Life history and systematic position of *Heteroralfsia saxicola* gen. et comb. nov. (Ralfsiaceae, Phaeophyceae)*

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The phenology, morphology and life history of *Saundersella saxicola* were studied in culture. At Ohma, Aomori Prefecture, Japan, the species is an annual appearing in March, growing during spring, and maturing in May. In culture, the zoospores show a mediate discal-type of germination, and develop into *Ralfsia*-like crustose thalli forming intercalary plurilocular sporangia with terminal sterile cells. Erect filamentous thalli develop on the crustose thalli, forming radiate multicellular assimilatory filaments and unilocular sporangia. The following characters of the species suggest its distant systematic relation with *Saundersella* and rather closer position to *Ralfsia* and its relatives including *Analipus*: single sinuate cup-shaped chloroplast without pyrenoid per cell; mediate discal-type of germination; and intercalary plurilocular sporangia with terminal sterile cells. Accordingly, a new genus *Heteroralfsia* to accommodate the species is proposed.

INTRODUCTION

Saundersella saxicola (Okamura et Yamada) Inagaki (Inagaki 1958) was originally described as *Gobia saxicola* Okamura et Yamada (Yamada 1928). Yamada (1928) placed the species in the genus *Gobia* (Reinke 1889) based on its morphological resemblance to *Gobia simplex* Setchell et Gardner. In 1958, Inagaki transferred the species to the genus *Saundersella,* following the treatment of Kylin (1940) who transferred *G. simplex* to his new genus *Saundersella. Saundersella saxicola* has been placed in the Chordariaceae, Chordariales. However, compared with *Saundersella simplex,* the type of the genus, *S. saxicola* has several distinctive characters (e.g. less slimy and tougher thalli, well developed crustose holdfasts, pigmented and almost isodiametric medullary filaments), which suggest that it may be generically distinct from *Saundersella.* Furthermore, there has been no prior report on the phenology or life history of this species. The purpose of the present study was to provide phenological data for this species, to examine its life history in culture, and to elucidate its systematic position.

MATERIALS AND METHODS

Field observations and collections of specimens were made at Ohma, Aomori Prefecture facing the Tsugaru Strait (41°29′N, 140°55′E) on 23 May 1984, 10 February, 21 March 1985, 27 April, 12 May, 6 September, 3 December 1986, and 2 March 1987.

Morphological observations by light microscopy were made on living materials or on specimens preserved in 3–5% formaldehyde-sea water. For the observations by TEM, materials were fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer, postfixed in 2% OsO_4 in 0.1 M cacodylate buffer, dehydrated in acetone series and embedded in Spurr's epoxy resin, 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.

Cultures were started from swarmers released from unilocular sporangia on erect thalli collected on 23 May 1984 and 8 May 1985. 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 : 16 h LD), 5°C LD (long day; 16 : 8 h LD), 10°C SD, 10°C
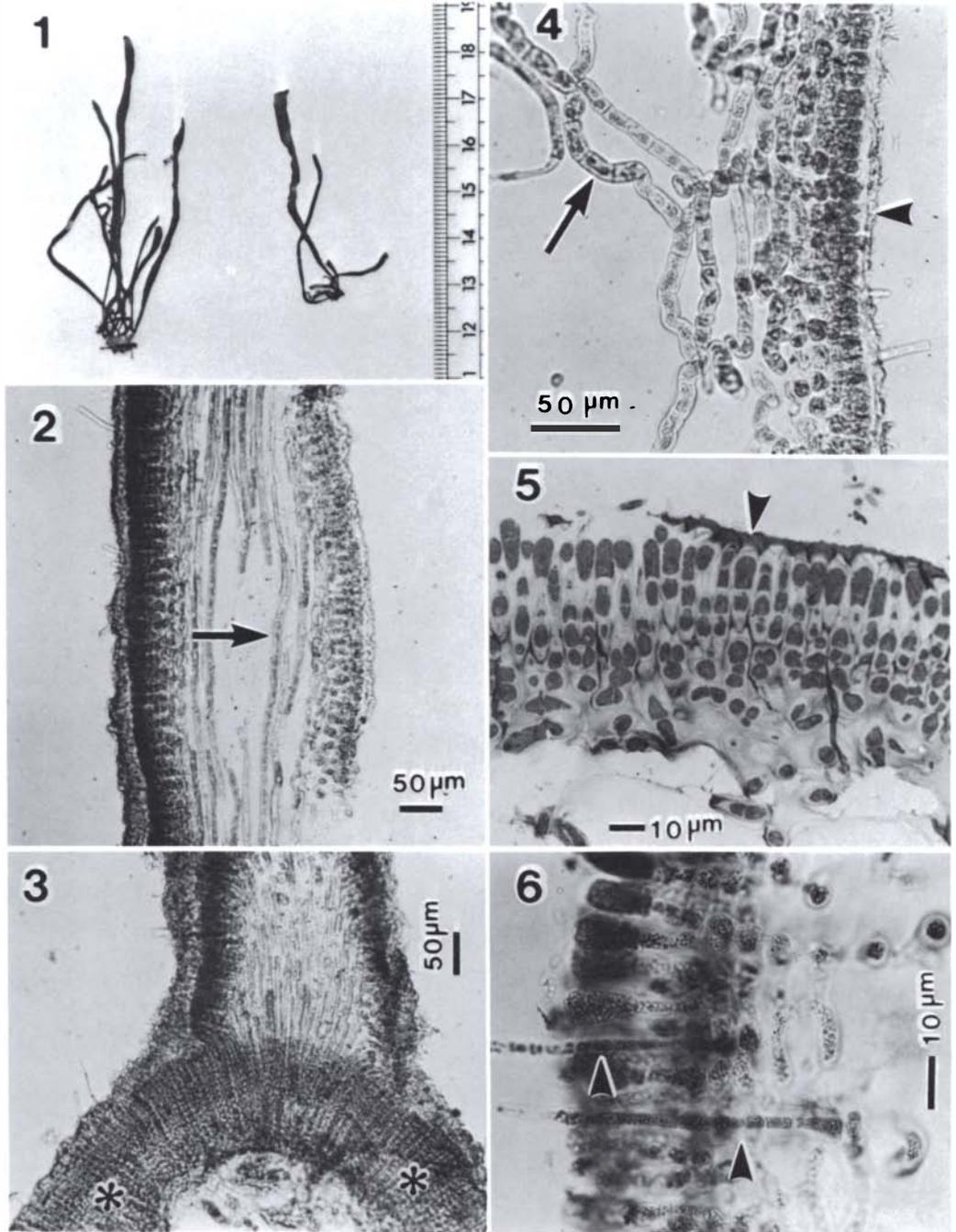
Figs 1–6. Habit and anatomy of *Heteroralfsia saxicola* (Okamura et Yamada) Kawai gen. et comb. nov. in the field.
   Fig. 1. Habit of the plant collected on 29 May 1983 at Ohma, Shimokita Peninsula. Scale numbers denote centimetres.
   Fig. 2. Longitudinal section of the young erect thallus (arrow shows simple pigmented medullary filament).
   Fig. 3. Longitudinal section of the crustose holdfast (asterisks) and the erect thallus which issues from it.
   Fig. 4. Longitudinal section of the young erect thallus (arrow shows reticular pigmented medullary filament, arrowhead shows cuticle).

LD, 15°C SD, 15°C LD, 20°C SD and 20°C LD, under white fluorescent lighting of approximately 28 μmol m^{-2} s^{-1} (5°C) or 46 μmol m^{-2} s^{-1} (10°C, 15°C, 20°C). Lux values were measured using a photocell illuminometer and converted to quantum irradiance using the following relation: 250 lux = 4.6 μmol m^{-2} s^{-1}.

RESULTS

Phenology and morphology

Saundersella saxicola (Fig. 1) grows on rocks in the upper intertidal zone of rather sheltered areas, accompanied by *Gloiopeltis furcata* (Postels et Ruprecht) J. Agardh, *Ishige okamurae* Yendo and *Petrospongium rugosum* (Okamura) Setchell et Gardner. Individuals are composed of caespitose erect portions and basal crustose portions. New erect portions appear in March, grow during spring and attain maximum length at the end of April and mature in May. After maturation, erect portions are lost.

The basal crustose portions resemble *Ralfsia* in appearance, but are slightly softer, greenish- to reddish-brown in colour, and irregular in circumference. The construction of the crustose portion agrees with the unilateral structure type in *Ralfsia* (Tanaka & Chihara 1980), composed of a basal cell layer and closely packed, parallel, erect filaments which issue from it (Fig. 3). Erect filaments are usually simple, about 20 cells and 200–300 μm in length. Each cell contains a sinuate cup-shaped chloroplast and many physode-like bodies (Fig. 10). Pyrenoids were not detected. The surface of the crustose portion is covered with a thick cuticle. Vegetative crustose portions of the species were observed in September; however, they could not be detected in winter due to the difficulties in distinguishing this species from other similar crustose algae.

The erect portions of thalli are multiaxial, pseudoparenchymatous, and originate by the further development and branching of erect filaments (Fig. 3). There is a transition between the relatively short cells of the crust and the elongate medullary cells of the erect portion of the thallus.

Erect portions of thalli are simple, cylindrical, roundish at the tip, attenuated towards the base, and slightly slimy, elastic, yellowish- to reddish-brown in colour (Fig. 1). They become leathery, darker and adhere weakly to paper when dried. They are solid near the base (Figs 2, 3) and hollow in the middle or upper part (Figs 4, 5). Medullary filaments are densely packed and simple near the base, rather loose and connected with each other here and there in the middle and upper parts, resulting in the formation of a reticular medullary layer (Figs 4, 9). The cells of the medullary filaments contain single lobed or several fragmented chloroplasts that are irregular in shape. When young the erect thalli are covered with a cuticle on the surface in the same manner as the basal crustose portions of the thalli (Figs 2, 4). Following the development of multicellular assimilatory filaments (paraphyses), however, this cuticle is shed (Figs 5, 6). Assimilatory filaments form from the cortical cells, and are 3–5 cells long, isodiametric but end in slightly larger cells (Figs 5–7, 9). Cells of assimilatory filaments contain many physode-like bodies and a single sinuate cup-shaped or several fragmented chloroplasts without pyrenoids. The terminal cells are usually deep red in colour and richer in physode-like bodies, but their chloroplasts have degenerated (Figs 6–8). In well developed erect portions of thalli, degenerated terminal cells enlarge to function as new terminal cells (Fig. 7). Colourless hairs occur among the assimilatory filaments issuing from the cortical layer or the medullary layer (Fig. 6). These hairs differ from typical phaeophycean hairs in the absence of basal meristematic regions and in containing more cellular contents. Unilocular sporangia are obovoid and sessile on the basal cells of assimilatory filaments (Fig. 9). Plurilocular sporangia were not detected on erect portions of thalli throughout the growing season.

Culture experiments

The swarmers released from unilocular sporangia (unispores) are teardrop-shaped, 10–13 μm in length and 6–8 μm in width, with two lateral flagella, and a single chloroplast. Pyrenoids were

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Fig. 5. Cross-section of the erect thallus showing the development of the assimilatory filaments and sloughing cuticle (arrowhead) (embedded in Spurr's epoxy resin and stained with Toluidine Blue).

Fig. 6. Cross-section of the erect thallus showing the hairs (arrowheads) issuing from the medullary or cortical layer (prepared in corn syrup and stained with Cotton Blue).
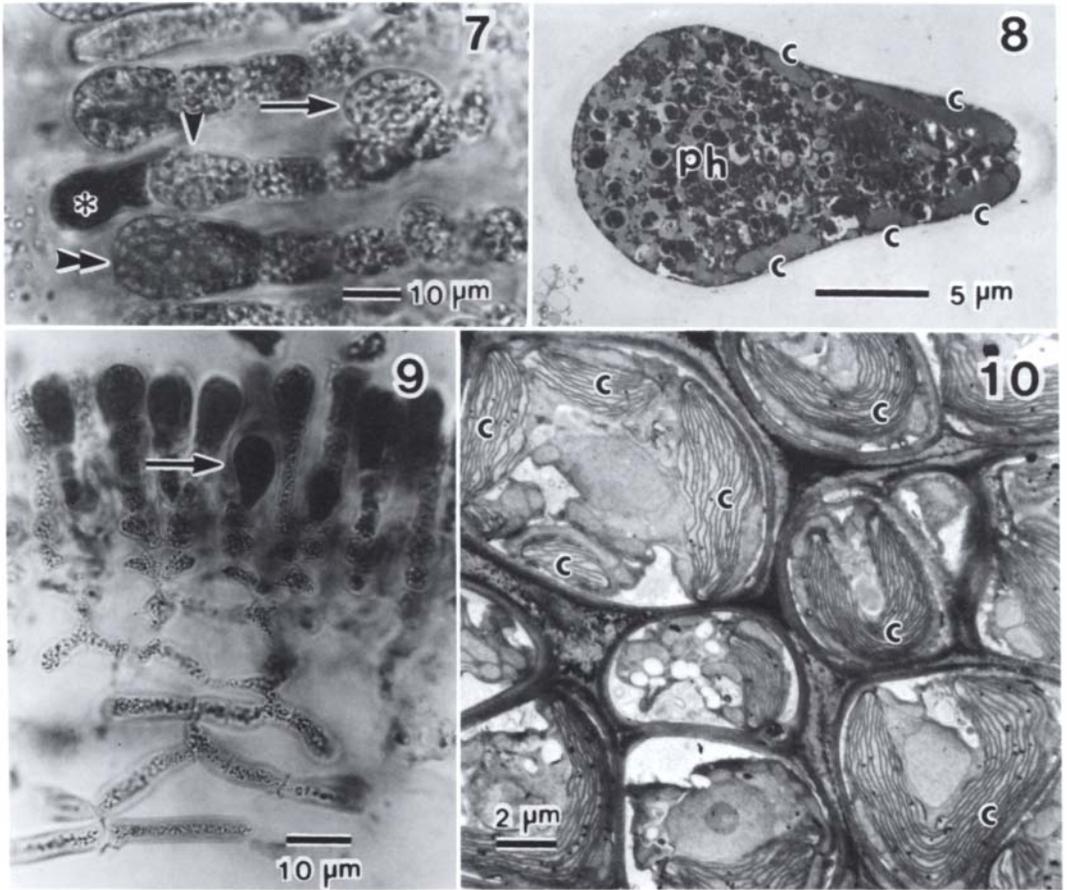
Figs 7–10. Anatomy of *Heteroralfsia saxicola* (Okamura et Yamada) Kawai gen. et comb. nov.
  Fig. 7. Regeneration of terminal cells of assimilatory filaments (asterisk shows degenerated original terminal cell, arrowhead shows developing subterminal cell, double arrowhead shows regenerated new apical cell, arrow shows initial of unilocular sporangium).
  Fig. 8. TEM micrograph of terminal cell of assimilatory filament containing abundant physode-like bodies (ph) and degenerated lobed chloroplasts (c) in longitudinal section.
  Fig. 9. Cross-section of mature erect thallus (arrow shows unilocular sporangium) (prepared in corn syrup and stained with Cotton Blue).
  Fig. 10. TEM micrograph of the cells of the crusts in cross-section, each cell contains a cup-shaped or sinuate chloroplast (c) without pyrenoids.

not observed. They swim for a few minutes and then settle on the glass. In 1–2 days they germinate by forming a tube (Fig. 11). Most of the cell contents of the spore migrates into the tube, and the original germinated spore-wall becomes almost empty. Then germlings produce lateral branches which cohere to form a circular disc with a marginal row of apical cells (Fig. 12). Phaeophycean hairs occur on the discs (Figs 12, 13). Cells of the disc contain a sinuate cup-shaped chloroplast in each cell. The disc then expands by transverse and oblique divisions of the marginal apical cells. Coupled with horizontal expansion of the disc, vertical elongation of the

basal cells is followed by transverse divisions which result in the development of polystromatic crustose thalli (Fig. 13). Well developed crustose thalli grow to about 1 cm in diameter, 9–18 cells high and 80–125 μm thick (Figs 15, 19). Phaeophycean hairs are scattered on the crustose thalli (Fig. 14). Rhizoidal filaments often issue from the basal layer of crustose thalli where they are out of contact with the substratum. In 9–12 months, the crustose thalli form intercalary plurilocular sporangia at 10°C SD and 15°C SD. They are formed by divisions of subterminal cells of erect filaments of the crustose thalli, one to two seriate and 14–18 cells and 38–63 μm in
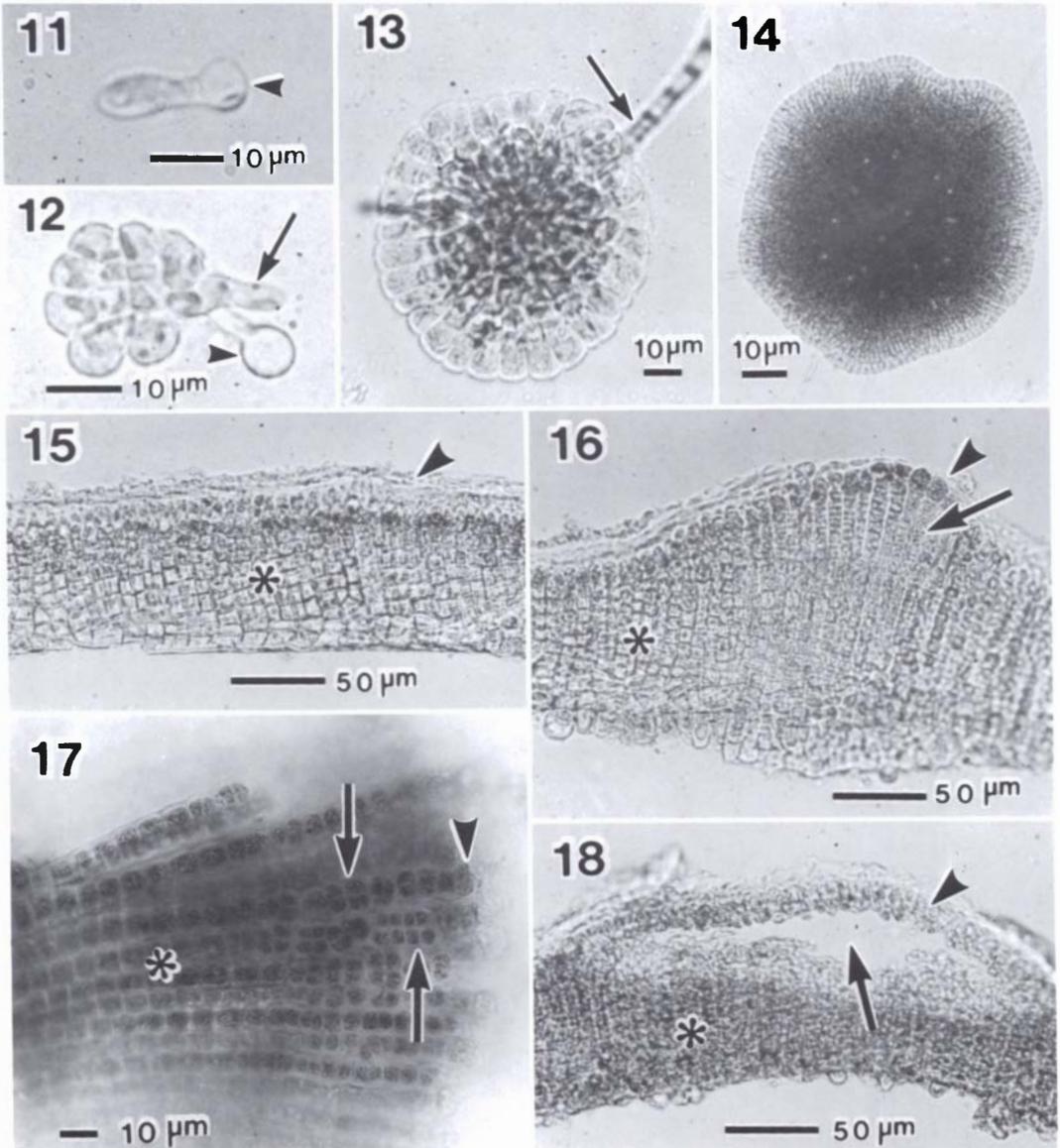
Figs 11–18. *Heteroralfsia saxicola* (Okamura et Yamada) Kawai gen. et comb. nov., development of crusts.
Fig. 11. Germling of zoospore, showing the migration of cell contents from original spore-wall (arrowhead) into germination tube.
Fig. 12. Monostromatic discal germling (arrowhead shows emptied original spore, arrow shows initial of hair).
Fig. 13. Discal germling with central polystromatic area (arrow shows hair).
Fig. 14. Developed crust with scattered hairs.
Fig. 15. Longitudinal section of vegetative crust (arrowhead shows cuticle, asterisk shows vegetative erect filaments).
Fig. 16. Longitudinal section of mature crust (arrowhead shows cuticle and terminal sterile cells, arrow shows intercalary plurilocular sporangia, asterisk shows vegetative erect filament).
Fig. 17. Squeezed preparation of intercalary plurilocular sporangia (arrows), terminal sterile cells (arrowhead), and vegetative erect filaments (asterisk) (prepared in corn syrup and stained with Cotton Blue).
Fig. 18. Longitudinal section of mature crust showing emptied plurilocular sporangia (arrow) and remaining terminal sterile cells bonded with the cuticle (arrowhead, asterisk shows vegetative erect filament).
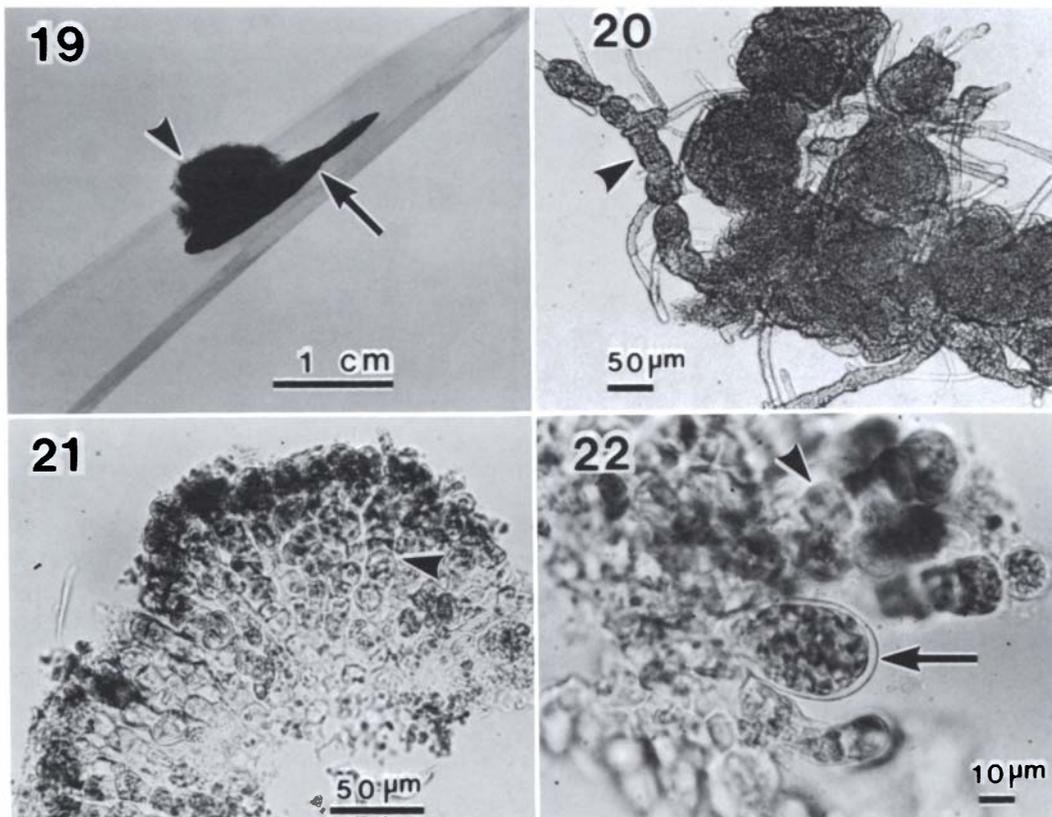
Figs 19–22. *Heteroralfsia saxicola* (Okamura et Yamada) Kawai gen. et comb. nov., development of sporophyte in culture.
Fig. 19. Well developed crust (arrow) and gregarious erect filamentous thalli on it (arrowhead).
Fig. 20. Thickened part of erect thalli with longitudinal walls (arrowhead).
Fig. 21. Cross-section of thickened part of erect filamentous thalli showing outwardly radiating multiseriate assimilatory filaments (paraphyses, arrowhead).
Fig. 22. Unilocular sporangium (arrow) among the multicellular assimilatory filaments (arrowhead).

length (Figs 16, 17). Spore release from the plurilocular sporangia takes place through the cleavage formed on the surface of the crustose thalli. Terminal cells of erect filaments of the crustose thalli remain sterile. Accordingly, the peripheral cells of the crustose thalli bonded by thick cuticle on them remains even after the release of the swarmers (Fig. 18). Released swarmers (plurispores) show a similar appearance to unispores. Mating reactions between the plurispores were not observed. Settled plurispores germinate and form crustose thalli again in similar developmental processes as unispores. Some of the germlings show filamentous development in their early stage; however, they finally develop into crustose thalli.

Several to many erect filaments issue directly from the surface of the crustose portion of thalli, irrespective of temperature or photo-regime, before or after the formation of plurilocular sporangia (Fig. 19). The erect filaments often form longitudinal walls (Fig. 20). Their cells contain a sinuate cup-shaped or several fragmented chloroplasts which are irregular in shape. The terminal cells of the erect filaments contain rich physode-like bodies, having a similar appearance to apical cells of the crustose portion of thalli. In 10°C and 15°C long-day conditions, the erect filaments produce outwardly radiating branched assimilatory filaments (paraphyses) (Fig. 21), which results in the development of cylindrical thalli. Sessile elliptical or obovoid unilocular sporangia are formed (Fig. 22) among the assimilatory filaments. Unispores released from the unilocular sporangia develop in a similar way as the original unispores.
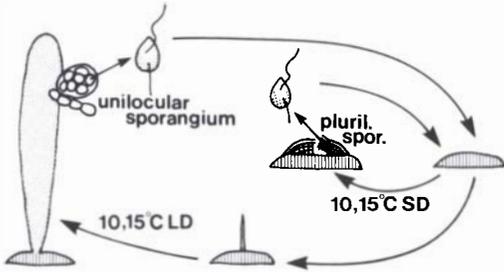
Fig. 23. A diagram of the life history of *Heteroralfsia saxicola* (Okamura et Yamada) Kawai in culture.

DISCUSSION

The crustose portion of the thallus of *Saundersella saxicola* is shown to form intercalary plurilocular sporangia and reproduce by itself in culture (Fig. 23). Although the erect filamentous growths which arose on crustose thalli did not develop into multiaxial cylindrical erect portions identical with field collected plants, they formed radiate multicellular assimilatory filaments and unilocular sporangia. They are regarded as a sporophytic generation, since in brown algae meiosis generally takes place in the unilocular sporangia. No independent gametophytic generations were observed in the field or in culture. The crustose portion of the thallus functions not only as a basal system for the erect sporophytic thalli, but it also reproduces by forming plurilocular sporangia. Therefore, considering the possibility of somatic diploidization (e.g. *Elachista stellaris,* Müller & Schmidt 1988), the crustose portion of the thallus may be a potential (or reduced) gametophytic generation.

The following characters of the crustose por-

tion of *Saundersella saxicola* show a close systematic affinity with the genus *Ralfsia* (Table 1): a) construction of thallus, composed of a radially expanding basal layer and densely packed parallel erect filaments, b) thick cuticle which covers the surface of the crust, c) intercalary plurilocular sporangia which originate from subterminal cells, d) mediate discal-type of germination of swarmers, e) single sinuate cup-shaped chloroplast lacking a pyrenoid (Fletcher 1978). *Saundersella saxicola* also shows affinities with *Analipus* (*Heterochordaria*) spp. in the nature of chloroplast (single cup-shaped without pyrenoids), mediate discal-type of germination, presence of abundant physodes, multicellular paraphyses and intercalary plurilocular sporangia with terminal sterile cells (Table 1). The systematic affinities between *Analipus* and *Ralfsia* and its relatives have been repeatedly discussed (Nakamura 1972; Wynne 1972; Tanaka & Chihara 1980), although both sporophyte and gametophyte are erect in *Analipus* and crustose in *Ralfsia*. Since *Saundersella saxicola* has an erect thallus portion similar to *Analipus* spp. forming unilocular sporangia, and the crustose portion forming intercalary plurilocular sporangia resembling *Ralfsia* spp., the species may be regarded as an intermediate type between the two taxa.

On the other hand, *Saundersella simplex* (Saunders) Kylin (Chordariaceae, Chordariales), the type of the genus, has a filamentous gametophyte forming terminal plurilocular sporangia, whose cells contain several chloroplasts with obvious pyrenoids, characteristic of the Chordariales (Table 1; Wynne 1972; Kawai, unpubl.). The germination pattern of the swarmers is 'unipolar germination type A (Pedersen 1981)' (Kawai, un-

Table 1. A comparison of distinguishing characters among *Heteroralfsia* (gen. nov.), *Saundersella, Ralfsia* and *Analipus*

	Heteroralfsia	*Saundersella*	*Ralfsia*	*Analipus*
Life history pattern	direct?	heteromorphic	isomorphic or direct	isomorphic
Sporophyte	erect, tough	erect, gelatinous	crustose, tough	erect, tough
Holdfast	crustose	rhizoidal	—	crustose
Chloroplast	single, lobed or fragmented	many, discoidal	single, cup-shaped	single cup-shaped or many discoidal (in holdfast)
Pyrenoid	−	+	−	−
Physode	abundant	not abundant	abundant	abundant
Cuticle	+	−	+	+
Plurilocular sporangium	on crustose part, intercalary	on filamentous thallus, terminal	on crustose thallus, intercalary	on erect thallus, intercalary
Germination pattern	mediate, discal	immediate, unipolar type A	mediate, discal	mediate, discal

publ.). The basal portions of the erect thalli are composed of rhizoidal filaments (Inagaki 1958). In addition, the isodiametric and pigmented medullary layer or the cortical layer of the erect portion of the thallus is also distinctive. Such characteristic features of *Saundersella saxicola* as discussed before suggest that it is inappropriate to place the species in the genus *Saundersella.* However, its former generic assignment to *Gobia* cannot be used, since its type *G. baltica* is regarded as a taxonomic synonym of *Dictyosiphon chordaria* Areschoug emend. Du Rietz [Rosenvinge & Lund 1947 (Dictyosiphonaceae, Dictyosiphonales)]. Accordingly, a new generic name, *Heteroralfsia* gen. nov., is proposed to accommodate this species.

Heteroralfsia appears to have close systematic relationships with the Ralfsiaceae and the Heterochordariaceae. However, the definitions and the ordinal assignment are controversial. Nakamura (1972) proposed establishing the order Ralfsiales to include the Ralfsiaceae, Lithodermataceae and Nemodermataceae, based on the following characters: a) isomorphic life history, b) discal-type of development of thallus, c) single parietal plate-shaped chloroplast without pyrenoid per cell. He also suggested that *Heterochordaria* (= *Analipus*) has a strong systematic relationship with the Ralfsiales in spite of the erect nature of its thalli. Since then, there have been repeated discussions about the value of the order. Tanaka & Chihara (1980, 1982) emphasized the unreliability of the third character (single chloroplast per cell), but in general they accepted the Ralfsiales and included their new family, the Mesosporaceae, in the order. In contrast, Wynne & Loiseaux (1976) questioned the reliability of all characters. Furthermore, Nelson (1982) urged abandoning the order, referring to exceptions to each of the three characters. She also proposed to include the Lithodermataceae in the Ralfsiaceae and emphasized the independence of the Heterochordariaceae (Ectocarpales) to accommodate *Analipus.* She did not refer to the ordinal position of the Ralfsiaceae. Later, Bold & Wynne (1985) placed the Ralfsiaceae (including *Analipus*) in the Ectocarpales. On the other hand, Fletcher (1987) proposed to include *Ralfsia* in the Scytosiphonaceae, but he did not consider ordinal assignment. Thus, the systematic position of *Ralfsia* and its relatives is still uncertain.

In my own opinion, it does not make sense placing the Ralfsiaceae and its relatives in the Ectocarpales, since it only makes the order more heterogeneous. It may not be proper to place *Ralfsia* (*sensu stricto*) in the Scytosiphonaceae because the taxonomic value of the presence or absence of pyrenoid and germination patterns are not fully known. The order Ralfsiales itself remains invalid because of the lack of a Latin diagnosis (ICBN, Art. 36.2; see Greuter 1988), and its distinguishing characters need re-examination. Accordingly, I will place *Heteroralfsia* in the Ralfsiaceae but with some hesitation. Its ordinal systematic position should be reconsidered after the systematic revision of the Ralfsiaceae and its relatives.

The shedding and subsequent regeneration of terminal cells of the assimilatory filaments in developed thalli may have a protective function against severe desiccation and strong insolation, caused by the upper intertidal habitat of the species. In other words, in the present species, the superficial (outermost) cells might have differentiated to play a protective role and have lost their assimilatory and meristematic abilities. The terminal sterile cells in the plurilocular sporangia on the crustose thalli may have similar protective roles. Many members of the *Ralfsia*-group (including *Analipus*), which grow in the intertidal (often upper intertidal) zone, have similar terminal sterile cells in the plurilocular sporangia. This character as well as the presence of a thick cuticle may be useful in re-examining the distinguishing characters of the *Ralfsia*-group.

In culture, the development of crustose portions of thalli and formation of erect filamentous portions occurred under 5°C and 10°C irrespective of daylength. The crustose thalli formed plurilocular sporangia at 10°C and 15°C during short days, whereas the development of assimilatory filaments and the maturation of erect filamentous portions occurred at 10°C and 15°C during long days which correspond to autumn, winter, and spring respectively at Ohma. This result agrees with the phenological observations and suggests that the seasonal growth pattern of the species is controlled mainly by daylength, and the maturation of the crustose generation occurs in winter.

DESCRIPTION AND DIAGNOSIS

Heteroralfsia Kawai gen. nov.

Thalli erecti caespitosi, simplices, cylindrici, cum filamentis medullaribus fere isodiametris pigmentalibus, cellulis corticalibus, filamentis assimilanti-

bus multicellularibus, pilis, sporangiis unilocularibus. Cellulae thallorum erectorum cum physodibus abundantibus et chloroplastis cupulatis singularibus vel pluribus fragmentibus sine pyrenoidibus. Thalli crustosi cum stratis cellularibus basalibus, filamentis erectis isodiametris, cuticula crassa, pilis phaeophyceanis, sporangiis plurilocularibus intercalaribus cum cellula sterili terminali singulari. Cellulae crustae cum physodibus et chloroplastis cupulatis singularibus sine pyrenoidibus.

　　　SPECIES TYPI: *Heteroralfsia saxicola* (Okamura et Yamada) Kawai.

Heteroralfsia saxicola (Okamura et Yamada) Kawai comb. nov.

BASIONYM: *Gobia saxicola* Okamura et Yamada in Yamada 1928, pp. 507–509, fig. 9.

SYNONYM: *Saundersella saxicola* (Okamura et Yamada) Inagaki 1958, pp. 161–162, fig. 64.

Heteroralfsia Kawai gen. nov.

Erect thalli caespitose, cylindrical, simple, having almost isodiametric pigmented cylindrical medullary filaments, cortical cells, multicellular assimilatory filaments, hairs, and unilocular sporangia. Cells of erect thalli contain abundant physodes, single cup-shaped or several fragmented chloroplasts without pyrenoids. Crustose thalli with basal cell layer, isodiametric erect filaments, thick cuticle, phaeophycean hairs, intercalary plurilocular sporangia with a terminal sterile cell. Cells of crusts with abundant physodes and a cup-shaped chloroplast without pyrenoid.

　　The genus is distinguished from *Saundersella* in having a thick cuticle, plurilocular sporangia with terminal sterile cells, chloroplasts without pyrenoids, and almost isodiametric pigmented medullary filaments.

ACKNOWLEDGMENTS

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