Jpn. J. Phycol. (Sôrui) 39: 319–328, December 10, 1991

Critical review of the taxonomy and life history of *Kjellmania arasakii* (Dictyosiphonales, Phaeophyceae)

Hiroshi Kawai

Department of Botany, Faculty of Science, Hokkaido University, Sapporo, 060 Japan

Kawai, H. 1991. Critical review of the taxonomy and life history of *Kjellmania arasakii* (Dictyosiphonales, Phaeophyceae). Jpn. J. Phycol. 39: 319–328.

A taxonomic review of *Kjellmania arasakii* based on the materials newly collected at Yashiro Island, Seto Inland Sea, Japan revealed that the species is identical with *Stictyosiphon soriferus*, which is distributed widely in North Atlantic Ocean. At Yashiro Island, *Stictyosiphon soriferus* grows on subtidal artificial substrata at a depth of 3–4 m. The thallus is 3–4 times irregularly branched, delicate, attaining about 20 cm in height and forms abundant plurilocular sporangia. In culture the swarmers from plurilocular sporangia developed into protonemata on which erect thalli directly arose. The polystichous, branched erect thalli grew well and formed plurilocular sporangia between 5–20°C, although best between 10 and 15°C. Unilocular sporangia were formed only in 5°C short day conditions.

Key Index Words: *Dictyosiphonales*—Kjellmania arasakii—*Life history*—*Phaeophyceae*—Stictyosiphon soriferus—*Taxonomy*.

Yamada (1953) described *Kjellmania arasakii* based on some drift materials collected at Fukagawa in Tokyo Bay by S. Arasaki during 1951 and 1952. However, this report was preliminary, lacking Latin descriptions and detailed descriptions of the species. Yamada mentioned that he intended to publish a second report including a detailed description, but it has not been published. Arasaki and Nozawa (1953) cultured the same material as Yamada studied and reported the occurrence of erect filamentous gametophytes from the swarmers of the field plant; however, they could not complete the life history. They reported a *Laminaria*-type of germination of the swarmers in which most cellular contents migrated into the germination tube forming a emptied embryospore. However, such a germination pattern is rather uncommon in the Dictyosiphonales in which the genus is placed, and does not agree with previous reports on the life history of *Kjellmania* and its closely related genus *Stictyosiphon* (Sauvageau 1929, Rosenvinge 1935, South and Hooper 1976).

The genus *Kjellmania* was established by Reinke (1889) based on *Kjellmania sorifera* Reinke collected at Kiel, Baltic Sea. However, the distinction between *Kjellmania* and *Stictyosiphon* has been disputed, and *Kjellmania* is generally now recognized as a taxonomic synonym of *Stictyosiphon* (Rosenvinge 1935, Rosenvinge and Lund 1947, Naylor 1958, South and Hooper 1976). On the other hand, the characters used to distinguish *Kjellmania arasakii* from *Kjellmania sorifera* (=*Stictyosiphon soriferus*), such as the manner of branching, and presence or absence of intercalary plurilocular sporangia, seem to be rather variable and need revision. In addition, the life history of *K. arasakii* is not yet fully clear. Accordingly, this paper aims to reexamine the morphology and life history of *K. arasakii* using the type specimen and newly collected materials referable to the species, and to compare it with specimens of Atlantic *Stictyosiphon soriferus*, including authentic materials, to clarify its systematic status.

Materials and Methods

Collections of specimens were made at

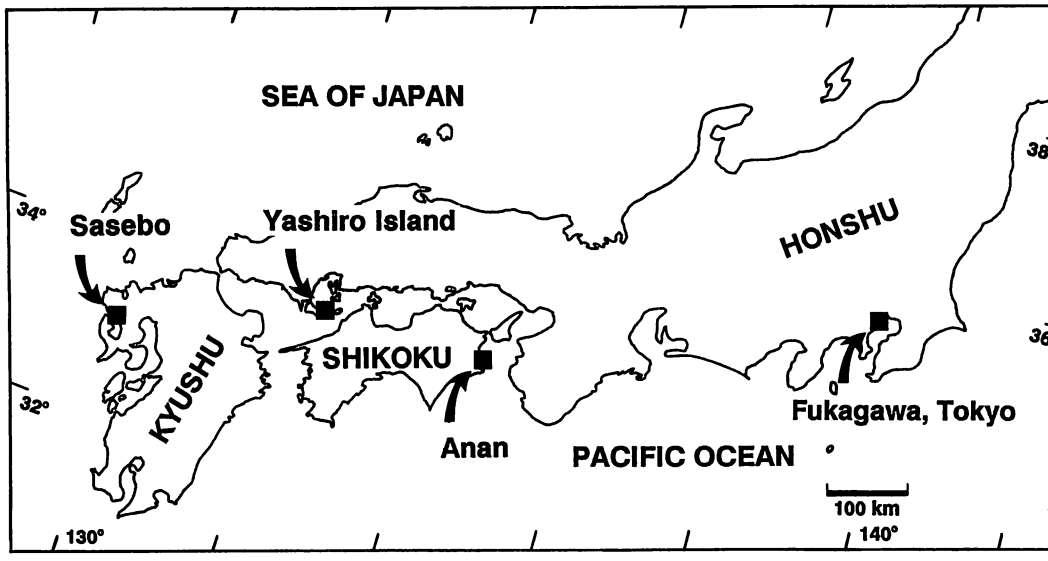


Fig. 1. Distribution of *Stictyosiphon soriferus* (Reinke) Rosenvinge in Japan. Squares show the localities of collections.

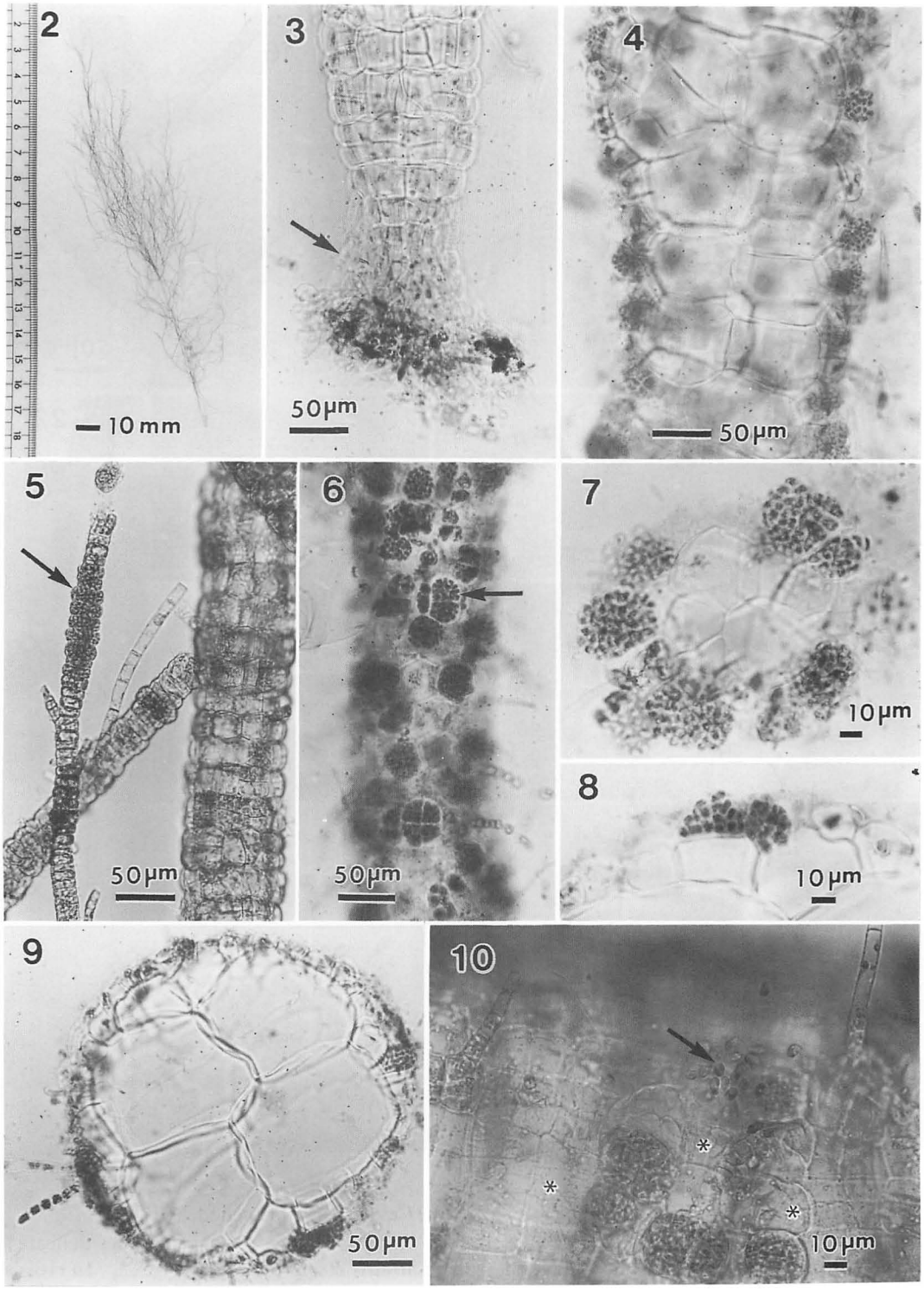
Yashiro Island, Yamaguchi Prefecture, Seto Inland Sea (Fig. 1, 33°55′N, 132°20′E) on 15 May 1986 using SCUBA. The type specimen of *Kjellmania arasakii* (SAP 027286, Fukagawa, Tokyo Bay, Fig. 1, leg. S. Arasaki, 4 February 1951) and permanent preparations made from the type material by Y. Yamada, as well as some additional herbarium specimens collected by Arasaki (2 January 1951, 26 January, 2, 23, 25, 26 February 1952) were examined. Additional materials as follow were also examined: Japanese herbarium specimens referable to *Kjellmania arasakii* collected at Sasebo, Nagasaki Pref. (Fig. 1) (leg. S. Migita, April 1955) and Anan, Tokushima Pref. (Fig. 1) (−5 m deep, leg. S. Arai, 14 February 1984); herbarium sheet of *Stictyosiphon soriferus* (as *Kjellmania sorifera* Reinke, January and June 1888, Kiel, collected and identified by Reinke placed in B. M.); permanent preparation of *Stictyosiphon soriferus* (leg. P. Kornmann and P.-H. Sahling, 26 August 1960, Helgoland); fresh and liquid preserved material of *Stictyosiphon soriferus* (15 April 1989, Portsmouth, England).

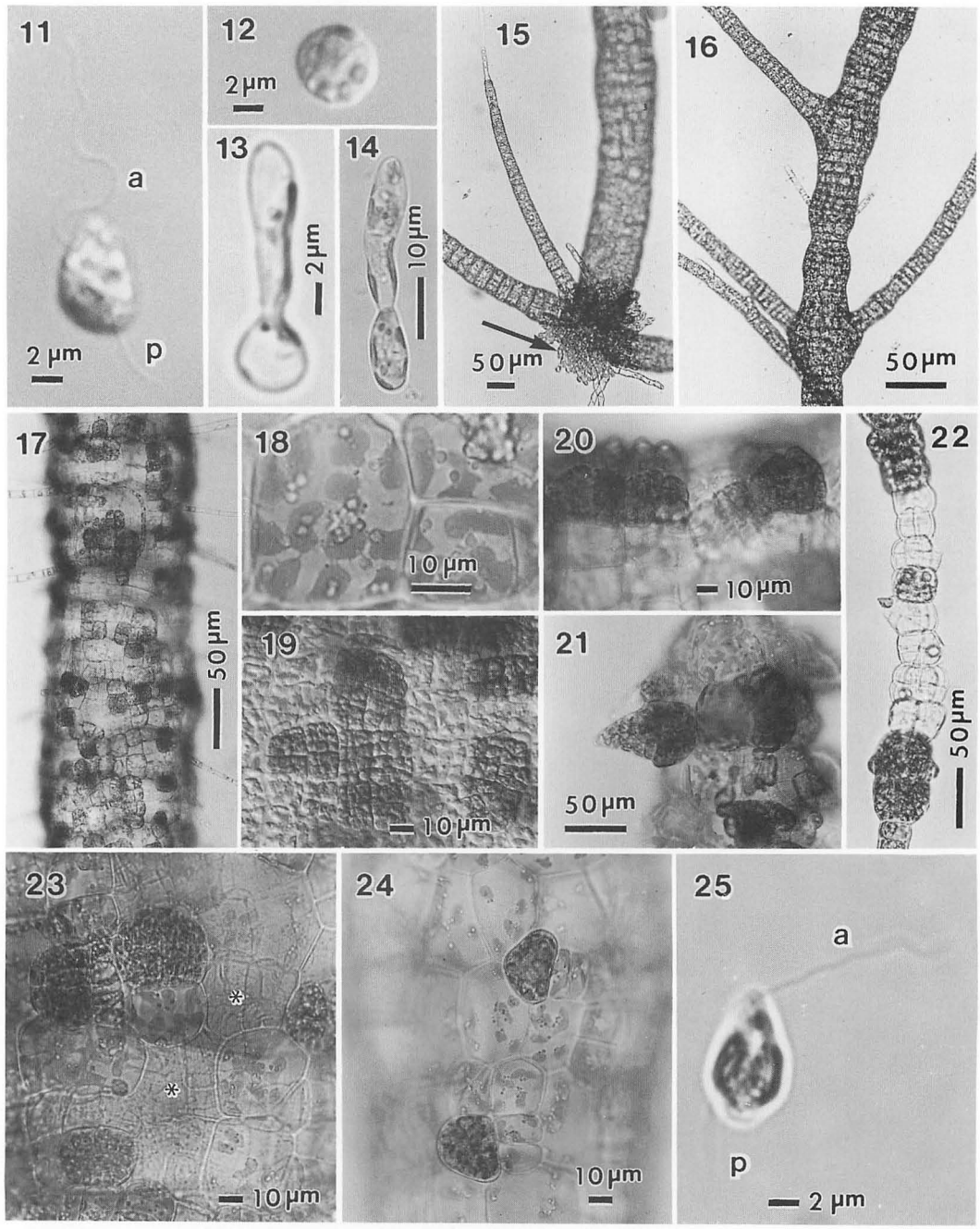
Morphological observations by light microscopy were made on living materials, specimens preserved in 3-5% formaldehyde-seawater and permanent preparations made from dried herbarium specimens.

Cultures were started from swarmers released from plurilocular sporangia on the erect thalli collected on 15 May 1986 at Yashiro Island, Seto Inland Sea. For comparisons in the morphology, life history and response to day length-temperature conditions, culture strains of *Stictyosiphon soriferus* from Portsmouth, England (Kawai SSO-1), Denmark (Pedersen strain no. 42), and Bergen, Norway (Kawai SSO-3) were also cultured. Swarmers were pipetted onto glass slides and cultured in glass vessels containing 200 ml of PESI medium (Tatewaki 1966). The sets of culture conditions used were 5°C SD (short day; 8: 16hLD), 5°C LD (long day; 16: 8hLD), 10°C SD, 10°C LD, 15°C SD, 15°C LD, 20°C SD and 20°C LD, under white fluorescent lighting of approximately 30 μmolm^{-2}s^{-1} (5°C) or 50 μmolm^{-2}s^{-1} (10°C, 15°C, 20°C). A temperature gradient plate was also used to investigate high lethal temperatures under long-day conditions (16: 8hLD).

Results

Habitat and morphology of the plant at Yashiro Is-


2
10 mm
3
50μm
4
50μm
5
50μm
6
50μm
7
10μm
8
10μm
9
50μm
10
10μm



land and morphology of other Japanese materials

The plants grow densely on concrete experimental substrata for algae at a depth of 3-4 m below Mean Low Water Level, together with *Punctaria* sp. The erect thallus is 3-4 times irregularly branched, without an obvious main axis, pale yellow in color, delicate and attains 20 cm in height (Fig. 2). In cross section the thallus consists of four large colorless central cells surrounded by 1-2 layers of

small pigmented peripheral cells (Fig. 9). In longitudinal section the central cells are rounded, 80–110 × 70–100 μm in size (Fig. 4). Terminal and lateral (often opposite) phaeophycean hairs are present (Figs. 5, 6, 9, 10). Plurilocular sporangia form by repeated divisions of peripheral cells (Figs. 6–10). They are usually formed in groups of 2–4 sporangia each containing 4–8 loculi in the surface view, square to rectangular in the shape, 12–16 × 10–14 μm in length and width in surface view (Figs. 5, 10). In the terminal thinner branches of the thallus where inner cells are not differentiated, entire peripheral cells transform into plurilocular sporangia which appear as intercalary sporangia (Fig. 5). The basal part of the plant attaches to the substratum by rhizoidal filaments (Fig. 3). Unilocular sporangia were not detected.

The materials from Sasebo and Anan (Fig. 32) agreed well with the specimens from Yashiro Island in general appearance and internal structure. Both materials had plurilocular sporangia which agreed with those of Yashiro Island in morphology (Figs. 33, 34). Unilocular sporangia were not detected.

Culture experiments on the plant from Yashiro Island

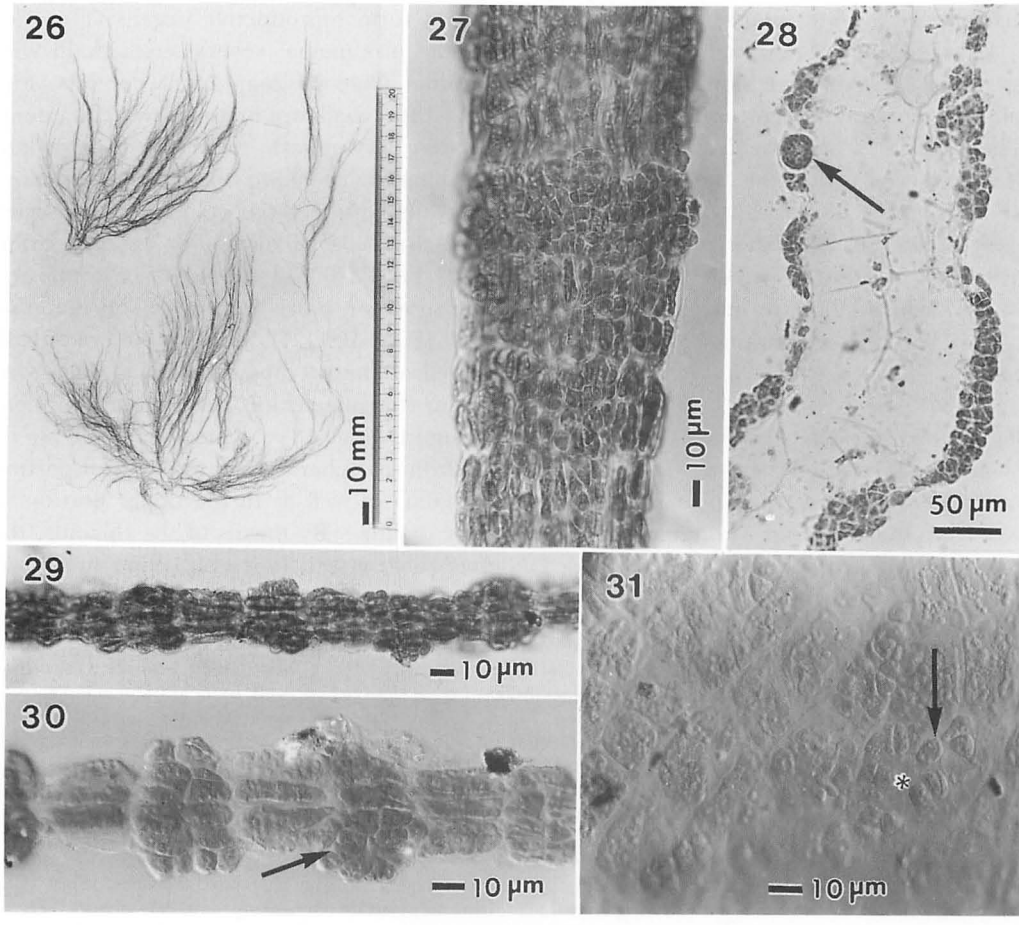
Swarmers released from plurilocular sporangia (plurispores) are pear-shaped, 6–11 × 5–7 μm in length and width, containing a chloroplast with an eyespot, and provided with two laterally inserted flagella, a longer anterior (14–16 μm in length) and a shorter posterior one (ca. 6 μm in length) (Fig. 11). Released swarmers swim for some minutes and then settle on the glass (Fig. 12). Sexual fusions among the swarmers were not observed. Abnormal swarmers in which two or more individual swarmers coalesced with each other, when released through the release pores of the sporangia, were often observed. Such abnormal swarmers settled and developed in the same way as normal swarmers. In 1–2 days they germinate forming a germ tube (Figs. 13, 14), and develop into branched prostrate filaments (protonemata) which do not form reproductive organs (Fig. 15). On the protonema, several erect thalli with terminal phaeophycean hairs develop (Fig. 15). Erect thalli are first uniseriate filaments of intercalary growth, then they undergo longitudinal divisions to become polystichous and differentiate large colorless inner cells. Erect thalli form irregular or opposite branches (Fig. 16). Lateral, often opposite, phaeophycean hairs are present on the erect thalli (Figs. 16, 17). Cells of the erect thalli as well as the protonema contain many discoid or elongated chloroplasts with prominent pyrenoids (Fig. 18). Rhizoidal filaments issue from peripheral cells in the basal portion of thallus as well as in the upper portion in older thallus. By means of the rhizoids, the erect thalli attach to the substrata firmly, or

Figs. 2–10. *Stictyosiphon soriferus* (Reinke) Rosenvinge in the field. (Figs. 3–9. Preserved materials stained with toluidine blue). Fig. 2. Habit of the field plant collected at Yashiro Island, Seto Inland Sea on 15 May 1986. Fig. 3. Basal part of the erect thallus showing rhizoidal filaments (arrow). Fig. 4. Micrograph focused on the central part of the thallus showing large rounded inner cells. Fig. 5. Parenchymatous branches and intercalary plurilocular sporangia on a terminal branch (arrow). Fig. 6. Surface view of mature erect thallus forming abundant plurilocular sporangia (arrow). Fig. 7. Cross section of upper thin part of mature erect thallus forming protruded conical plurilocular sporangia. Fig. 8. Cross section of thicker part of mature thallus forming immersed plurilocular sporangia. Fig. 9. Cross section of thicker part of thallus showing rounded inner cells. Fig. 10. Surface view of erect thallus showing plurilocular sporangia, released swarmers (arrow) and emptied sporangia (asterisks).

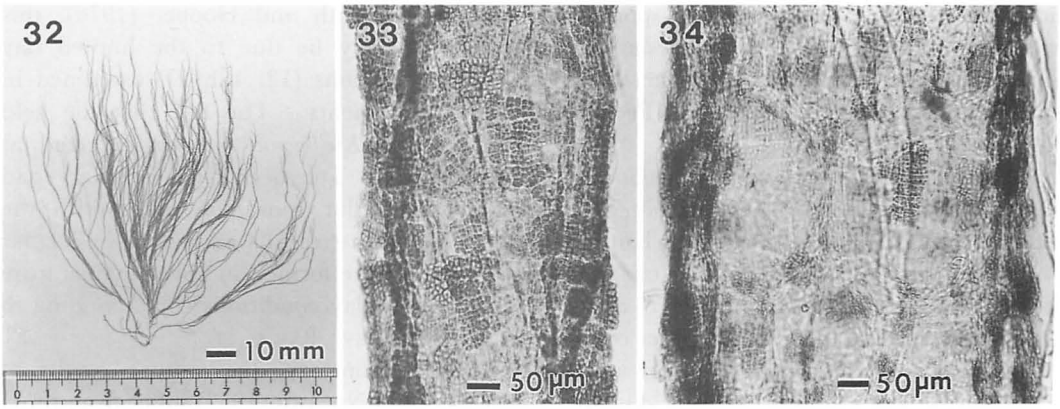
Figs. 11–25. *Stictyosiphon soriferus* (Reinke) Rosenvinge in culture. Fig. 11. Swarmer (pluri-spore) released from plurilocular sporangium. a, anterior flagellum; p, posterior flagellum. Fig. 12. Settled swarmer. Figs. 13, 14. Germination of swarmer. Fig. 15. Young erect thalli arising on prostrate filaments (protonema, arrow). Fig. 16. Opposite and unilateral branches on erect thallus. Fig. 17. Surface view of mature erect thallus. Fig. 18. Peripheral cells containing many discoid chloroplasts with prominent pyrenoids. Fig. 19. Surface view of thicker part of mature thallus showing grouped plurilocular sporangia among vegetative peripheral cells. Figs. 20, 21. Lateral views of immersed and protruded type of plurilocular sporangia. Fig. 22. Intercalary plurilocular sporangia formed on terminal thin part of the thallus. Fig. 23. Emptied plurilocular sporangia (asterisks). Fig. 24. Unilocular sporangia. Fig. 25. Zoospore (uni-spore) released from unilocular sporangium. a, anterior flagellum; p, posterior flagellum.

entangle with each other.

The erect thalli developed and formed plurilocular sporangia in all culture conditions examined, but they grew faster, and attained their maximum length of 15-20 cm in 10°C and 15°C. In 5°C short day conditions they formed unilocular sporangia, sometimes mixed with plurilocular ones. Plurilocular sporangia are formed by repeated divisions of the peripheral cells. The shapes of them are rather variable depending on their position on the thallus, age and culture conditions (Figs. 17, 19-23). Almost flat plurilocular sporangia as well as protruded ectocarpoid ones are observed. In the terminal part of the thallus where inner cells do not develop, the whole surface of the thallus transforms into plurilocular sporangia, which appear as intercalary sporangia (Fig. 22). Unilocular sporangia are conical or irregularly spherical, sessile, formed from the peripheral cells, 28-30 × 20-28 μm in length and width (Fig. 24). Zoospores (uni-spores) released from unilocular sporangia are about 7 × 5 μm in length and width provided with two, longer anterior and shorter posterior, flagella (Fig. 25). Swarmers from plurilocular sporangia as well as zoospores from unilocular sporangia germi-



Figs. 26–31. Type specimen and permanent preparations of *Kjellmania arasakii* Yamada. Fig. 26. Habit of the type material (SAP 027286). Fig. 27. Surface view of the type material forming immersed plurilocular sporangia. Fig. 28. Longitudinal section of mature erect thallus forming both unilocular (arrow) and plurilocular sporangia in the preparation of Y. Yamada. Figs. 29, 30. Terminal thinner part of the thallus forming plurilocular sporangia (arrow) in Yamada's preparation. Fig. 31. Surface view of mature erect thallus in Yamada's preparation showing individual swarmers (arrow) and emptied loculi (asterisk) of plurilocular sporangia.



Figs. 32–34. Herbarium specimens of Japanese *Stictyosiphon soriferus* (Reinke) Rosenvinge. Figs. 32, 33. Habit and surface view of the specimen forming plurilocular sporangia collected at Anan, Tokusima Pref. on 14 February 1984 by S. Arai. Fig. 34. Surface view of the specimen forming plurilocular sporangia collected at Sasebo, Nagasaki Pref. on April 1955 by S. Migita.

nated and developed in the same manner as the original swarmers. *In situ* germinations of the swarmers or zoospores in the sporangia were often observed, especially in old cultures. The high lethal temperature was 25–26°C in the Yashiro Island strain.

Morphological observations on the type specimen of Kjellmania arasakii

The erect thallus is 3–4 times irregularly branched, without an obvious main axis, and attains 15 cm in height (Fig. 26). In longitudinal section the thallus consists of large rounded colorless central cells of about 100×90 μm in longitudinal section, surrounded by 1–2 layers of small pigmented cells (Fig. 28). Plurilocular sporangia are abundant, formed by divisions of peripheral cells, $35\text{–}40 \times 25\text{–}30$ μm in surface view, somewhat protruded from the surface (Fig. 27, 31). In the terminal thinner part of the thallus each loculus of the sporangia is strongly protruded (Figs. 29, 30), however, not completely independent as shown in fig. 15 in Arasaki & Nozawa (1953). Rounded sessile unilocular sporangia immersed in the peripheral cells are also present, about 30×25 μm in length and width (Fig. 28).

Culture experiments on Atlantic Stictyosiphon soriferus

All of the three European strains of *Stictyosiphon soriferus* (SSO-1, SSO-3, Pedersen no. 42) showed direct type of life histories and formed plurilocular sporangia. In the Denmark strain a few unilocular sporangia were formed in 3°C short day conditions. The high lethal temperature in the Portsmouth strain was 24–25°C.

Discussion

The specimens from Yashiro Island agreed well with the type material of *Kjellmania arasakii*, in appearance and general anatomical features, such as size and branching pattern of erect thalli, and shape, arrangement and size of inner and peripheral cells. The plurilocular sporangia of the Yashiro Island plant also agreed with figs. 1–4 of Yamada (1953) and those of the type specimen and his permanent preparations. Plurilocular sporangia are formed by repeated divisions of peripheral cells, as in *Kjellmania* and *Stictyosiphon*. Although the nature of the sporangia is a little obscure in figs. 1–3 of Yamada (1953), the examination of type permanent preparations (Figs. 29, 30) revealed that they are the same as those of Yashiro Island plant (Figs. 2, 22). However, the plurilocular sporangia shown in fig. 15 of Arasaki and Nozawa (1953) seem to be rather different from them, because each loculus of the sporangium is independent at the base in cross sec-

tion. Such kinds of plurilocular sporangia are reminiscent of those of *Coelocladia arctica* Rosenvinge and *Litosiphon subcontinuus* (Rosenvinge) Lund (Rosenvinge 1898, Pedersen 1976).

Naylor (1958) reviewed the genus *Stictyosiphon* and its four European species (e.g. *S. tortilis* (Ruprecht) Reinke, *S. adriaticus* Kützing, *S. soriferus*, and *S. griffithsianus* (Le Jolis) Holmes et Batters). According to her, *S. adriaticus* and *S. soriferus* have rounded inner cells in longitudinal sections, while *S. tortilis* and *S. griffithsianus* have longer ones. Furthermore, *S. soriferus* is distinguished from *S. adriaticus* in having a solid thallus and more uniformly sized and arranged inner cells. In Europe the former has a more northern distribution than the latter. Compared with these species, *Kjellmania arasakii* agrees well with *Stictyosiphon soriferus* in its anatomical features. Yamada (1953) distinguished *Kjellmania sorifera* and *K. arasakii* in the manner of branching and absence of intercalary sporangia in the latter. However, the differences in the branching manner are apparently within the range of variations caused by age and growing conditions. As mentioned above, in this species the intercalary sporangia are essentially the same as those formed on the surface of the thicker thallus. Furthermore, since the specimens Yamada (1953) examined were all drift materials, terminal thinner mature portions could have been already lost. Detailed comparisons with the herbarium specimens and live or liquid preserved materials of European specimens of *Stictyosiphon soriferus* (cited in Materials and Methods) with those of *Kjellmania arasakii* in the present study also showed no distinctive differences between the two taxa.

In culture, the plants from Yashiro Island showed a direct type of life history and formed unilocular and plurilocular sporangia. This life history pattern agreed well with the culture results of Rosenvinge (1935) and South and Hooper (1976) on *Stictyosiphon soriferus*, as well as the results on the Atlantic culture strains in the present study. Although unilocular sporangia were not reported in the culture of South and Hooper (1976), this difference may be due to the limited day length conditions (12: 12hLD) examined in their experiments. The fact that the field material of *Kjellmania arasakii* collected at Fukagawa in Tokyo Bay on February had some unilocular sporangia agree with the present culture results in which unilocular sporangia were formed in lower temperature (5°C) short day conditions corresponding to winter at Tokyo Bay.

On the contrary, the culture results of Arasaki and Nozawa (1953) differ from those in the previous reports and present work on *S. soriferus* in the following points; 1) *Laminaria*-type of germination in which most cellular contents migrate into germ tube and the embryospores become almost empty; 2) the thalli derived from swarmers developed into erect (gametophytic) filaments and formed clustered plurilocular sporangia resembling those of *Botrytella* (=*Sorocarpus*); 3) swarmers from the plurilocular sporangia were supposed to be gametes, (actual copulations were not observed but presumptive zygotes with two stigmata were found) and the presumptive zygotes developed into parenchymatous sporophytes. With regard to 1), *Laminaria*-type (mediate filamentous type) germination is rather rare in the order Dictyosiphonales and not reported in *Stictyosiphon*. The rare known exception in the order is the case in *Coelocladia arctica* (Pedersen 1976). About 2), as Arasaki and Nozawa (1953) also mentioned, such plurilocular sporangia differ from those known in *Stictyosiphon*, and are rather similar to those of *Coelocladia arctica*. Concerning 3), since they did not observe actual copulations nor complete the life cycle, their explanation of the erect filaments derived from the original swarmer as gametophytes is questionable. In fact, the presumptive gametophytic filament illustrated in fig. 7 of Arasaki and Nozawa (1953) has some longitudinal walls, resembling those in the sporophytic thallus in their fig. 13. Settled swarmers provided with two (or more) stigmata can also be caused by abnormal coalescences of the swarmers as observed in the present culture. This

phenomenon may occur by too low or high temperature treatment during transportation or storage. Accordingly, it is presumed that the material Arasaki and Nozawa (1953) used for culture (at least the swarmers from which cultures were started) was somehow different from the specimens sent to Yamada. Judging from the germination pattern and the morphology of the erect thalli and sporangia, the entity of the material Arasaki and Nozawa cultured is most likely a *Coelocladia*. This hypothesis is also supported by the recent finding of *Coelocladia arctica* from Japanese waters (at Oshoro, Japan Sea coast of Hokkaido; Kawai and Sato 1991). However, specimens referable to *Coelocladia* were not found in the herbarium specimens sent by Arasaki to Yamada and deposited in SAP.

In conclusion, through the detailed morphological comparisons and culture experiments in the present work, there are no essential differences distinguishing *Kjellmania arasakii* from *Stictyosiphon soriferus*. Accordingly, *Kjellmania arasakii* is considered to be taxonomically identical with *Stictyosiphon soriferus* at the species level. The species is distributed widely in the central part of Japan as shown in Fig. 1. Although the geographical distribution of the species in Japan seems to be a little more to the south than in Europe, there were no remarkable differences in the high lethal temperatures between Japanese and European strins. Judging from the culture results, the species could be expected to have a much wider distribution in Northern Japan and other Pacific Ocean areas.

Acknowledgments

I am grateful to Dr. G. Robin South (University of the South Pacific) for his critical reading and improving the English of the manuscript and to Dr. T. Yoshida for his valuable comments. I am also grateful to Mr. K. Yoshikawa (Naisei Regional Fisheries Research Laboratory), Dr. Tore Lein (University of Bergen) and Dr. R. L. Fletcher (Portsmouth Polytechnic) for their help in collecting specimens, and to Miss. N. Uesugi (Tokyo Kyuei, Co. Ltd.), Dr. S. Migita (Nagasaki Univ.), Drs. P. Kornmann and P.-H. Sahling (Helgoland Marine Station), Dr. P. M. Pedersen (Copenhagen Univ.) and Mr. S. Arai (Kaisou-kenkyusho Co. Ltd.) for providing field and culture materials, and staff members of British Museum for their help in examining the specimens. A part of this work was conducted during my stay in Dr. D. G. Müller's laboratory as Alexander von Humboldt Fellow.

References

Arasaki, S. and K, Nozawa. 1953. On the life-history of *Kjellmania arasakii* Yam. and its systematic position. Bull. Jap. Phycol. Soc. **1**: 5–9.

Kawai, H. and N. Sato. 1991. Morphology and life history of Japanese *Coelocladia arctica* (Dictyosiphonales, Phaeophyceae). (In Japanese, abstract of 15th annual meeting of Jpn. Phycol. Soc.). Jpn. J. Phycol. **39**: 100.

Naylor, M. 1958. Observations on the taxonomy of the genus *Stictyosiphon* Kütz. Rev. Algol. n.s. **4**: 7–24.

Pedersen, P. M. 1976. Culture studies on marine algae from West Greenland II. *Coelocladia arctica* (Dictyosiphonales, Coelocladiaceae fam. nov.). Norw. J. Bot. **23**: 243–249.

Reinke, J. 1889. Algenflora der westlichen Ostsee deutschen Antheils. Prussia. Kommission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel. Berlin, xiv+101 pp.

Rosenvinge, L. K. 1898. Deuxième Mémoire sur les algues marines du Groenland. Meddr Grønland **20**: 1–125.

Rosenvinge, L. K. 1935. On some Danish Phaeophyceae. Mém. Acad. R. Sci. Lett. Dan., Copenhagen. Sect. Sci. **6**: 1–40.

Rosenvinge, L. K. and S. Lund. 1947. The marine algae of Denmark. Contribution to their natural history. Vol. II. Phaeophyceae. Part III. Encoeliaceae, Myriotrichiaceae, Giraudiaceae, Striariaceae, Dictyosiphonaceae, Chordaceae, and Laminariaceae. K. Dan. Vidensk. Selsk. Biol. Skr. **4**: 1–99.

Sauvageau, C. 1929. Sur le développement de quelques Phéosporées. Bull. Stat. Biol. Arcachon. **26**: 253–420.

South, G. R. and R. Hooper, 1976. *Stictyosiphon soriferus* (Phaeophyta, Dictyosiphonales) from eastern North America. J. Phycol. **12**: 24–29.

Tatewaki, M. 1966. Formation of a crustaceous sporophyte with unilocular sporangia in *Scytosiphon lomentaria*. Phycologia **6**: 62–66.

Yamada, Y. 1953. What is Okamura's Samezu-gusa? Bull. Jap. Phycol. Soc. **1**: 1–4.

川井浩史：褐藻サメズグサ（*Kjellmania arasakii*, ウイキョウモ目）の分類と生活史の再検討

褐藻サメズグサの分類について瀬戸内海・屋代島において新たに採集した材料などにもとづき再検討した結果，本種は北大西洋に広く生育する *Stictyosiphon soriferus* と同一種であると結論した。本種は屋代島においては水深 3–4 m の亜潮間帯の人工的な基物の上に生育しており，藻体は高さ 20 cm に達し，3–4回不規則に枝分かれし，柔らかく，表面に複子嚢を生ずる。培養下では複子嚢に由来する遊走細胞はプロトネマに発達し，その上に直接直立藻体を形成した。直立藻体は多列形成的となり，分枝しながらよく成長し 5–20°C で複子嚢を生じたが，10°C と 15°C で特によく成長した。単子嚢は 5°C 短日条件でのみ形成された。（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）