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Morphology and life history of *Kurogiella saxatilis* gen. et sp. nov. (Chordariales, Phaeophyceae)

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Kurogiella saxatilis gen. et sp. nov. (Leathesiaceae, Chordariales) is described from the cold-water area of Hokkaido. It grows on exposed rocks in the intertidal zone. *K. saxatilis* is an annual, appearing in spring and maturing in winter. Erect thalli are pulvinate, solid, rugose, gelatinous and yellowish to dark brown. They are composed of a holdfast, closely packed colourless cylindrical medullary filaments and a cortical layer. The latter consists of 4–8(–11)-celled assimilatory filaments, colourless hairs and ellipsoid or long-lanceolate unilocular sporangia. Each cell contains several discoid chloroplasts with pyrenoids. Plurilocular sporangia are unknown. *Kurogiella* is closely related to *Leathesia* sect. *Primariae,* but is distinguished by its much larger, epilithic, solid thallus having almost isodiametric assimilatory filaments. In culture, unispores develop into prostrate filaments, from which pulvinate erect thalli arise directly. Further development of erect thalli occurred under long-day conditions of 5°C and 10°C, and formation of unilocular sporangia occurred under 5°C short-day conditions. The direct type of life history of *K. saxatilis,* lacking a gametophytic generation, is considered to be an adaptation to the winter field conditions influenced by ice.

INTRODUCTION

During a study of the benthic algal flora in the cold-water area of Hokkaido, Japan, an unknown chordarialean brown alga was found at several localities growing on the most exposed intertidal rocks. The alga was slimy, solid and rugose pulvinate. To clarify its systematic position, seasonal collections, morphological observations and culture experiments were carried out. This paper describes the morphology and life history of the new taxon, *Kurogiella saxatilis* gen. et sp. nov. (Leathesiaceae, Chordariales). Its adaptation to the winter sea conditions of the Okhotsk Sea coast is discussed, and it is proposed that the ice cover may have played a role in eliminating the gametophytic generation.

MATERIALS AND METHODS

Field observations and collections were made at the following localities (Fig. 1): Rishiri Is. (12.viii.1986, 19.vi.1991); Kitami-Esashi (15.v.1979, 9.vii.1979); Saruru (10.viii.1979, 8.ix.1979, 15.x.1980, 23.xi.1980, 22.xii.1980, 2.vi.1981); Abashiri (23.vii.1978, 11.vii.1979, 9.viii.1979, 29.vii.1980, 4.vi.1981, 21.vi.1981); Sashirui in Shiretoko Peninsula (3.vi.1981, 28.vii.1981); Tohsamporo (25.v.1982, 23.vi.1982, 21.vii.1982) and Hanasaki (28.vi.1980) in Nemuro Peninsula; Akkeshi (14.vi.1980, 28.vi.1980, 19.i.1981, 30.vi.1981, 25.viii.1981, 27.xi.1981, 9.i.1982, 14.i.1983, 28.vi.1992). Liquid-preserved specimens of *Corynophlaea crispa* (Harvey) Kuckuck (Anglesey, UK, 21.xi.1985, leg. et det. R.L. Fletcher) were examined for morphological comparison. Light microscopy was performed on live material and on specimens preserved in 3–5% formaldehyde-seawater. Cultures were started from swarmers released from unilocular sporangia on erect thalli collected at Akkeshi on 19.i.1981 and 14.i.1983. Swarmers were pipetted onto glass slides and cultured in glass vessels containing 200 ml PESI medium (Tatewaki 1966). The culture conditions used were 5°C SD (short day; 8:$\overline{16}$ h), 5°C LD (long day; 16:$\overline{8}$ h), 10°C SD, 10°C LD, 15°C SD, 15°C LD, 20°C SD and 20°C LD, under a photon flux of 30 $\mu mol\ m^{-2}\ s^{-1}$ (5°C) or 50 $\mu mol\ m^{-2}\ s^{-1}$ (10°C, 15°C, 20°C) (white fluorescent tubes).

RESULTS

Kurogiella saxatilis Kawai gen. et sp. nov.

Figs 2–16

Description: Thalli erecti, annui, epilithici, pulvinati, usque ad 80 mm diametro, usque ad 5 mm alti, solidi, rugosi, mucilaginei, flavidi vel atrobrunnei, cum hapteris rhizoideis, filamentis medullaribus crebris hyalinis cylindricis, filamentis assimilantibus multicellularibus fere isodiametricis, pilis, sporangiis unilocularibus. Filamenta assimilantia simplicia, 4–5 cellularia, 113–270 μm longa. Cellulae thalli cum chloroplastis aliquot discoideis cum pyrenoidibus. Sporangia unilocularia longe lanceolata vulgo sessilia, 73–163 μm longa, 18–35 μm diametro. Sporangia plurilocularia ignota.

Erect thallus annual, epilithic, pulvinate, up to 80 mm in diameter, up to 5 mm in height, solid, rugose, mucilaginous, yellowish to dark brown, with rhizoidal holdfast, closely packed cylindrical hyaline medullary filaments, almost isodiametric assimilatory filaments, hairs and unilocular sporangia. Assimilatory filaments simple, 4–5 celled, 113–270 μm long. Cells of the thallus contain several chloroplasts with pyrenoids. Unilocular sporangia long-lanceolate, mostly sessile, 73–163 μm in length and 18–35 μm in diameter. Plurilocular sporangia unknown.

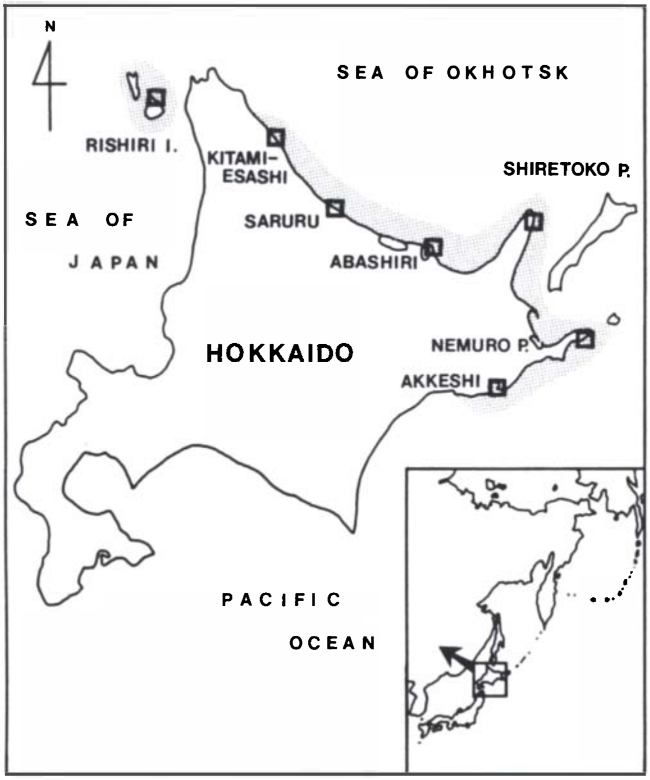


Fig. 1. Geographical distribution of *Kurogiella saxatilis* gen. et sp. nov.

ETYMOLOGY: The generic name commemorates the late Dr Munenao Kurogi (1921–1988), Professor Emeritus of Hokkaido University, for his contributions to phycology.

TYPE SPECIES: *Kurogiella saxatilis* sp. nov.

HOLOTYPE: SAP057969, 26.vii.1987. Akkeshi, Hokkaido, Japan.

MORPHOLOGY OF THE PLANT IN THE FIELD: The erect thallus is initially subspherical or compressed-subspherical (Figs 2a, 4). It expands horizontally and becomes rugose, attaining 70–80 mm in width and 5 mm in height (Figs 2b, 3). The thallus is yellowish brown, becoming dark brown with age, somewhat slimy, and is attached tightly to the substratum.

The thallus is composed of basal layer (holdfast), medullary layer and cortical layer (Figs 4, 5). In the juvenile thallus, the basal holdfast is located in the central ventral part of the thallus, and composed of densely entangled colourless multicellular rhizoidal filaments, 13–20 μm in diameter (Fig. 4). The medullary layer is composed of large, cylindrical, dichotomously branched, closely packed medullary filaments (Figs 7, 10), which are radially arranged from the holdfast (Fig. 5). Cells of the medullary filaments are almost colourless, containing many physode-like granules in the central part (Figs 6, 7). These cells are 75–200(–350) μm long and 33–70 μm wide. Secondary rhizoidal filaments issue from the ventral surface of the expanded thallus which is in contact with the substratum (Fig 5). The assimilatory filaments are simple, almost isodiametric throughout the length, 4–8(–11) celled and 113–270 μm long and 8–13 μm wide (Figs 6, 8, 9, 11). Cells of the assimilatory filaments are cylindrical to ellipsoid, 15–40 μm long, containing several discoid chloroplasts with pyrenoids. Hyaline hairs are scattered among assimilatory filaments and 5–7 μm in diameter (Figs 9, 11). Unilocular sporangia are formed on the basal part of assimilatory filaments; they are sessile or pedicellate, ellipsoid to elongated lanceolate, 73–163 μm long and 18–35 μm wide (Figs 8, 11). Plurilocular sporangia were not detected.

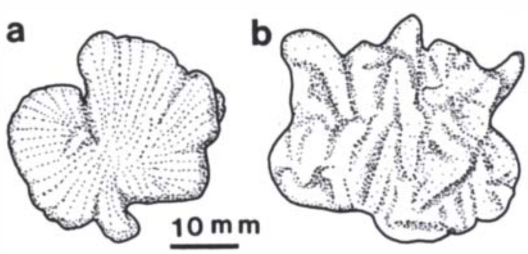


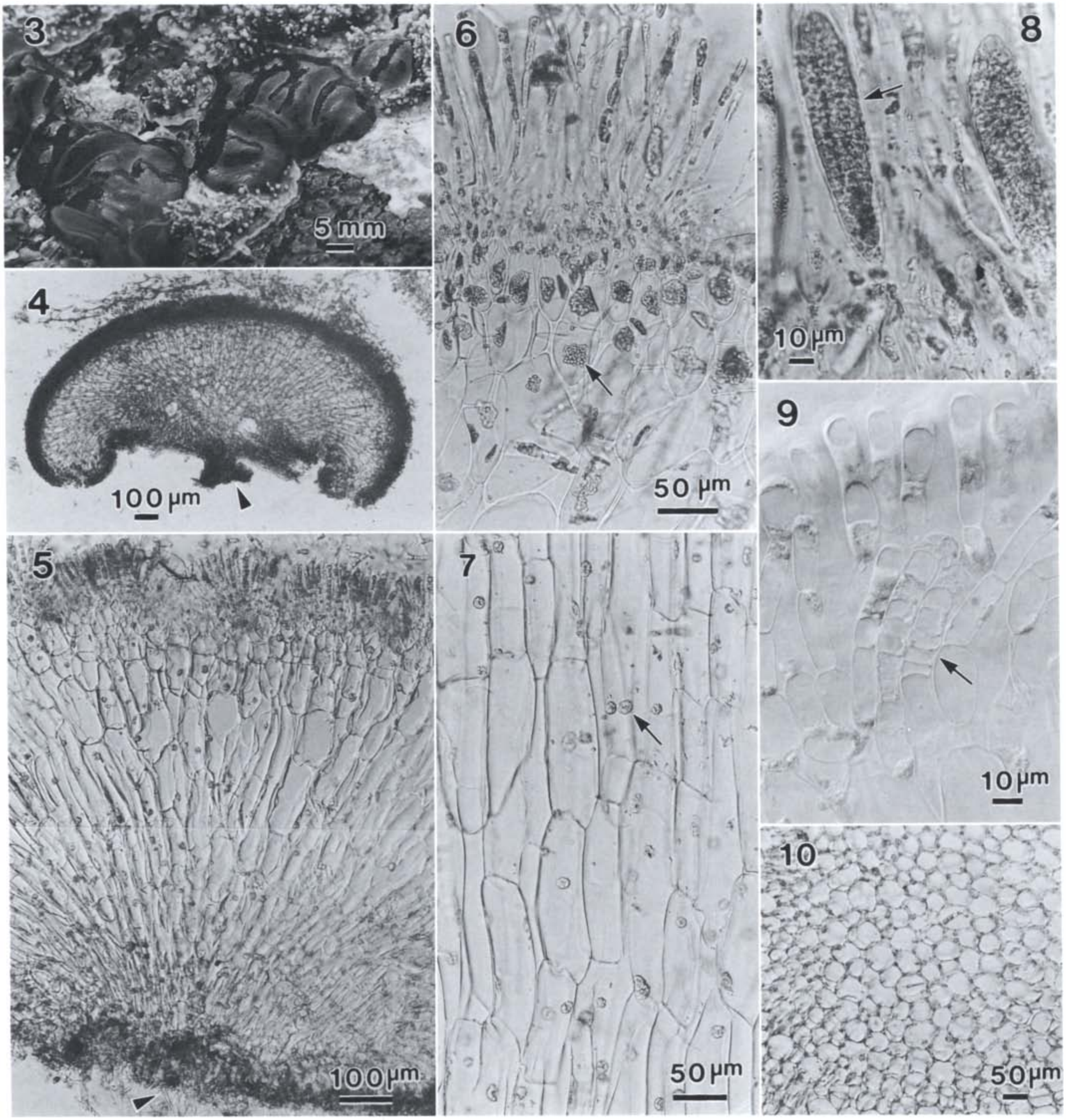
Fig. 2. General appearance of young (a) and mature rugose plants (b) of *Kurogiella saxatilis* gen. et sp. nov.

PHENOLOGY AND GEOGRAPHICAL DISTRIBUTION: *Kurogiella saxatilis* grows on the most exposed rocks in the intertidal zone, accompanied by *Corallina pilulifera* Postels et Ruprecht, *Delamarea attenuata* (Kjellman) Rosenvinge and *Chordaria flagelliformis* (Müller) C. Ag. f. *chordaeformis* Kjellman. New plants appear in April to May, grow relatively slowly during spring and summer, and attain the maximum size in July–August. They mature in December–January. After maturation, the macroscopic plants disintegrate.

Kurogiella saxatilis is distributed in the cold-water area of Hokkaido (Fig. 1). It has not been observed in adjacent warmer areas despite intensive collections at many sites.

Culture experiments

The swarmers released from unilocular sporangia were pear-shaped, 5.5–7 μm long and 3.5–5 μm wide, with a long anterior and a short posterior flagellum inserted laterally. They contained a single chloroplast with stigma and pyrenoid. The swarmers swam for a few minutes showing negative phototaxis and then settled on the glass. They germinated after several days by unipolar germination and developed into branched prostrate filaments (Figs 12, 13). Cells of the filaments contained several discoid chloroplasts with pyrenoids. The filaments grew well under long- and short-day conditions of 5°C, 10°C and 15°C, but not at 20°C. The prostrate filaments did not form any reproductive organs during the experiments. After 3 weeks, plants in some of the cultures formed pseudoparenchymatous subspherical erect thalli on the prostrate filaments, starting with a single-layered compact basal disc (Fig. 14), that later issued erect assimilatory filaments. Medullary cells developed below the assimilatory filaments, and the erect thallus became spherical (Figs 15, 16). The development of the erect thallus occurred only when the prostrate filaments remained in firm contact with the substratum (Fig. 14), never in non-attached filaments. Under long-day conditions of 5°C and 10°C, but not under the other conditions examined, the erect thallus developed into a macroscopic subspherical or spherical plant resembling a young field thallus (Figs 15, 16). Rhizoidal filaments issued from the central ventral part of the thallus (Fig. 15). Hyaline hairs were scattered among the assimilatory filaments, 4–5 μm in diameter; however, their basal



Figs 3–10. *Kurogiella saxatilis* gen. et sp. nov. collected in the field.
Fig. 3. Habit of vegetative plants (Akkeshi, 28.vi.1992).
Figs 4, 5. Longitudinal section of very young subspherical plants with holdfast (arrowheads).
Fig. 6. Assimilatory filaments and upper part of medulla in longitudinal section. Arrow shows abundant physode-like granules.
Fig. 7. Closely packed hyaline medullary filaments in longitudinal section. Arrow shows physode-like granules.
Fig. 8. Unilocular sporangia (arrow) among assimilatory filaments.
Fig. 9. Young assimilatory filaments and initial of phaeophycean hair (arrow).
Fig. 10. Closely packed medullary filaments in cross (tangential) section.

meristems were not obvious (Fig. 16). Assimilatory filaments in well-developed thalli were 4–6 celled, 93–135 µm long and 9–12 µm wide (Fig. 16). Erect thalli from 10°C LD transferred to 5°C SD formed unilocular sporangia. The erect thalli did not mature under other culture conditions. Unilocular sporangia were formed on the basal cells of assimilatory filaments. They were 65–83 µm long and 25–33 µm in diameter. Unilocular sporangia released unispores that developed into pros-

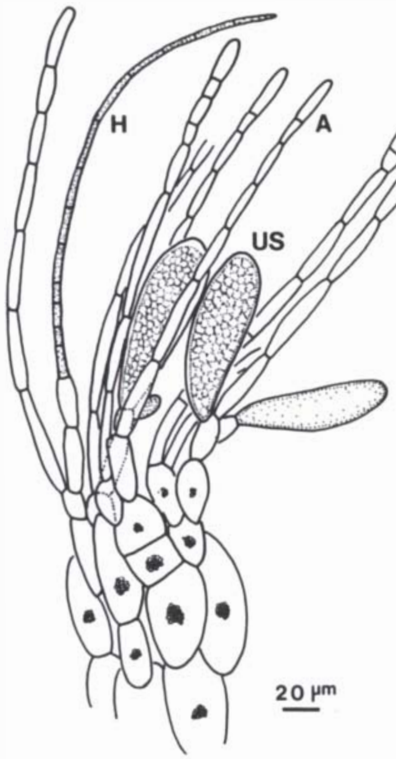
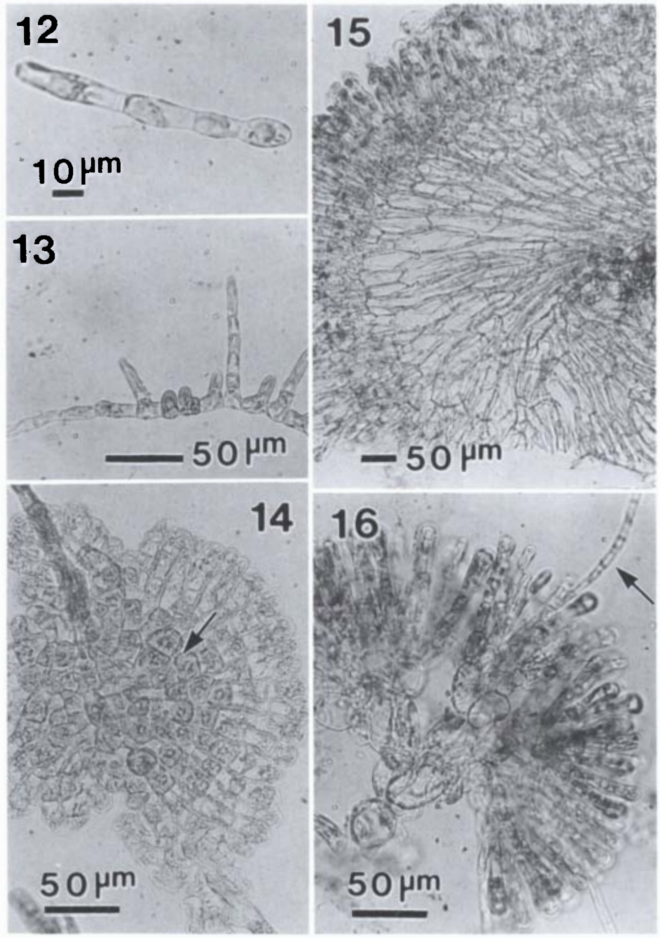


Fig. 11. *Kurogiella saxatilis* gen. et sp. nov. Longitudinal section of mature plant collected in the field. A, assimilatory filament; H, hair; US, unilocular sporangium.

trate filaments in the same manner as unispores from field material. Plurilocular sporangia were not formed.



Figs 12-16. *Kurogiella saxatilis* gen. et sp. nov. in culture.
Figs 12, 13. Germlings of unispores isolated from field collected plants.
Fig. 14. Compact prostrate thallus with central di- or tristromatic area (arrow) from which erect thalli issue.
Fig. 15. Longitudinal section of erect thallus.
Fig. 16. Assimilatory filaments and phaeophycean hair (arrow).

DISCUSSION

The pulvinate, pseudoparenchymatous thallus and the chloroplast morphology suggest that *Kurogiella saxatilis* is a member of the order Chordariales, related to *Petrospongium, Leathesia* and *Corynophlaea.* It is easily distinguished from *Petrospongium* by the closely packed medullary filaments, the lack of rhizoidal filaments in the medulla, and the shape of the unilocular sporangia (Table 1).

The taxonomy of *Leathesia* and *Corynophlaea* is somewhat confused. In *Leathesia,* the thallus is more or less hollow, comprising reticulate medullary filaments. *Corynophlaea* is solid, at least in the juvenile stage, and the medullary filaments are closely packed and arranged in parallel. However, Setchell & Gardner (1925) included *Corynophlaea* in *Leathesia,* arguing that the above-mentioned differences are not significant. Inagaki (1958), who studied the morphology of Japanese *Leathesia* and related taxa, generally followed Setchell & Gardner's generic concept, but classified Japanese *Leathesia* into two groups, section *Leathesia* and section *Primariae.* He used the arrangement of the medullary filaments and the nature of the medulla as distinguishing characteristics. Section *Leathesia* has a reticulate, more or less hollow medulla, and section *Primariae* has a closely packed, compact and solid medulla. Inagaki's section *Primariae* appears to correspond to *Corynophlaea* in European material; however, the relationship between the two is not fully clear. Inagaki listed 8 taxa in the section *Primariae,* including three new species. Many of these need further taxonomic study, and the boundaries between the taxa are not clear. More recently, Fletcher (1987) distinguished *Corynophlaea* from *Leathesia* by its smaller thallus, the less irregularly contorted and non-stellate medullary cells, and the longer and less compact assimilatory filaments. However, he commented that these two taxa are very similar.

In its anatomical construction, the present species has closest affinity to members of *Leathesia* section *Primariae,* having solid thalli composed of closely packed medullary filaments (Table 1). Section *Leathesia* (e.g. *Leathesia difformis* (Linnaeus) Areschoug) is relatively distant in having a reticulate, more or less hollow medulla and swollen assimilatory filaments. *Corynophlaea* has more loosely arranged medullary filaments, and assimilatory filaments of round swollen cells which are usually curved distally, compared with *Leathesia* sect. *Primariae* (Kützing 1858; Kuckuck 1929; Fletcher 1987, personal observations). In the section *Primariae, Leathesia primaria* Takamatsu has isodiametric assimilatory filaments with relatively long cylindrical cells, whereas other species have round, swollen assimilatory cells and enlarged terminal cells (Inagaki

Table 1. Comparison of *Kurogiella saxatilis* gen. et sp. nov., *Leathesia* sect. *Primariae, L.* sect. *Leathesia, Corynophlaea* and *Petrospongium.* After Inagaki (1958), Ajisaka (1984), Fletcher (1987) and Womersley (1987)

	Kurogiella saxatilis	*Leathesia* sect. *Primariae*	*Leathesia* sect. *Leathesia*	*Corynophlaea*	*Petrospongium*
Habitat	Epilithic	Epiphytic	Epilithic or epiphytic	Epiphytic	Epilithic
Size (diam.)	80 mm	*c.* 5 mm	*c.* 100 mm	*c.* 5 mm	*c.* 100 mm
Assimilatory filament with larger swollen terminal cell	Absent	Present or absent	Present	Absent	Absent
Medulla	Solid, closely packed	Solid, closely packed	More or less hollow, loosely packed	Solid, closely packed	More or less solid, loosely packed
Medullary cells	Cylindrical	Cylindrical	Anastomosing	Cylindrical	Cylindrical
Horizontal rhizoidal filaments in medulla	Absent	Absent	Absent	Absent	Present
Unilocular sporangia	Ellipsoid, terminal	Obovoid, terminal	Obovoid, terminal	Obovoid, terminal	Kidney-shaped or ellipsoid, laterally inserted or terminal
Plurilocular sporangia on erect thalli	Unknown	Present	Present	Present	Unknown
Life history	Direct	Heteromorphic	Heteromorphic	Unknown	Heteromorphic

1958). All known taxa in *Leathesia* section *Primariae* are minute (several millimetres in diameter) and epiphytic.

In conclusion, *Kurogiella saxatilis* most closely resembles *Leathesia* sect. *Primariae* but is distinct from any known member of that section in the much larger, tough, epilithic thallus. It differs also in the very long growing season (more than 9 months) and the lack of plurilocular sporangia. It is therefore proposed to classify the taxon as a new species in a separate genus.

Figure 17 summarizes the life history of *Kurogiella saxatilis* based on the present culture results. In culture, although prostrate filaments occasionally formed on erect thalli, development of pulvinate erect thalli was restricted to long days at 5°C and 10°C. Formation of unilocular sporangia on the erect thalli occurred only under low temperature, short-day conditions. These conditions correspond to spring–summer and winter, respectively, in the distribution area of *K. saxatilis.* The developmental responses of *K. saxatilis* in culture thus agree with the phenology of the species in the field.

In the related genus *Leathesia,* Dangeard (1965) and Ajisaka (1984) reported heteromorphic life histories in *Leathesia difformis* and *L. japonica* Inagaki, respectively. *Kurogiella saxatilis* showed a direct type of life history without a microscopic gametophytic generation and plurilocular sporangia were absent. Such a life history pattern is not common in the Chordariales (Kawai 1986; Peters 1987). Considering that macroscopic thalli of *K. saxatilis* disappear only for 2–3 months in nature, it is likely that it lacks a gametophytic stage also in the field. The intertidal zone of the Okhotsk Sea coast of Hokkaido (Kitami-esashi, Saruru, Abashiri and Shiretoko Peninsula, see Fig. 1) is regularly covered with packed drift ice in January–March. Nemuro Peninsula and Akkeshi on the Pacific Ocean

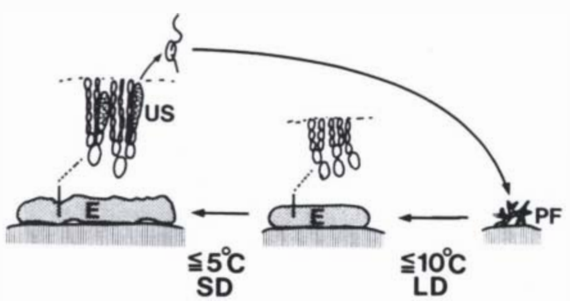


Fig. 17. Diagram of the life history of *Kurogiella saxatilis* gen. et sp. nov. deduced from culture. E, erect thallus; PF, prostrate filament; US, unilocular sporangium.

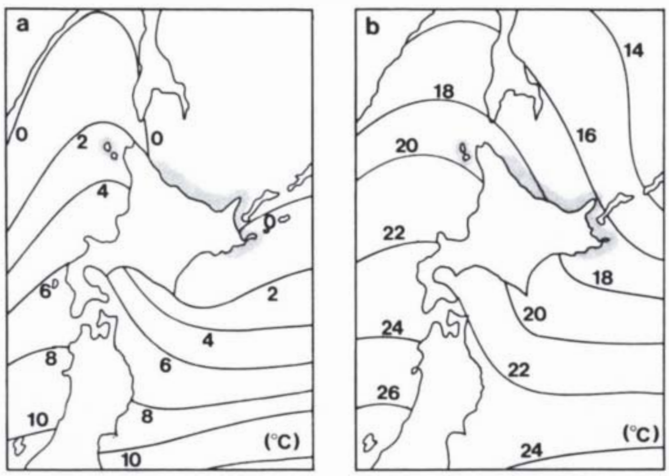


Fig. 18. Average surface water temperature around Hokkaido and its vicinity in February (a) and August (b), and the known geographical distribution of *Kurogiella saxatilis* Kawai gen. et sp. nov. Isotherms after National Astronomical Observatory, Japan (1991).

side (Fig. 1) are also under the influence of drift ice in March, and the intertidal zone is often covered and scoured by ice. Under such conditions, growth of benthic algae and reproduction by flagellated gametes may be inhibited, and an alga that grows in the intertidal zone of exposed areas would suffer severe damage. *Kurogiella saxatilis* probably survives this period as vegetative prostrate filaments, without forming reproductive organs. Its life history may be an example of an adaptation to the severe winter sea conditions in the Okhotsk Sea coastal area.

Figure 18 shows monthly average surface seawater temperature isotherms around Hokkaido in February and August, when the temperatures are lowest and highest, respectively. The coastal area in Hokkaido where such conditions occur in winter is more extensive than the known distributional area of *K. saxatilis,* especially on the Pacific coast. Therefore, high summer temperatures in the area may act as a limiting factor and define the southern distributional boundary. On the other hand, *K. saxatilis* may be expected to occur also in the colder adjacent areas of Hokkaido (e.g. Saghalien, Kurile Islands).

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