

Life history of Japanese *Stypocaulon durum* (Sphacelariales, Phaeophyceae)

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SUMMARY

Phenology, morphology, life history and responses to different temperature and photoperiod conditions were studied in Japanese *Stypocaulon durum* (Ruprecht) Okamura. Erect thalli of the species were collected year-round, but the mature thalli forming either unilocular sporangia or two different types of plurilocular structures (evidently gametangia) on separate thalli were found only in winter. In culture, an isomorphic life history is suggested for the species, alternating between a sporophyte forming unilocular sporangia and gametophytes forming plurilocular macro- (female) and micro- (male) gametangia. Contents of unilocular sporangia were not released, but germinated *in situ*, developing into erect thalli forming plurilocular gametangia. Macrogametangia released aplanogametes (oospores), but male gametangia appeared to be non-functional, although flagellated cells were once formed in the loculi. This is the first report of plurilocular gametangia in the species. Although the species grew well and matured under considerably lower temperature conditions than European *Stypocaulon scoparium* (L.) Sauvageau, its temperature requirements showed similarity to northwestern Atlantic *Stypocaulon* species. This supports the notion that northwestern Atlantic *Stypocaulon* is conspecific with *S. durum*.

Key words: *Halopteris*, life history, Phaeophyceae, Sphacelariales, *Stypocaulon durum*, taxonomy.

INTRODUCTION

Taxonomic assignment of the *Halopteris* (or *Stypocaulon*) species (Stypocaulaceae, Sphacelariales) that are distributed in the cold-water regions of the northwestern Pacific has been confused because two problems have not been clarified: (i) the generic relationship between *Halopteris* and *Stypocaulon* (i.e. the validity of the genus *Stypocaulon*); and (ii) the specific relationship between European plants and northeastern Pacific (and perhaps northwestern Atlantic) plants. For example, in Japan and its vicinity, Okamura (1902) first assigned the specimens collected in Hokkaido to *Stypo-*

caulon durum (Ruprecht) Okamura (*Sphacelaria dura* Ruprecht 1850), but Tokida (1931) identified the specimens from Sakhalin as *Halopteris scoparia* (L.) Sauvageau. Okamura (1936) and later authors (Segawa 1956; Kawai and Kurogi 1982; Yoshida *et al.* 1985) followed Tokida's opinion and referred Hokkaido plants to *H. scoparia*. In contrast, in Russia, Zinova (1930) combined *S. dura* with the genus *Halopteris* and, hence, the species was referred to as *Halopteris dura* (Ruprecht) Zinova (Zinova 1930, 1954; Perestenko 1980).

Regarding the generic problem, both the genus *Halopteris* and the genus *Stypocaulon* were first described by Kützing (1843). Later Sauvageau (1903) united all species of both genera in the single genus *Halopteris*. Prud'homme van Reine (1991, 1993) recently re-separated *Stypocaulon* from *Halopteris* based on the differences in the branching pattern, presence of special meristematic cells (pericysts) and the reproductive structures (Table 1). However, the life history and the sexual reproductive organs have not been studied in the Japanese plants; hence, the specific relationship between European, northwestern Pacific and northeastern Atlantic plants remained problematic. Therefore, in order to clarify these problems, we investigated phenology, morphology, life history and responses to different temperature conditions of Japanese *Stypocaulon* and compared them with plants from other geographical regions.

MATERIALS AND METHODS

Seasonal observations and collections were made using SCUBA at several sites at Abashiri, Hokkaido (44°02'N, 144°17'E), facing the Okhotsk Sea, from June 1986 to April 1987 at 1–2-month intervals. Observations could not be made in February and March when the sites were completely covered with ice.

Type material of *Sphacelaria dura* Ruprecht 1850 collected at Guba Nichta, Okhotsk Sea on 24 July 1843 (or 1844; date ambiguous from the notes on the type material or the original description) housed in the Her-

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Communicating editor: T. Motomura.

Received 25 June 1998; accepted 15 August 1998.

barium, Botanical Institute, Academy of Science, Leningrad was examined for morphological comparisons.

Unialgal cultures were started from apical fragments of vegetative thalli collected at Abashiri in August 1986. Culture conditions used were 5°C SD (short day; 8 h light (L):16 h dark (D)), 5°C LD (long day; 16L:8D), 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (5°C) or 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (10°C, 15°C, 20°C). A 3°C SD condition (30 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was also used in some experiments. Cultures were inoculated in plastic Petri dishes or glass vessels containing PESI medium (Tatewaki 1966). For transmission electron microscope observations, materials were prefixed in 3% glutaraldehyde in 0.1 mol/L cacodylate buffer for 3 h, post-fixed in 2% OsO₄ in 0.1 mol/L cacodylate buffer for 1 h (or fixed in a mixture of 2% glutaraldehyde and 1% OsO₄ in seawater for 40 min for released oospores), dehydrated in an acetone series and embedded in Spurr's epoxy resin (Spurr 1969), sectioned with a diamond knife and stained with uranyl acetate and lead citrate.

RESULTS

Phenology and morphology of field plants

At Abashiri, *S. durum* grew at a depth of 3–5 m below mean sea level, on semi-exposed subtidal rocks very close to sandy bottoms and plants often suffered serious damage from moving sand. The erect thalli were gregarious on rigid disc-shaped holdfasts (Figs 1,2), and are evidently perennial. Plants were collected year-round; however, fertile thalli were encountered only in winter during December and April. This coastal region was usually completely covered with drift ice from January to March. Therefore, spore release evidently took place under ice cover, perhaps in almost complete darkness when the ice surface was covered with snow.

Three morphologically different reproductive structures were found on fertile thalli, unilocular sporangia (Fig. 3) and two different types of plurilocular structures (Figs 4–7). These three structures were found on separate thalli in our field material. Unilocular sporangia were axillary, formed in groups, pedicellate, globose and measuring approximately 120 μm in length and 100 μm in diameter (Fig. 3). They became darker as they matured; however, no release of flagellated zooids or emptied sporangia was observed in the field material. Plurilocular structures, evidently gametangia, were also axillary, formed solitarily or in groups, but in smaller numbers than unilocular sporangia (Figs 4,6). They were pedicellate, elongated and approximately 200 μm in length and 160 μm in diameter (Figs 4–7). There were two types of gametangia; macrogametangia with locules 18–20 μm in width (Figs 4,5) and microgametangia with locules 4–5 μm in width (Figs 6,7). No release of flagellated zooids or emptied locules was observed from these gametangia, unlike in unilocular sporangial thalli. Macro- and micro-

gametangia were borne on separate erect thalli, so the species is evidently diecious.

Observations of type material of *Sphacelaria dura* Ruprecht

The general morphology of apical cells (Fig. 8) and branching of the type material (Figs 9–11) agreed with Japanese materials. No reproductive structures were found (Fig. 10). The basal part of the erect thalli was composed of densely interwoven rhizoidal filaments (Figs 9,11).

Culture experiments

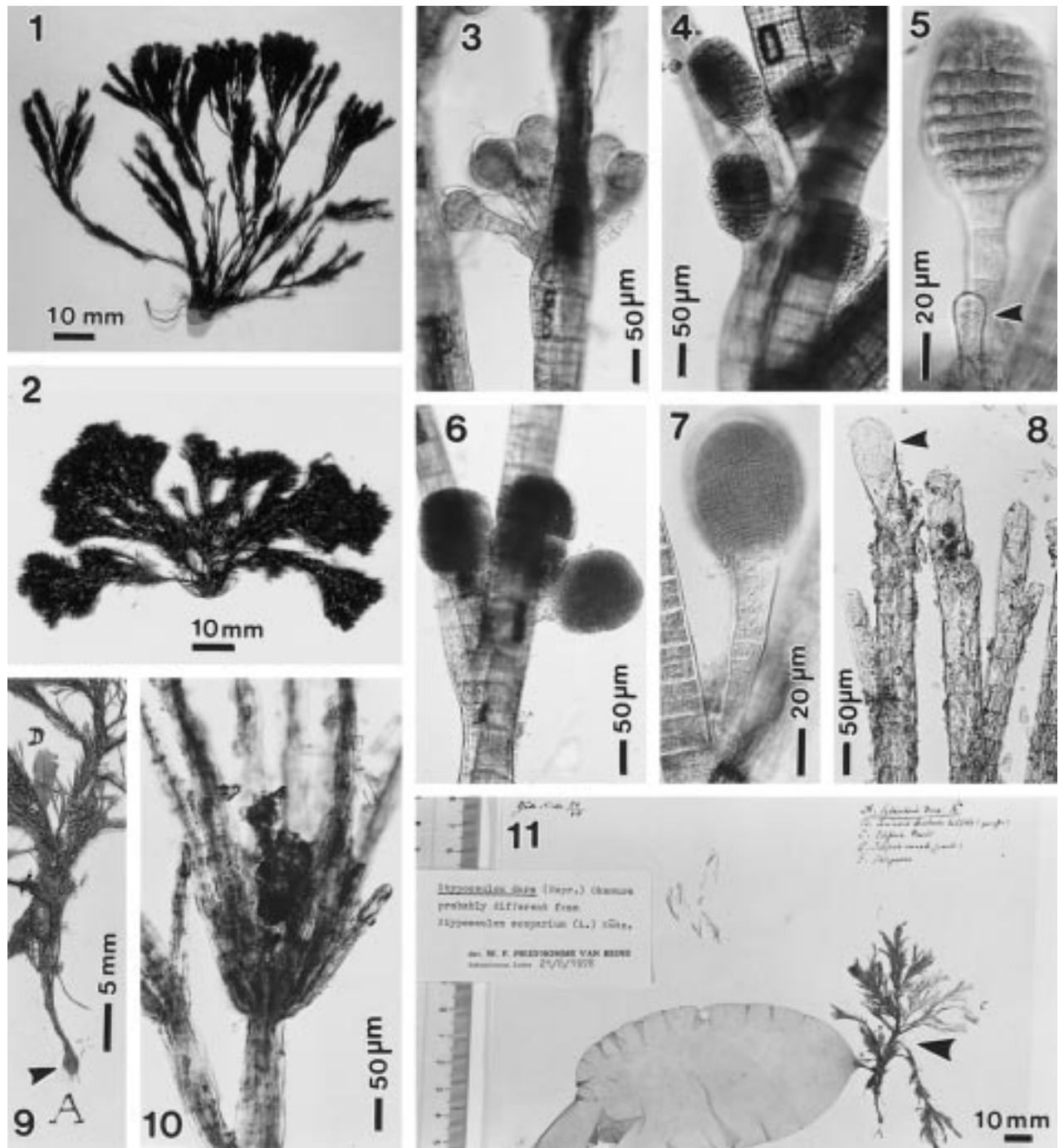
Among unialgal culture strains established from apical fragments, two culture strains, one forming unilocular sporangia and the other forming plurilocular gametangia, were used for further culture studies. In unilocular sporangial thalli, release of flagellated unispores (zooids) did not occur, but the contents of the unilocular sporangia germinated *in situ* below 5°C. Those germlings developed into compact discs and formed new erect thalli having characteristic apical cells (Fig. 12). They further developed into similar erect thalli and formed initials of plurilocular gametangia (Fig. 13) but their fate could not be traced. Both vegetative growth and formation of reproductive structures were rather slow and it usually took more than 6 months for a juvenile fragment to grow into a fertile thallus.

Cultures started from plurilocular gametangial thalli formed macrogametangia (Figs 14–16) and sometimes produced both macro- and microgametangia on the same thalli (Fig. 20). Macrogametangia released aplano-macrogametes (or oospores, Fig. 17). Flagella and stigmata were not detected by transmitted light or epifluorescence microscopy. Each oospore contained large vacuoles and many disc-shaped chloroplasts without pyrenoids (Figs 16,17). These oospores germinated parthenogenetically (Figs 18,19) and developed into erect thalli forming unilocular sporangia (Fig. 23). In contrast, no gamete release or *in situ* germination of the contents was seen in the microgametangia (Fig. 21). Transmission electron microscopy of these structures suggested the formation of flagellated cells (Fig. 22), but they soon degenerated without release.

Both the unilocular and plurilocular erect thalli formed reproductive structures at 3, 5, 10 and 15°C short-day conditions; however, release of oospores occurred only at 3 and 5°C.

DISCUSSION

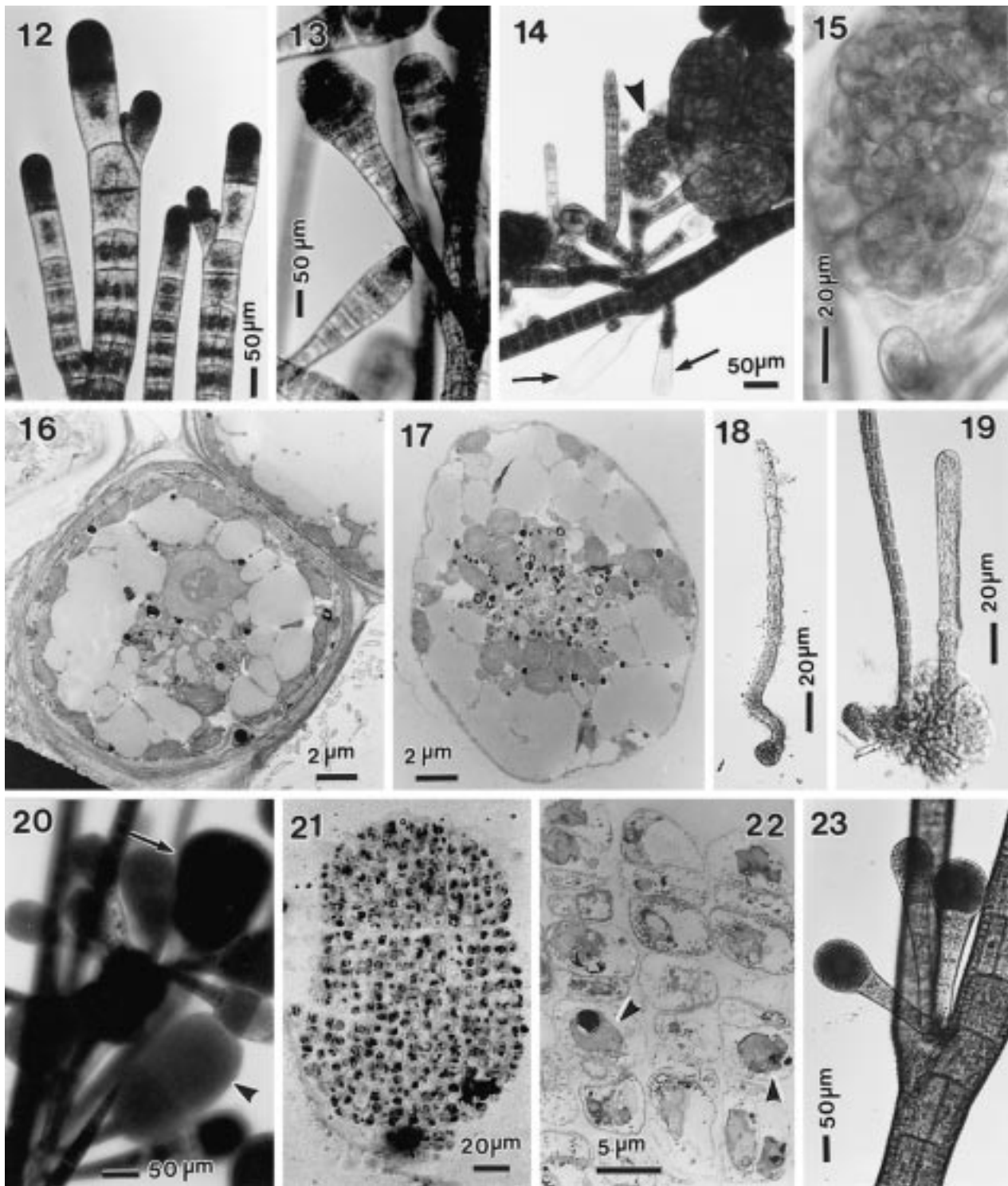
On the basis of the differences summarized in Table 1, the Japanese plants most probably belong to the genus *Stypocaulon*. However, the occurrence of putative plurilocular macro-gametangia and occasional occurrence of axillary laterals suggest a close relationship to the



Figs 1–11. Field plants of *Stypocaulon durum* (Ruprecht) Okamura from Japan (1–7) and the type material of the species (8–11). 1, 2. Field plants from Abashiri, Hokkaido, collected on 12 December 1978. 3. Unilocular sporangia formed in clusters. 4. Macrogametangia (female gametangia) formed in clusters. 5. Macrogametangium and initial (arrowhead). 6, 7. Microgametangia (male gametangia). 8. Apical cells (arrowhead). 9. Basal part of the erect thallus with rhizoidal filaments (arrowhead). 10. Middle part of the erect thallus. 11. Habit of the type material (arrowhead).

genus *Halopteris* as well. Morphological differences between the vegetative plants of *Stypocaulon scoparium* and *S. durum* are not very obvious. Japanese *Stypocaulon* tends to appear darker than European *S. scoparium*. In Japanese *Stypocaulon* the disc-shaped holdfast is a genuine basal disc formed by the attached spore and developing from a monostromatic to a polystromatic

disc, although it can be covered with rhizoidal filaments. In *S. scoparium*, however, the attachment of mature plants is never by a genuine basal disc. According to Sauvageau (1904, 1908, 1909) germlings of unilocular sporangia of *S. scoparium* exclusively form small monostromatic germination discs, which are not transformed to polystromatic discs or basal crusts. Ac-



Figs 12–23. Cultured plants of *Styocaulon durum* (Ruprecht) Okamura from Japan. 12. Apical cells. 13. Initials of plurilocular gametangia. 14. Macrogametangia with *in situ* germinating aplanogametes (arrowhead) and their emptied walls (arrows). 15. Germinating aplanogametes. 16. Transmission electron micrograph of a locule of a macrogametangium. 17. Transmission electron micrograph of a released macrogamete (aplanogamete). 18. Germling of a macrogamete. 19. Young erect filaments of apical growth from a prostrate disc developed from a macrogamete. 20. Macro- (darker color, arrow) and microgametangia (lighter color, arrowhead) formed on the same erect thallus. 21. Longitudinal section of a microgametangium embedded in Spurr's resin and stained with toluidine blue. 22. Transmission electron micrograph of a part of microgametangia. Each locule includes flagellated cells (microgamete, arrowheads), but somewhat degenerated. 23. Unilocular sporangia formed on the erect thalli developed from a macrogamete.

Table 1. Characters used to re-separate the genera *Halopteris* and *Stypocaulon*. For a glossary of terms see Prud'homme van Reine (1982)

Character	<i>Halopteris</i>	<i>Stypocaulon</i>
Secondary growth of segments	Always absent (leptocaulous)	Usually absent (leptocaulous) but rarely present in axial segments close to the basal disc (slightly auxocaulous)
Axillary cell in acroheteroblastic branching site	Does not divide or divides into 2–4 cells only	Divides usually into 4–32 small cells
Number of axial unilocular and plurilocular sporangia per branching site	1 (–2)	16 or more
Number of axial hairs per branching site	Usually none	Usually 4–16
Axial branches	Common	Rare
Pericysts	Absent	Present
Adventitious branches	Absent	Usually present
Rhizoid arise from	Peripheral cells of the first inferior secondary segment of a lateral	Pericysts
Macrogametangia	Plurilocular	Unilocular (oogonia)
Microgametangia	Plurilocular	Plurilocular

roheteroblastic laterals of *S. scoparium* often fragment and form small plantlets that may function like propagules. The cells of these fragments are able to form rhizoids, which attach the plantlets to their parent plants or to other substrata. These rhizoids never form attachment discs, but new erect axes may arise directly from these plantlets as well as from their rhizoids. Other differences between *S. scoparium* and *S. durum* are in the irregular branching pattern of the latter species, which is, according to Ruprecht (1850), irregularly dichotomic. Also, the occurrence of mainly appressed rhizoids in *S. durum*, contrasting with the more divaricate woolly rhizoids of *S. scoparium*, is probably a good differentiating character. In *S. durum*, the axillary cells in the acroheteroblastic branching site occasionally form one or more (up to four) spine-like determinate laterals, which have not been observed in *S. scoparium*.

Type material of *S. durum* basically agreed with the Japanese specimens, but was also similar to European *S. scoparium* in vegetative structure. The type material is sterile and does not contribute to the comparison of reproductive structures. However, based on the following features, we identified the Japanese materials as *S. durum* due to: (i) the difference in the morphology of female gametangia (unilocular, monosporangium-like structures in *S. scoparium* (Prud'homme van Reine 1991, 1993) versus plurilocular macrogametangia in Japanese specimens (current paper); and (ii) the difference in the tolerance to lower and higher temperatures [Table 2; Novaczek *et al.* (1989) and the present paper]. Japanese as well as northwestern Atlantic materials are considerably more tolerant to lower temperature conditions than European *S. scoparium*, but less tolerant to higher temperatures.

Considering the morphological resemblance and similarity of its temperature tolerances, the northwestern

Table 2. Responses to different temperature conditions in culture of Japanese *Stypocaulon durum*, Atlantic Canadian *Stypocaulon* sp. (presumably *S. durum*) and European *S. scoparia* [data compiled from Novaczek *et al.* (1989) and this paper].

Temperatures (°C)	Japanese <i>Stypocaulon durum</i>	Canadian (Atlantic) <i>Stypocaulon</i> sp.	European <i>Stypocaulon scoparium</i>
–2	nd	++	–
0	+	++	–
3	+	nd	nd
5	nd	++	+–
10	++	nd	nd
12	nd	+	+
15	++	nd	nd
16	nd	+	++
20	+	+	++
22	nd	+	++
25	–	–	++
27	nd	–	++
30	nd	–	+–

nd, no data; ++ undamaged; + alive but damaged; +– dead or damaged; – dead.

Atlantic taxon of *Stypocaulon* appears to be identical with *Stypocaulon durum*, as suggested by Novaczek *et al.* (1989), although the nature of the reproductive structures is not yet clarified.

Figure 24 represents the life-history pattern in culture of Japanese *S. durum*. This species, in principle, shows an isomorphic life-history common in the order Sphacelariales. The culture results suggest that this species requires short-day conditions for maturation and extreme cold temperature (below 5°C) for spore release. Such conditions correspond to winter conditions

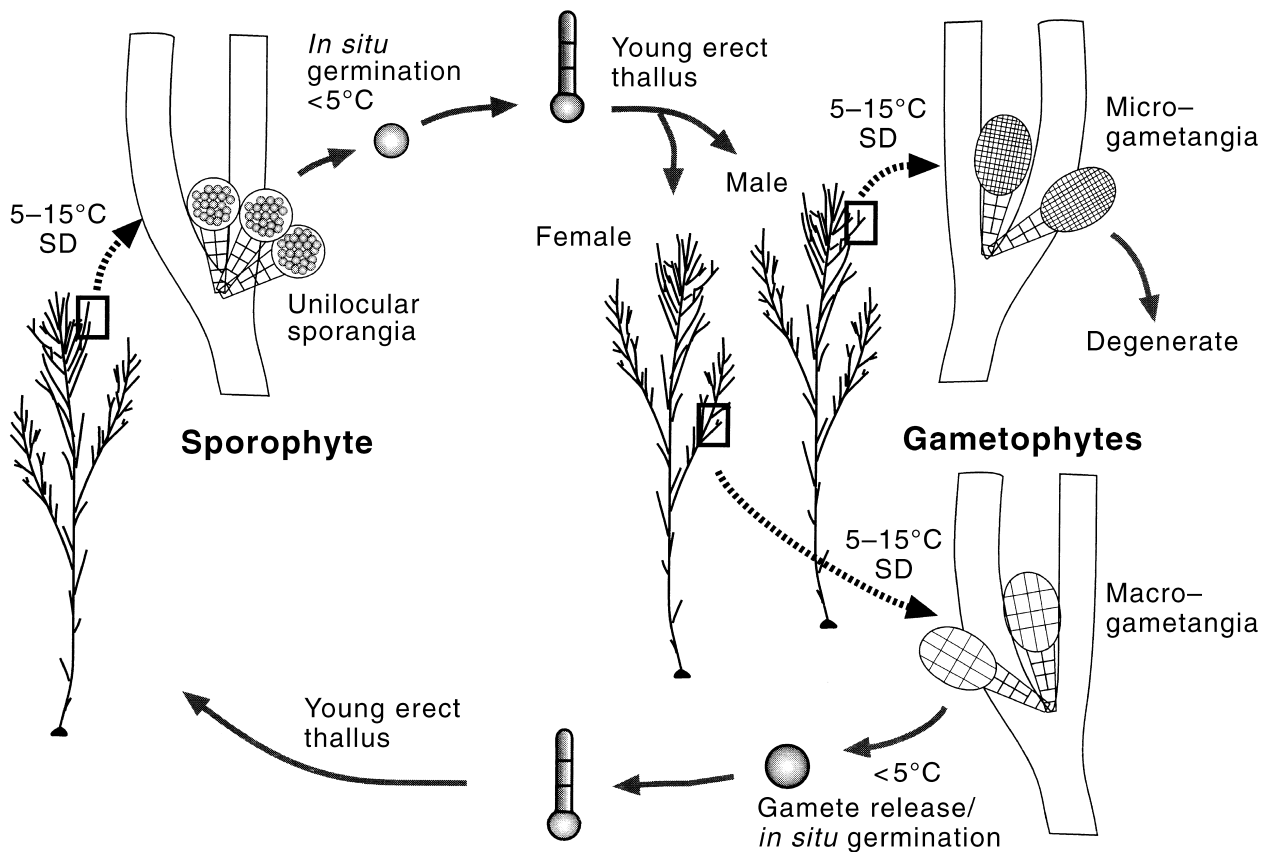


Fig. 24. Diagrammatic summary of the life history of *Stypocaulon durum* (Ruprecht) Okamura from Japan. SD, short day.

at Abashiri and agree well with the phenology of the species.

No release of flagellated reproductive cells was observed in culture or in field-collected plants; however, the non-flagellated oospores were released and the unispores germinated *in situ*. Unispores developed into gametophytes forming plurilocular organs and oospores parthenogenetically developed into sporophytes. Male gametes were not released or germinated *in situ*. Considering these results and the fact that no gamete release or emptied plurilocular male gametangia were found in field-collected plants, these male gametangia might be residual and not functional. Similar non-functional male gametangia and male gametes associated with non-functional oospores are reported in species of Tilopteridales (Kuhlenkamp and Müller 1985; Hooper *et al.* 1988) and this may be a similar phenomenon.

The family Stypocaulaceae Oltmanns currently includes five genera (*Alethocladus* Sauvageau, *Halopteris* Kützing, *Phloiocaulon* Geyler, *Ptilopogon* Reinke and *Stypocaulon* Kützing, Prud'homme van Reine 1993). Among them, the life history in culture has been studied only in a few taxa (Moore 1951; Ernst-Schwarzenbach 1957; Prud'homme van Reine 1982, 1991, 1993; Keum *et al.* 1995). No sexual reproductive structures have been reported in many species and in some species even neither asexual nor sexual sporangia/

gametangia have been described so far. In the monotypic genus *Alethocladus*, only unilocular sporangia-like structures resembling those of *Halopteris platycena* Sauvageau (Lindauer *et al.* 1961) were noted (Y.S. Oh, pers. comm. in Prud'homme van Reine 1993). In *Halopteris*, among the four species recognized in Prud'homme van Reine (1993) [*H. filicina* (Grateloup) Kützing, *H. novae-zelandiae* Sauvageau, *H. obovata* (Hooker and Harvey) Sauvageau, *H. platycena* Sauvageau], sexual reproductive structures are only known in *H. filicina*. This species forms anisogamous planogametes on monocious gametophytes (Sauvageau 1903; Ernst-Schwarzenbach 1957; Keum *et al.* 1995). In cultures of *H. filicina* Ernst-Schwarzenbach (1957) observed apomictic development of plurilocular sporangia with small loculi (microgametes) as well as of plurilocular sporangia with larger loculi (macrogametes). That author never observed copulation of gametes in *H. filicina*, although she observed simultaneous release of both micro- and macrogametes in the populations she had sampled. Often, however, the spores from plurilocular sporangia of both sizes did not release and apomictic development occurred within the plurilocular sporangia. Keum *et al.* (1995), however, observed *in situ* conjugation between plurizoids of different sizes (evidently female and male gametes) released from a plant in culture. The macrogametes were observed to

settle earlier than the microgametes, while macrogametes that did not fuse with microgametes always developed parthenogenetically into haploid germlings. Keum *et al.* (1995) counted 16 chromosomes in mitotically dividing nuclei of unilocular sporangia as well as in gametophytes and in haploid germlings. These results are fully in accordance with an isomorphic diplohaplontic life history, which seems to be usual in Sphacelariales (Prud'homme van Reine 1982). In *H. filicina*, sexual reproduction is by anisogamy, whereas in other genera isogamy and oogamy are also assumed to occur, although complete observations, like those by van den Hoek and Flinterman (1968) and by Keum *et al.* (1995) are often still lacking. Our observations on occurrence of plurilocular sporangial structures in *S. durum* do not change this general picture. The suggested occurrence of aposporic female gametes and non-functional male gametangia is conceivable, but it is also possible that the gametes in the cultures in this study did not develop normally. This is very similar to the contrasting observations on gametophytic *Halopteris filicina* in the papers by Ernst-Schwarzenbach (1957) and Keum *et al.* (1995), respectively. To this can be added that chromosome counts in *H. filicina* by Ernst-Schwarzenbach (1957) suggested a haploid chromosome number of $n = 8$. In nuclei of young unilocular sporangia she counted the diploid chromosome number $2n = 16$. Mathias (1935), however, had already published chromosome counts of 32 chromosomes in the not yet meiotically divided nuclei of young unilocular sporangia. In both cases, the specimens had been collected at Naples in Italy. Thus, counts by Mathias (1935) agree with those made by Keum *et al.* (1995), but are twice as large as the counts by Ernst-Schwarzenbach (1957). The latter author suggested that the thalli observed by Mathias might have been tetraploid, a suggestion which could then also be applied to the Korean specimens.

Members of the genera *Phloiocaulon* and *Ptilopogon* also form anisogamous gametes on monocious gametophytes (Sauvageau 1904, 1907; Moore 1951; Womersley 1987), although the detailed life histories have not been studied in culture. In the genus *Stypocaulon*, among the four species recognized by Prud'homme van Reine (1993) [i.e. *S. scoparium* (L.) Kützinger, *S. durum*, *S. funiculare* (Montagne) Kützinger and *S. paniculatum* (Suhr) Kützinger], only *S. durum* (present paper) has plurilocular female gametangia forming aplanogametes, while the rest are monocious and oogamous with monosporangium-like female gametangia (Sauvageau 1904, 1907; Womersley 1987; Prud'homme van Reine 1993). It is noteworthy that only *S. durum* shows diecism in field plants. As summarized above, all known gametophytes in Stypocaulaceae have been reported to be monocious, although those structures are only known in cultured plants in *H. filicina* (Ernst-Schwarzenbach 1957; Keum *et al.* 1995). However, Sauvageau (1931) and Ernst-Schwarzenbach (1957) ob-

served that young plants of *H. filicina* bearing plurilocular sporangia occasionally only form loculi of the larger sizes, while older plants form loculi of both larger and smaller sizes. Considering that *S. durum* also showed monecism in culture, it might be possible that field plants of the species also show monecism later in the fertile season. It would be interesting to study the reproductive structures of American North Atlantic *Stypocaulon*.

ACKNOWLEDGEMENTS

We are grateful to Dieter G. Müller for the use of laboratory facilities, to Eric Henry for critically reading and improving this manuscript, to the Botanical Institute, Academy of Science, Russia for the loan of the type of *Sphacelaria dura* Ruprecht, to Irene Novaczek for providing cultures of North Atlantic *Stypocaulon* sp.

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