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Morphology and life history of *Petalonia zosterifolia* (Reinke) O. Kuntze (Scytosiphonales, Phaeophyceae) from Japan

Kazuhiro Kogame* and Hiroshi Kawai**

*Department of Botany, Faculty of Science, Hokkaido University, Sapporo, 060 Japan
**Department of Biology, Faculty of Science, Kobe University, Rokkodai Nadaku, Kobe, 657 Japan

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The morphology and life history of Japanese *Petalonia zosterifolia* were studied based on materials collected from sixteen localities. Erect thalli collected in the field were flat, linear, basically solid or with small cavities, attaining 20(–30) cm in length and 0.5–8 mm in width. Plurilocular sporangia were closely packed without paraphyses. In culture, swarmers from plurilocular sporangia developed into filamentous prostrate thalli (microthalli) that formed unilocular sporangia. The prostrate thalli never developed into distinctly crustose thalli. Erect thalli (macrothalli) issued directly from the prostrate thalli, and developed best in temperature less than 10°C and short day conditions, and formed plurilocular sporangia. In some isolates, unilocular sporangia also formed on the erect thalli bearing plurilocular sporangia. Swarmers from plurilocular and unilocular sporangia developed in the same manner as the original plurispores, representing a direct type of life history. Sexual reproduction was not observed.

Field plants collected at Oshoro, Hokkaido, which were morphologically referable to *Compsonema saxicolum* (Kuckuck) Kuckuck, developed in culture into erect thalli identical with *Petalonia zosterifolia*. Therefore, *Compsonema saxicolum* is considered to be a sporophytic stage of *P. zosterifolia*.

Key Index Words: Compsonema saxicolum—*Life history*—Petalonia zosterifolia—*Phaeophyceae*—*Scytosiphonales*—*Taxonomy*.

In the genus *Petalonia* Derbès et Solier, three species are generally recognized; *P. fascia* (O. F. Müller) O. Kuntze, *P. zosterifolia* (Reinke) O. Kuntze and *P. filiformis* (Batters) O. Kuntze (Wynne 1969, Fletcher 1987). *Petalonia zosterifolia* is distributed along the North Atlantic coast (Newton 1931, Hamel 1931-39, Rosenvinge and Lund 1947) as well as the North Pacific coast [Setchell and Gardner (1925) as *Ilea fascia* f. *zosterifolia* Setchell et Gardner].

The life history of *Petalonia zosterifolia* has been studied in culture by several authors. Dangeard (1962, 1963) reported a heteromorphic life history alternating between erect thalli (macrothalli) forming plurilocular sporangia and filamentous prostrate thalli (microthalli) forming unilocular or plurilocular sporangia, based on the materials collected at Gironde, France. However, Wynne (1969 pp. 51, 52) doubted the taxonomic assignment of Dangeard's material as *P. zosterifolia*, because a part of his culture bearing ectocarpoid plurilocular sporangia on the prostrate thalli contained more than one plastid in each vegetative cell. On the other hand, Dangeard (1963 pp. 25, 30, 42-44) also reported sessile plurilocular sporangia based on different isolates. The swarmers from these sessile plurilocular sporangia did not form erect thalli and unilocular sporangia. On British materials, Fletcher (1974) reported a direct type of life history in which erect thalli issued directly from the filamentous prostrate thalli. On materials from North Carolina, Boone and Kapraun (1989) reported the occurrence of erect thalli and filamentous prostrate thalli with unilocular sporangia.

Based on study of Japanese material, Nakamura and Tatewaki (1975) reported a heteromorphic and biphasic life history includ-

Table 1. Localities and collection dates of Japanese *Petalonia zosterifolia* used for morphological observations, and no. of culture strains established from them.

Locality	Collection date		Culture strain
Oshoro	11 March	1987	2
Oshoro	7 November	1987	3, 4
Oshoro	9 December	1987	5, 6
Oshoro	21 January	1988	7, 8
Oshoro	17 February	1988	
Oshoro	18 March	1988	
Oshoro	14 May	1988	9
Ofuyu	2 May	1988	14
Rausu	1 July	1988	17
Hanasaki	7 September	1987	13
Akkeshi	30 June	1988	15
Akkeshi	14 July	1988	16
Hiroo	12 February	1989	20
Samani	11 February	1989	19
Muroran	22 January	1989	18
Shikabe	4 March	1986	1
Kashiwazaki	27 March	1988	21
Shiiya	27 March	1989	
Shirakami-Misaki	19 March	1987	12
Esashi	15 May	1988	
Setana	18 March	1987	11
Shiraito-Misaki	18 March	1987	10
Iwanai	1 May	1988	

ing sexual reproduction. However, their material had unicellular paraphyses among plurilocular sporangia. Such paraphyses are uncommon in *P. zosterifolia*, so their findings require reexamination. Therefore, the aim of this study was to reexamine the morphology and life history of *Petalonia zosterifolia* from Japan.

Materials and Methods

Localities and collection dates of the materials for morphological and culture studies are shown in Table 1 and Fig. 1. For morphological observations both living materials and preserved materials in 5% formaldehyde-seawater were used. The following herbarium specimens were also examined; Esashi, 3 April 1943 (SAP 042481); Esashi, 3 April 1944 (SAP 025419); Setana, 28 March 1945 (SAP 025362); Sirakami-Misaki, 7 April 1947 (SAP 042483). We also examined herbarium specimens of *P. zosterifolia* from which the cultures of Nakamura and Tatewaki (1975) were established, collected at Muroran on 30 March 1967.

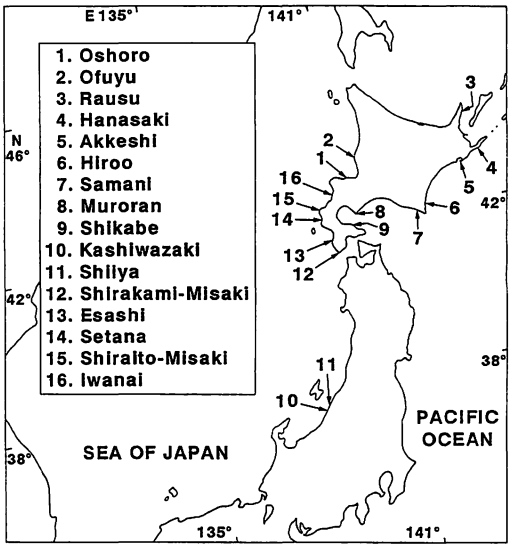


Fig. 1. Collection sites of Japanese *Petalonia zosterifolia* examined in the present paper.

Cultures were started from the swarmers released from plurilocular sporangia on erect thalli. The swarmers were pipetted onto cover glasses and cultured in glass vessels containing 100 ml of PESI medium (Tatewaki 1966). Filamentous thalli morphologically referable to *Compsonema saxicolum* (Kuckuck) Kuckuck were collected at Oshoro on 23 September 1989. Unialgal culture of *Compsonema* was started from fragments of the thalli. Penicillin G potassium (48 U/ml) and GeO_2 (0.005 mg/ml) were added at the beginning of the culture of *Compsonema* in order to suppress the growth of bacteria and diatoms.

The sets of culture conditions used were 5°C SD (short day; 8 : 16 h light : dark cycle), 5°C LD (long day; 16 : 8 h light : dark cycle), 10°C SD, 10°C LD, 15°C SD, 15°C LD, 20°C SD and 20°C LD, under fluorescent lighting of approximately 30-50 μmol $m^{-2}s^{-1}$.

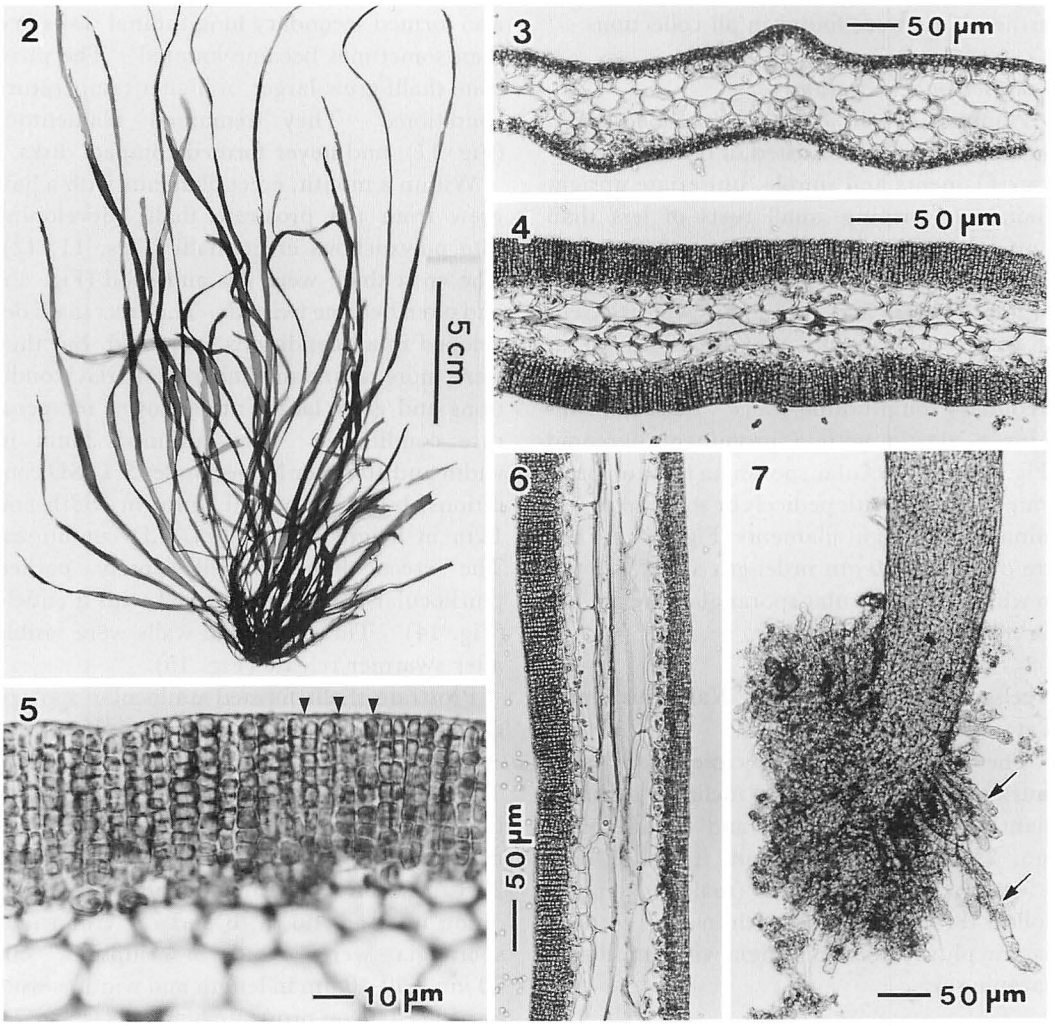
Results

Morphology and phenology

Petalonia zosterifolia

Erect thalli are gregarious, linear, flattened, simple, twisted in narrower thalli, 10-20 (up to 30) cm long, 2-5 (0.5-8) mm wide and tapered towards the base (Fig. 2). The thalli are 60-120 μm in thickness, composed of cortical cells (1-3 cells thick) and colorless medullary cells (Figs. 3, 4). Each cell of the thallus contains a plastid with a prominent pyrenoid. Medullary cells are rounded or oval and 22-54 × 8-24 μm in size in transverse section (Figs. 3, 4) and 20-270 μm (or more) in length in longitudinal section (Fig. 6). The thalli are solid or sometimes partly hollow. Rhizoidal filaments in the medullary layer and phaeophycean hairs are rare. The basal holdfast is composed of rhizoidal filaments (Fig. 7), and never forms an expanded mat.

Plurilocular sporangia may form anywhere on the surface of the thalli, sometimes in sori



Figs. 2-7. Habit and anatomy of *Petalonia zosterifolia* collected in the field. Fig. 2. Habit of the plant collected on 21 January 1988 at Oshoro. Fig. 3. Cross-section of the sterile thallus having small cavities in the medulla. Fig. 4. Cross-section of mature thallus bearing plurilocular sporangia. Fig. 5. Cross-section of mature thallus showing plurilocular sporangia with a cuticle (arrowheads). Fig. 6. Longitudinal section of mature thallus. Fig. 7. Rhizoidal filaments at the basal part of thallus (arrows).

which are often longitudinally elongated. Maturation of the thallus occurs basipetally. Plurilocular sporangia are closely packed, covered with a cuticle and 14–40 μm (6–12 loculi) in height (Fig. 5). Paraphyses were not observed.

P. zosterifolia is epilithic or epizoic, growing in the upper littoral zone of exposed areas. Erect thalli appeared in November and disappeared in May at Oshoro. Erect thalli were collected in winter and spring at other localities except for Akkeshi and Hanasaki where they were also observed in summer. Some fertile plants were found in all collections.

Compsonema saxicolum

Plants of *Compsonema saxicolum* collected in the field (Fig. 21) consisted of branched prostrate filaments and simple, uniseriate upright filaments, forming small tusts of less than 1 mm in diameter and up to 240 μm in height. Cells of upright filaments measure 6–14 μm in length and 7–12 μm in width. Cells of prostrate filaments measure 8–18 μm in length and 6–17 μm in width; they often form secondary longitudinal walls. Each cell contains a plastid with a prominent pyrenoid (Fig. 22). Unilocular sporangia form on prostrate filaments with pedicels or sometimes terminally on upright filaments (Fig. 21). They are ovoid, 30–50 μm in length and 15–25 μm in width. Plurilocular sporangia were not observed.

Herbarium specimens of Nakamura and Tatewaki (1975)

The "*P. zosterifolia*" specimens of Nakamura and Tatewaki (1975) included a female plant (marked as no. 18) and a male plant (no. 25). They were 3 mm in width, and 6.5 cm (female) and 9 cm (male) in length, hollow throughout the length in cross section, having plurilocular sporangia with unicellular paraphyses.

Culture results

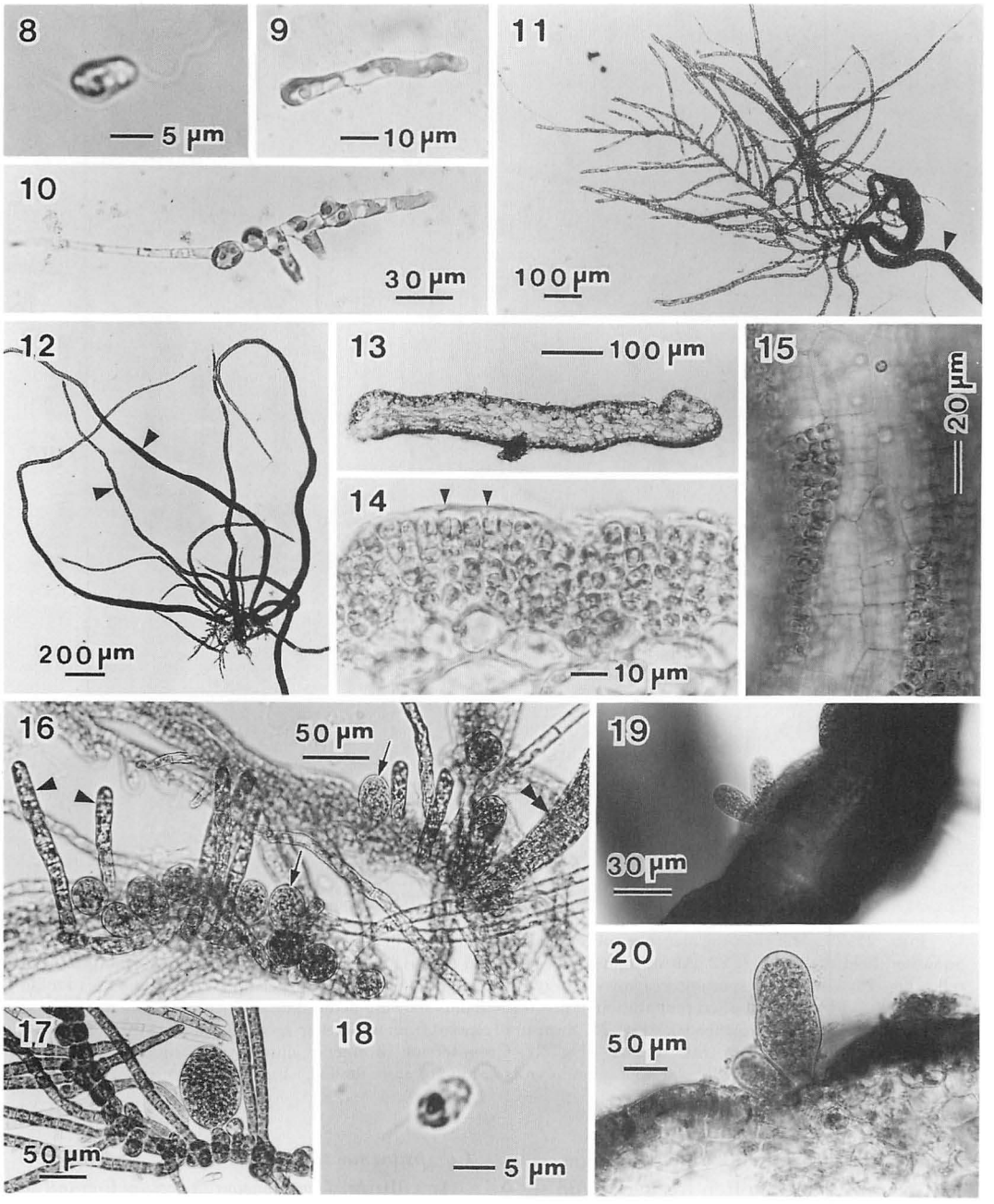
Petalonia zosterifolia

Swarmers released from plurilocular sporangia were teardrop-shaped, 7–8 μm × 4–5 μm in size, laterally biflagellated with a longer anterior and a shorter posterior flagellum (Fig. 8). They contained a plastid with a pyrenoid and a stigma. Sexual reproduction and fragrant odors of sexual pheromones were not observed. The swarmers showed negative phototaxis, and then settled on the substratum. Settled swarmers germinated in 1–5 days without leaving an emptied "embryospore" wall (Figs. 9, 10). The germlings developed into prostrate thalli of branched filaments from which uniseriate upright filaments arose. The cells of prostrate filaments also formed secondary longitudinal walls and then sometimes became knotted. The prostrate thalli grew larger in higher temperature conditions. They remained filamentous (Fig. 11), and never formed compact disks.

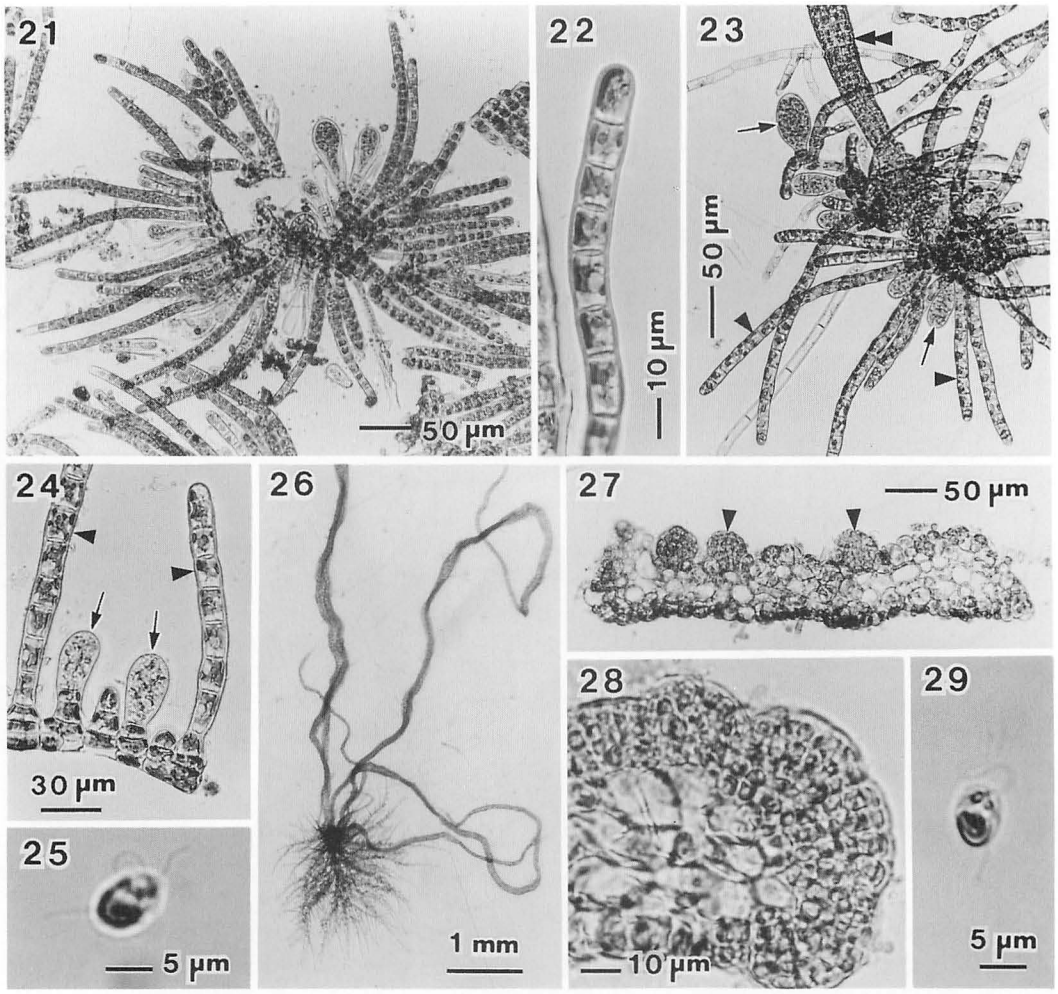
Within a month, erect filaments with a hair grew from the prostrate thalli, developing into polystichous erect thalli (Figs. 11, 12). The erect thalli were flat and solid (Fig. 13) and often became twisted. The erect thalli developed in all conditions examined, but they were more abundant under short day conditions and grew larger under lower temperature conditions. They attained 2 mm in width and 10 cm or longer under 5°C SD conditions, but were only 0.2 mm in width and 1 cm in length under 20°C LD conditions. The erect thalli formed closely packed plurilocular sporangia covered with a cuticle (Fig. 14). The sporangial walls were visible after swarmer release (Fig. 15).

Prostrate thalli formed unilocular sporangia only in strains no. 1, 2, 3, 5, 6, 7 (collected from Shikabe and Oshoro) (Fig. 16). They were formed under all culture conditions except 5°C in strain no. 1 and no. 5, under long day conditions of 10°C, 15°C and 20°C in strain no. 2, and under 20°C LD condition in strain no. 3, 6 and 7. Unilocular sporangia were ovoid or ellipsoid, 60–70 μm × 30–40 μm in length and width, sessile or pedicellate on prostrate filaments (Fig. 17).

Swarmers released from unilocular sporangia measured 7–8 μm × 4–5 μm in size (Fig. 18). They developed to filamentous prostrate thalli that formed erect thalli in the same man-



Figs. 8–20. *Petalonia zosterifolia* in culture. Fig. 8. Swarmer released from plurilocular sporangium on erect thallus. Figs. 9, 10. Germlings of swarmers from plurilocular sporangium. Figs. 11, 12. Prostrate thalli and erect thalli (arrowheads) issued from them. Fig. 13. Cross-section of flat and solid erect thallus. Fig. 14. Cross-section of plurilocular sporangia on erect thallus. Arrowheads show a cuticle. Fig. 15. Emptied plurilocular sporangia on mature erect thallus in surface view. Fig. 16. Prostrate thalli bearing unilocular sporangia (arrows), uniseriate upright filaments (arrowheads) and erect thallus (double arrowhead). Fig. 17. Unilocular sporangium on knot-shaped filament of prostrate thallus. Fig. 18. Swarmer released from unilocular sporangium on prostrate thallus. Fig. 19. Unilocular sporangia on erect thallus. Fig. 20. Cross-section of the erect thallus bearing unilocular sporangia.



Figs. 21–29. *Compsonema saxicolum* collected in the field (Figs. 21, 22) and in culture (Figs. 23–29). Fig. 21. Squashed field thalli. Fig. 22. An upright filament of field thallus showing one plastid with a pyrenoid in each cell. Fig. 23. Unilocular sporangia (arrows), uniseriate upright filaments (arrowheads) and erect thallus (double arrowhead). Fig. 24. Squashed preparation of prostrate thallus showing pedicellate unilocular sporangia (arrows) and upright filaments (arrowheads). Fig. 25. Swarmer released from unilocular sporangium on prostrate thallus. Fig. 26. Erect thalli on prostrate thallus. Fig. 27. Cross-section of erect thallus with plurilocular sporangia (arrowheads). Fig. 28. Plurilocular sporangia in cross-section of erect thallus. Fig. 29. Swarmer released from plurilocular sporangium on erect thallus.

ner as those from plurilocular sporangia.

Strains no. 1 and 2 often formed ovoid sessile unilocular sporangia on the erect thalli together with plurilocular sporangia under 15°C and 20°C (strain no. 1) and 20°C LD (strain no. 2) conditions (Figs. 19, 20). Swarmers released from those unilocular sporangia developed in the same manner as those from plurilocular sporangia.

Compsonema saxicolum

In culture, *Compsonema saxicolum* formed sessile or pedicellate unilocular sporangia on the prostrate filaments under 10°C LD, 15°C and 20°C conditions (Figs. 23, 24). Swarmers released from them (Fig. 25) developed into prostrate thalli. The prostrate thalli also formed erect thalli under all conditions examined (Figs. 23, 26). The erect thalli were flat (Fig. 27) or often twisted, similar to

Petalonia zosterifolia in culture. They formed densely packed plurilocular sporangia covered with a cuticle (Figs. 27, 28). Swarmers released from them (Fig. 29) developed into prostrate thalli forming unilocular sporangia and erect thalli.

Discussion

The morphology of our plants collected in various localities agreed well with the original description (Reinke 1889) and other previous reports of Atlantic *Petalonia zosterifolia* (Rosenvinge and Lund 1947, Clayton 1981, Fletcher 1987). The occurrence of filamentous prostrate thalli in Japanese plants also agrees with the previous culture results on the species (Fletcher 1974). *Petalonia zosterifolia* is taxonomically very close to *Petalonia filiformis* (Batters 1888, Kuckuck 1897). Newton (1931) and Fletcher (1987) distinguished *P. zosterifolia* from *P. filiformis* by the absence of fibrous rhizoidal mats at the bases, and in having broader thalli and different distributions, although these characteristics are not very clear. Therefore, considering that both of the species have filamentous prostrate thalli (Fletcher 1974, 1981), there remains a possibility that *P. zosterifolia* is conspecific with *P. filiformis*, or differs only at a lower taxonomic rank (e.g. variety or forma). However, until their taxonomic relations become more clear in Atlantic materials, we tentatively classify Japanese plants as *P. zosterifolia*.

In the present culture of *P. zosterifolia* prostrate thalli remained filamentous, and never formed *Ralfsia*-like crusts resembling that of *Scytosiphon lomentaria* (Lyngbye) Link and *Petalonia fascia* (Wynne 1969, Nakamura and Tatewaki 1975). Fletcher (1974) and Boone and Kapraun (1989) also mentioned that *Ralfsia*-like crusts were not observed in culture of *P. zosterifolia*. On the other hand, Dangeard (1963) reported glomerulus, myrionematoid and ralfsioid prostrate thalli. However, his results can not be generalized since his cultures contain contaminants of other brown algal species as mentioned above.

The morphology of prostrate thalli (sporophytes) are known to be more or less variable in the Scytosiphonaceae. For example, *Scytosiphon lomentaria* and *Petalonia fascia* occasionally form filamentous sporophytes in culture, although they are normally crustose. The quality of light or concentration of iodine or phosphate in the culture media are shown to affect on their morphology (Lüning and Dring 1973, Hsiao 1969, Roberts and Ring 1972). However, in the present species, the morphology of prostrate thalli was uniformly filamentous in any conditions examined, and we concluded that the prostrate thalli of *P. zosterifolia* is basically filamentous.

We believe that the filamentous prostrate thalli of *P. zosterifolia* are identical with *Compsonema saxicolum* encountered in the field. This hypothesis is supported by the present culture results in which field plants of *C. saxicolum* formed *P. zosterifolia*-like erect thalli.

C. saxicolum has been studied by several authors in culture. Fletcher (1987) reported the occurrence of erect thalli resembling *Petalonia* or *Scytosiphon* in the life history of *C. saxicolum*. He also mentioned that prostrate thalli of *Petalonia filiformis* in culture appear to show a marked similarity to *C. saxicolum* (Fletcher 1981). Loiseaux (1970) reported that *Compsonema sporangiiferum* Setchell and Gardner, which is taxonomically very close to *C. saxicolum*, formed minute *Scytosiphon*-like erect thalli. Therefore, it is likely that *C. saxicolum* generally represents a prostrate (sporophytic) stage of *P. zosterifolia*.

Although there has been a report on the life history of Japanese *P. zosterifolia* (Nakamura and Tatewaki 1975), detailed observations on their original material revealed that it was not *P. zosterifolia* but probably a new taxon of *Scytosiphon*, having hollow thalli and unicellular paraphyses among plurilocular sporangia. The occurrence of *Ralfsia*-like prostrate thalli in their culture, which is different from filamentous prostrate thalli in our results, also supports this conclusion. Therefore, this paper represents the first report on the life history of Japanese *P. zosterifolia*.

P. zosterifolia also resembles *Scytosiphon com-*

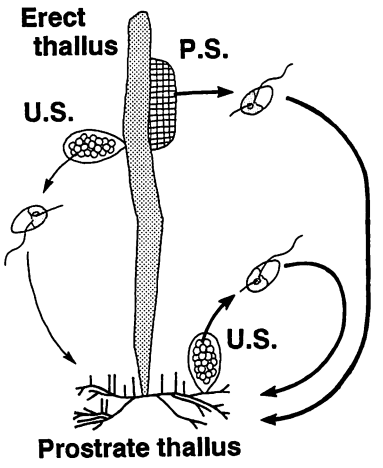


Fig. 30. Diagram of the life history of Japanese *Petalonia zosterifolia* in culture. P. S.: plurilocular sporangium, U. S.: unilocular sporangium.

planatus (Rosenvinge) Doty in morphology. Pedersen *et al.* (1987) doubted their distinctiveness. However, the erect thalli of *P. zosterifolia* are solid when young, while those of *S. complanatus* are essentially hollow (Rosenvinge and Lund 1947). Furthermore, *S. complanatus* forms crustose prostrate thalli (Pedersen 1980) which contrasts with the filamentous ones in *P. zosterifolia*. Therefore, in our opinion, these two are distinct species.

Fig. 30 summarizes the asexual, direct type of life history of Japanese *Petalonia zosterifolia* shown in the present culture study. This life history pattern in principle agrees with the reports of Fletcher (1974) and Boone and Kapraun (1989) on Atlantic materials. However, in our culture, in addition to the usual plurilocular sporangia, the erect thalli bore unilocular sporangia under 15°C and 20°C conditions. This is the first report on the occurrence of unilocular sporangia on the erect thalli in the Scytosiphonales, although they were not found in the field materials and can be artifact of culture experiment.

The order Scytosiphonales is generally known to form only plurilocular sporangia on (gametophytic) erect thalli, and only unilocular sporangia on (sporophytic) prostrate thalli. However, *Colpomenia peregrina* (Sauv.) Hamel forms additional plurilocular sporangia on prostrate thalli in culture (Sauvageau 1927, Dangeard 1963, Blackler 1981). As shown in the present study, erect thalli also form unilocular sporangia under certain conditions. These results suggest that the life history patterns of the Scytosiphonales are more complicated than so far believed.

Culture results of Japanese *P. zosterifolia*, in which erect thalli appeared under all culture conditions examined, does not explain why erect thalli could not be found during summer and autumn at Oshoro. However, the growth of erect thalli and the swarmer release from plurilocular sporangia were less abundant under 20°C culture conditions than other conditions. Since *P. zosterifolia* grows in the upper intertidal zone, higher air temperature and strong solar irradiation during summer may cause serious damage to the growth of *P. zosterifolia*. Therefore, the occurrence of *P. zosterifolia* may be suppressed by these factors. This notion is supported by the fact that the species showed longer growth periods at Akkeshi and Hanasaki where the air and water temperatures are much lower than at Oshoro.

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小亀一弘・川井浩史：日本産褐藻ホソバセイヨウハバノリ *Petalonia zosterifolia* (Reinke) O. Kuntze の形態と生活史

本種の直立藻体は，長さ 20(-30) cm, 幅 0.5–8 mm の偏平で細長い帯状で，中実だが部分的に中空になる。複子嚢の細胞列は互いに密に接着しており，側糸を欠く。複子嚢から放出された遊走細胞は培養下では糸状のほふく体に発達し，単子嚢を形成した。ほふく体は明かな盤状になることはない。直立体はほふく体から直接発出し，10°C 以下の低温短日条件下でよく発達し複子嚢を形成した。また，一部の培養株では，直立体上に複子嚢に混じって単子嚢が形成された。有性生殖は観察されず，複子嚢および単子嚢に由来する遊走細胞は，いずれも初めの遊走細胞と同様の直接型の生活史を示した。北海道忍路において形態上 *Compsonema saxicolum* (Kuckuck) Kuckuck と同定される藻体を採集し培養したところ，ホソバセイヨウハバノリと同定できる直立体を得た。このことから *Compsonema saxicolum* は本種の胞子体世代であると考えられる。(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)