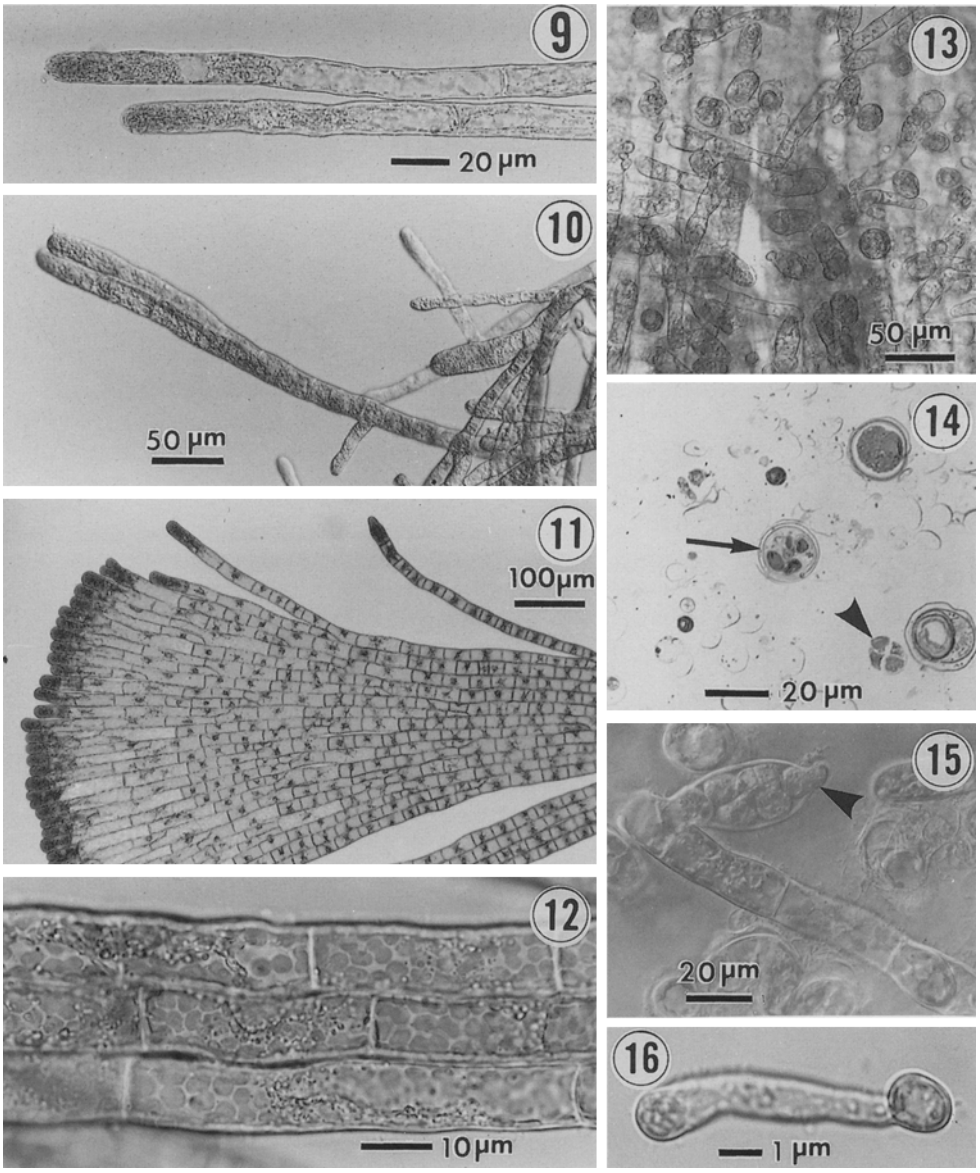
Morphological observations of the field plants

The present materials grow on subtidal shaded rocks at a depth of 5–7 m below Mean Low Water Level. In August, the plants are vegetative, thin fan-shaped, smooth-surfaced, attaining 20 mm in length and 25 mm in width (Fig. 1). They are attached to the substratum by holdfasts composed of entangled rhizoidal filaments (Fig. 3). The fan-shaped blade is composed of radially arranged round filaments, 16–28 μm in diameter, which coalesce laterally (Fig. 2). Tears often form between the filaments of the blade. Cross walls form in the plane parallel to the surface of the blade (Figs. 4, 6). Rhizoidal filaments issue from the lower surface of the blade, which becomes multi-seriate near the base (Figs. 3, 4). Mature blades of the plants collected in December bore dorsally 1–5 celled erect simple filaments (paraphyses) and unilocular sporangia (Figs. 5, 6). Unilocular sporangia are sessile or pedicellate, 25–30 μm in length and 15–18 μm in diameter, often surrounded by some sheath-like membranous structure, apparently formed by the generation of a new sporangium from the cell below a previously emptied sporangium (Fig. 6). Unilocular sporangia contained 8 to 16 walled spores, each of which often divided into a tetrad. Each of the tetrad cells contained a chloroplast with an obvious stigma. The release of flagellated cells (swarmers) from the sporangia was not observed, however several to many spherical walled spores were observed attached on the surface of emptied sporangia or paraphyses (Fig. 7). Some of the tetrads were empty (Fig. 8).

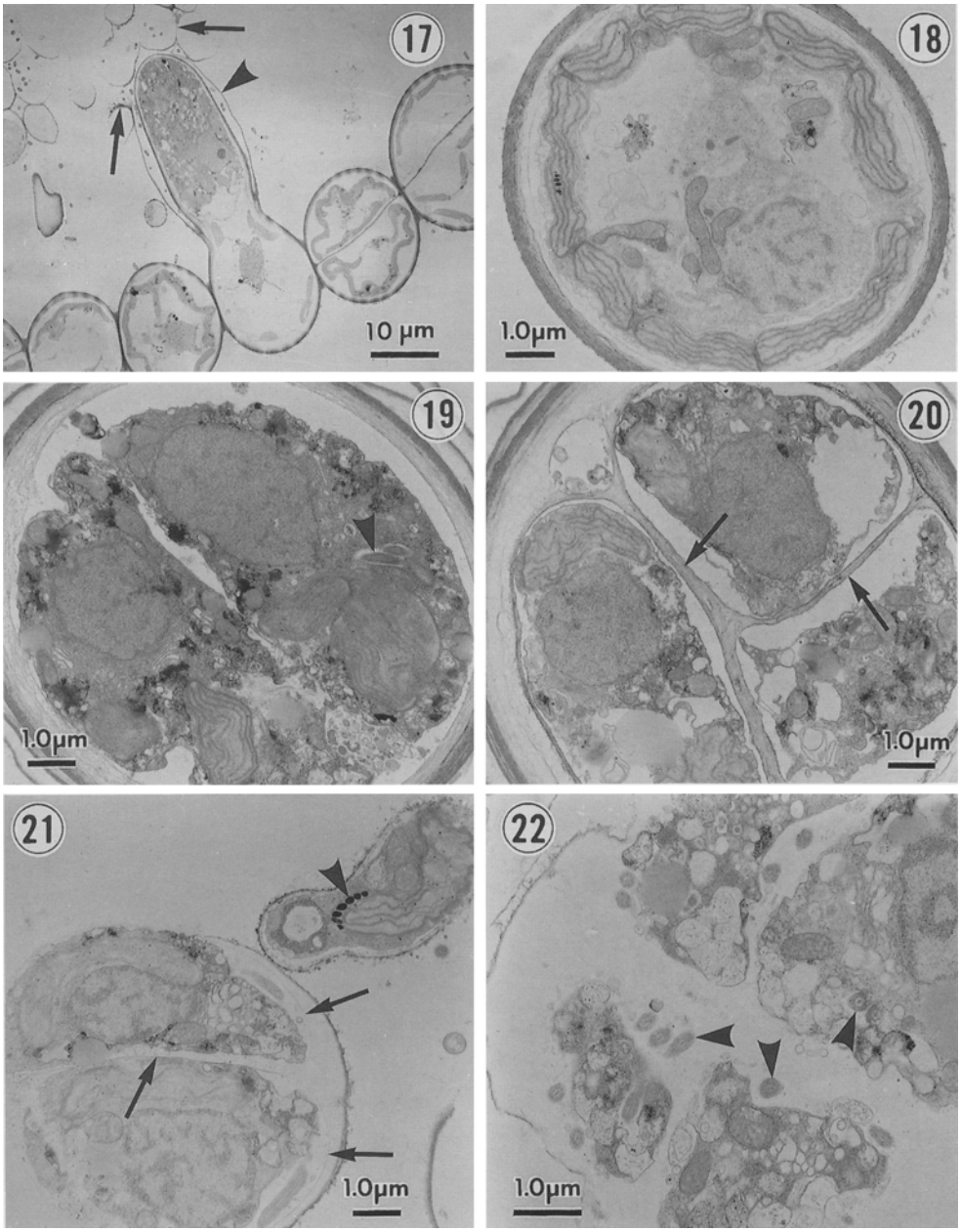
Our plants collected in the field agreed well with the type material of *Syringoderma abyssicola* in habit and general vegetative constructions of the thallus.

Culture experiments

The uniseriate filaments derived from apical segments of the field material elongated as individual filaments by apical growth (Fig. 9). They developed into bush-like branched filaments. At 20 C, they did not grow well. Under long-day conditions at 5 C and 10 C, some filaments coalesced as they elongated and branched forming a single-layered fan-shaped blade (Figs. 10, 11). Cells of the blade contained many discoid chloroplasts without pyrenoids (Fig. 12). These blades formed paraphyses and unilocular sporangia on the dorsal surface of the blade under short-day conditions at 5 C and 10 C (Figs. 13–15). Under the other culture conditions, they remained as vegetative individual filaments. Unilocular sporangia were obovoid and sessile, but became pedicellate when formed by regeneration from the subtending cells of emptied unilocular sporangia (Fig. 17). Paraphyses were also formed by such regenerations. Accordingly, unilocular sporangia were often surrounded by the walls of old emptied



Figs. 9–15. Japanese *Syringoderma abyssicola* in culture.
Fig. 9. Independent filaments of apical growth.
Fig. 10. Branched filaments.
Fig. 11. Fan-shaped blade formed by the coalescence of the branched filaments.
Fig. 12. Many discoidal chloroplasts without pyrenoid in each cell of the filaments.
Fig. 13. Surface view of mature thallus forming unilocular sporangia and paraphyses.
Fig. 14. Paradermal section of mature thallus showing the unilocular sporangia (arrow) and released tetrads attached on the wall of the sporangium (arrowhead).
Fig. 15. Releasing walled spore (arrowhead) from unilocular sporangium.
Fig. 16. Unipolar germination of settled swarmer.



Figs. 17–22. Spore formation in unilocular sporangia and walled spores observed by TEM.
Figs. 17, 18. Young unilocular sporangia in longitudinal (Fig. 17) and transverse (Fig. 18) secetions. Arrows show emptied spore walls attached to the sporangium. Arrowhead shows remnant cell walls of a previous sporangium produced from the same blade cell.
Fig. 19. Swarmers in unilocular sporangium. Arrowhead shows flagella.
Fig. 20. Walled swarmers in unilocular sporangium. Arrows show spore walls.
Fig. 21. Probable gametes and the germling (upper right). Arrows show inner walls in the reduced gametophyte, arrowhead shows stigma in gamete germling.
Fig. 22. Probable gametes in tetrads. Arrowheads show flagella.

sporangia, or became pedicellate (Figs. 14, 17). The contents of unilocular sporangia divided into 8 to 16 flagellated cells (Figs. 18, 19) which immediately formed cell walls in the sporangia before release (i.e. germinated, Fig. 20). Each flagellate cell appeared to contain several chloroplasts, however stigmata were not detected. Some of the walled cells were released from the sporangia and attached to the surface of emptied sporangia or erect filaments (Figs. 14, 15). Each of the walled cells divided into tetrads in situ or after release, and formed four swarmers containing a chloroplast with a stigma. The swarmers were separated by walls in individual compartments as in plurilocular sporangia (Figs. 21, 22). Neiter actual release of the swarmers nor their sexual fusion were observed, however, settled swarmers germinated by forming a germination tube (unipolar immediate type), elongated into uniseriate branched filaments (Fig. 16). From these initial filaments, thicker erect filaments having characteristic apical cells issued. The erect filaments formed fan-shaped blades and matured under the same conditions as mentioned above.

Discussion

Based on the morphological observations on fertile material, culture experiments and comparisons with the type material of *Syringoderma abyssicola*, we conclude that

Table 1. Comparisons of some characteristic features among Japanese *Syringoderma* and known species

Characters	Our plant	*S. abyssicola*	*S. australe*	*S. phinneyi*	*S. floridana*
distribution	N.W. Pacific	N.E. Pacific	Antarctic	N.E. Pacific	Florida
blade thickness	1-2 layers	1-2 layers	1-2 layers	1 layer	1 layer
blade height (mm)	≧20	20-30	≧40	5-10	10-20
filament cell size (μm)	20-52 (−87) ×18-25	16-24 ×10-12 (−20)	40-60 ×20-30 (−35)	26-120 ×15-22	20-90 ×13-22
apical cell length (μm)	48-112	30-50	≧110	74-285	95-180
paraphyses	present	present	present	absent	absent
unilocular sporangium	sessile or pedicellate	sessile or pedicellate*	pedicellate on erect filament	sessile	sessile
spore	non-motile	non-motile	unknown	motile	motile
gametophyte	reduced (4 cells)	reduced (4 cells)	unknown	branched filament	reduced (2 cells)
gamete	isogamous ?	isogamous ?	unknown	isogamous	isogamous
references	1),2)	3)-7)	8),9)	10)	11)

1) Present paper, 2) Matsunaga & Yamada (1974), 3) Setchell & Gardner (1924), 4) Setchell & Gardner (1925), 5) Walker & Henry (1978), 6) Henry (1984), 7) Type material of *Chlanidophora abyssicola* S. and G. (UC 229737), 8) Delépine (1969), 9) Levring (1940), 10) Henry & Müller (1983), 11) Henry (1984), * Henry, (pers. comm.)

Japanese *Syringoderma* from Rishiri Island should be identified as *Syringoderma abyssicola*, not *S. australe*. In *S. australe*, unilocular sporangia are formed on the branchlets on the erect filaments on the blade (Henry, 1984), whereas they are formed directly on the blade cells in *S. abyssicola* (Table 1). The unilocular sporangia of *Syringoderma* from Rishiri Island are often pedicellate, which we consider to be the result of regeneration from the subtending cells of the sporangia as demonstrated in culture. Eastern Pacific *Syringoderma abyssicola* is also known to become pedicellate at times (E. Henry, pers. comm.). The *Syringoderma* from Rishiri Island also agrees with *S. abyssicola* (Walker and Henry, 1978) in forming walled cells in the unilocular sporangia, which divide into tetrads containing flagellated cells. In *S. australe*, formation of cell walls around the products of unilocular sporangia before release has

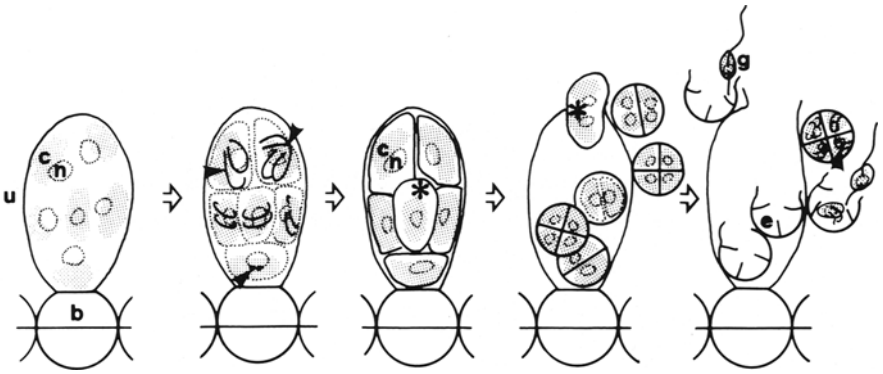


Fig. 23. Diagram of reproductive development of Japanese *Syringoderma abyssicola* in longitudinal section through unilocular sporangium. b, fan-shaped blade; c, chloroplast; e, emptied tetrad reduced gametophyte; g, gamete; n, nucleus; u, unilocular sporangium; arrowhead, flagellum; asterisk, walled spore = reduced gametophyte.

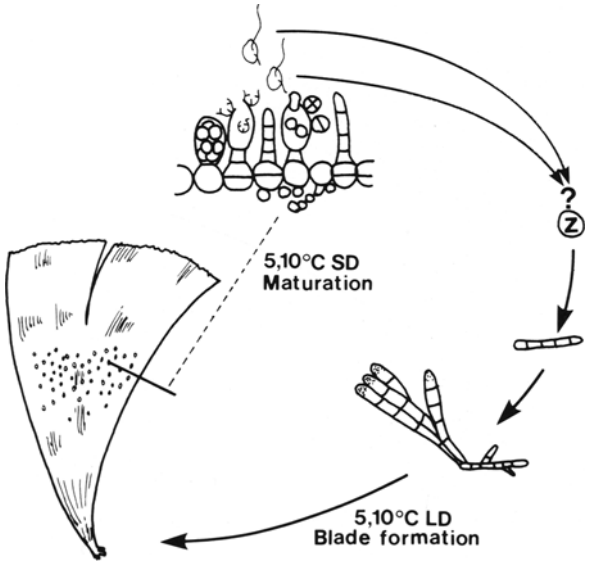


Fig. 24. Diagram of life history in culture of Japanese *Syringoderma abyssicola*

not been observed (Delépine, 1968; Henry, 1984). In *S. phinneyi* the contents of unilocular sporangia develop into swarmers which germinate to form branched filamentous gametophytes. In *S. floridana* the swarmers form cell walls immediately (reduced gametophyte), and then divide into two to form isogametes.

Japanese *Syringoderma abyssicola* is considered to have a heteromorphic life history alternating between fan-shaped sporophytes and reduced tetrad gametophytes as supposed by Henry (1984), although sexual reproduction was still not confirmed in the present study (Figs. 23, 24). We agree with the explanation of Henry (1984) of the life history of *S. floridana*, considering its close analogy with that of *S. phinneyi*. The finding of flagella in the first products of unilocular sporangia before forming cell walls in our study supports the explanation of Henry (1984) that they are reduced unispores. The fact that they lack stigmata may also show their reduced nature.

In culture, Japanese *S. abyssicola* formed the fan-shaped blade only under long-day conditions of relatively low temperature (5 C LD and 10 C LD). It formed unilocular sporangia under short-day conditions of low temperature (5 C SD and 10 C SD). These conditions correspond to spring and winter respectively at Rishiri Island. Accordingly, the seasonal growth pattern of the species is considered to be controlled by the responses to photoregime and temperature.

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