Female reproductive structures and strategy in a red alga, Constantinea rosa-marina (GMELIN) POSTELS et RUPRECHT (Dumontiaceae, Cryptonemiales)*

Sandra LINDSTROM**

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

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A morphological examination of female reproductive structures in the type species of the red algal genus *Constantinea*, *C. rosa-marina*, indicates that this genus should be retained in the Dumontiaceae despite some unique features of its reproductive apparatus. In particular, as the trichogyne elongates, subtending cells of the carpogonial branch, particularly the future nutritive cell, become lobed. Following fertilization in the spring and transfer of the fertilization nucleus to the nutritive cell, the female reproductive apparatus remains dormant until the fall when the fertilization nucleus is finally transferred by a connecting filament to a cell of a remote auxiliary cell branch from which the gonimoblast develops. Inner cortical cells form a nutritive network around the maturing carposporophyte. The summer dormancy of the female reproductive apparatus is hypothesized to be of evolutionary advantage to the species since male plants shed most of their blades in the spring after release of spermatia and therefore do not shade female and tetrasporangial plants which are accumulating starch in their blades during the summer to provide nutritive material for the relatively large spores produced in the fall.

Key Index Words: Constantinea; Cryptonemiales; Dumontiaceae; nutritive cell; reproductive morphology; reproductive strategy; Rhodophyta; Weeksiaceae.

Constantinea rosa-marina (GMELIN) POS-TELS et RUPRECHT is a subtidal perennial red alga with a peltate habit which occurs along the Pacific Rim from eastern Hokkaido, Japan, to Southeast Alaska, U.S.A. It was first described by GMELIN (1768) from plants collected by Steller near Cape Lopatka, Kamschatka Peninsula. POSTELS and RUPRECHT (1840) included the species in their *Illustrationes Algarum*, based on collections by Mertens near the type locality. Although

several other nineteenth century phycologists included *Constantinea* in their taxonomic works, probably only SCHMITZ and HAUPTFLEISCH (1897) in describing the cystocarps of *Constantinea* observed new material although SETCHELL (1906) considered that they may have instead observed *C. simplex* SETCHELL.

Although a number of authors have recorded its occurrence in Japan (OKAMURA 1910, 1936, NAGAI 1935, YAMADA and TANAKA 1944), in SAGHALIEN (TOKIDA 1954), in the Kurile Islands (NAGAI 1941), and in Alaska (SETCHELL 1899, SAUNDERS 1901, SETCHELL and GARDNER 1903), the species has generally remained poorly understood. FRITSCH (1945) included a figure of *C. sub-*

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ulifera SETCHELL under the name *C. rosa-marina* (based on FREEMAN'S 1899 identification—*C. subulifera* was not yet distinguished from *C. rosa-marina*), and KYLIN'S 1956 figure (after KÜTZING) resembles a rose more than *C. rosa-marina*. ABBOTT'S 1968 treatment of the genus, which deals mainly with *C. simplex*, includes several statements about the genus which apply only to *C. simplex*, and MASAKI (1953) presents observations based only on October and November collections.

Materials and Methods

Data in this paper are based on the following collections:

Date	Location	Habitat	Collector
Apr. 8, 1970	Cap Nosappu	Cast ashore	M. KUROGI
May 26, 1978	Kushiro	4-10 m	N. TAZAWA
Aug. 5, 1978	Cape Nosappu	Cast ashore	M. KUROGI
Sep. 5, 1978	"	"	Author
Oct. 17, 1978	"	"	"
Nov. 29, 1978	"	"	"

Slides were made from freezing microtome sections or squash preparations. Reproductive structures were stained with cotton blue.

Results

Carpogonial branches first appear in early spring. They arise from an inner cortical cell of the upper surface (never the lower surface) of the terminal blade (Fig. 1) and are (6-)7-9(-12) cells long. Frequently one or two immature carpogonial branches 1-7 cells in length arise from the same cortical cell or from the basal cell of a carpogonial branch.

The carpogonial branch initially grows downward toward the medulla (Fig. 1). After the future nutritive (fusion) cell is formed, the adjacent apical cell (carpogonium) begins to produce the trichogyne (Fig. 2), at the same time cutting off two sub-apical cells (Figs. 3, 4) such that the branch becomes strongly recurved at its distal end and the carpogonium remains in proximity to the nutritive cell, the trichogyne usually pointing back toward the upper surface of the blade (Fig. 4). As the trichogyne continues to elongate, first the nutritive cell begins to form lobes from its surface (Fig. 5), followed by the 2nd, 5th, 3rd, and 6th cells (Fig. 6; numbering begins from the top of the branch, the carpogonium being the 1st cell), none of which become as lobed as the nutritive cell. The trichogyne is strongly constricted just above the carpogonium and variously coiled.

Although trichogynes usually push their way through the upper surface of the blade, some extend across the medulla and push their way through the lower surface. In either case a conical elevation with a central pore is formed through which the trichogyne extends. Based on the number of pores visible on both upper and lower surfaces of a blade 130 mm in diameter, carpogonial branches can reach a density of at least 800/cm^2 near the margin of the blade; they decrease in density toward the stipe. After the trichogyne is retracted, presumably following fertilization, the conical elevations and pores disappear. The trichogyne remains intact and coiled within the blade for the duration of post-fertilization development.

No connection was observed between the fertilized carpogonium and other cells of the carpogonial branch. However, remnants of a cytoplasmic thread were occasionally seen extending from the carpogonium toward the nutritve cell (Fig. 7). The fertilization nucleus was presumably transferred to the nutritive cell via such a connection.

The ontogeny of auxiliary cell branches is the same as that of carpogonial branches, i.e., they arise from inner cortical cells in the spring. During the summer, as new cortical layers are added to the surface of the blade, the inner cortical cells to which the carpogonial and auxiliary cell branches are attached move closer to the medulla.
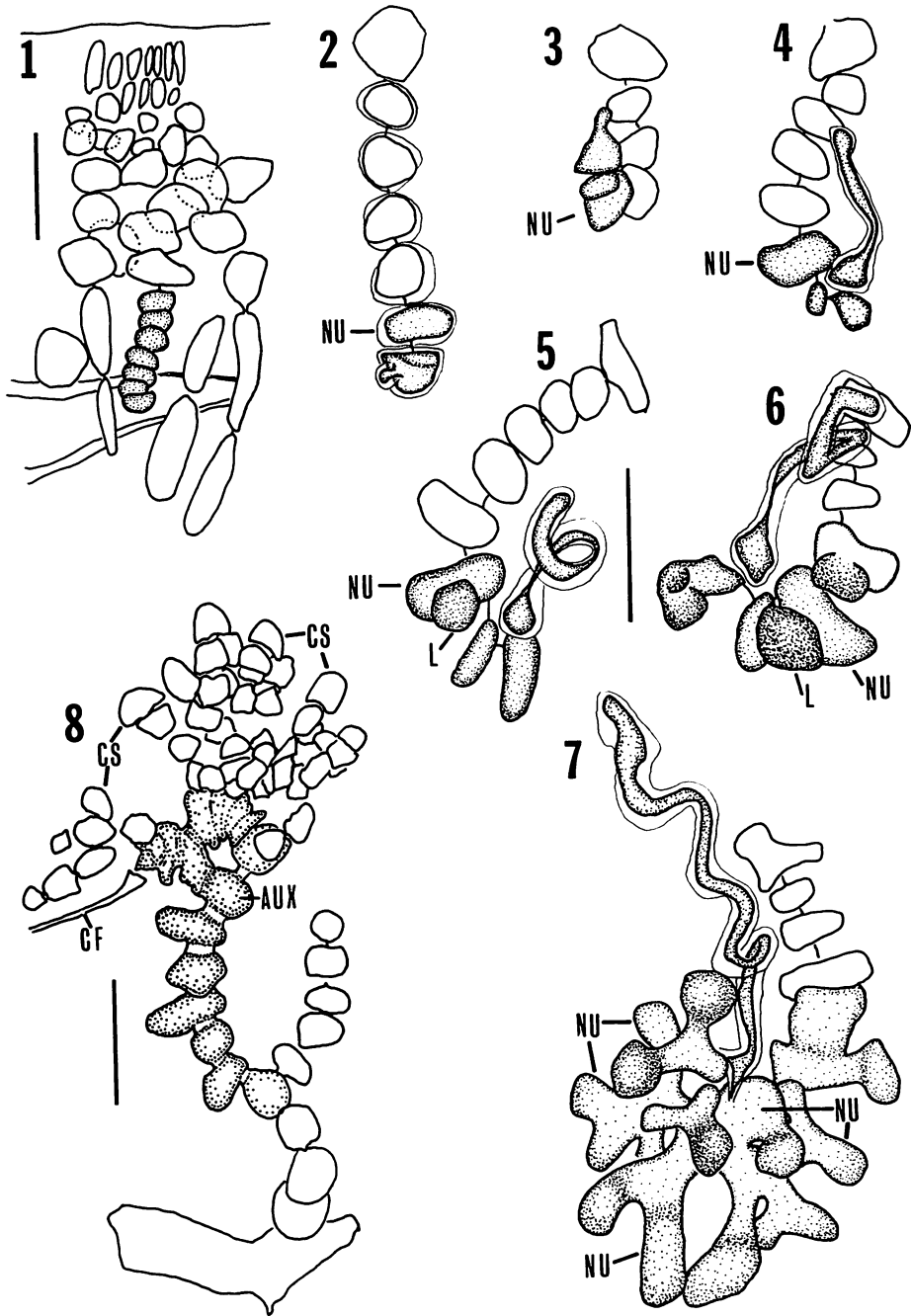
Figs. 1-8. *Constantinea rosa-marina* (GMELIN) POSTELS et RUPRECHT. All scales=30 μm. 1. Immature carpogonial branch arising from an inner cortical cell of the upper surface of the terminal blade; 2-4. Maturation of a carpogonial branch showing initiation and elongation of the trichogyne as cells 2 and 3 are cut off; 5. Initiation of a lobe from the nutritive cell; 6. Initiation of lobes from cells 2 and 5 as well as from the nutritive cell; 7. Remnant of a cystoplasmic thread between the carpogonium and the mature nutritive cell; 8. Development of a carposporophyte from the connecting filament where it attached to the second cell of an auxiliary cell branch. Also note development of the pedicel. AUX=auxiliary cell, CF=connecting filament, CS=carposporangia, L=lobes, and NU=nutritive cell.

This is also due in part to the elongation of the inner cortical cells beneath the upper surface of the blade. By mid summer, the auxiliary cell branches, which were originally oriented toward the medulla, now point toward the upper surface of the blade. They may bear one or two short lateral branches and are (8–)10–12(–15) cells long at maturity.

Connecting filaments were first observed in mid October. They frequently branch but are non-septate. After making contact with an auxiliary cell, the 2nd or occasionally the 3rd cell from the apex of a mature auxiliary cell branch, a connecting filament may branch and continue on or a new connecting filament may arise near the point of contact or on the opposite side of the auxiliary cell.

Gonimoblast filaments usually arise from the remnant of the connecting filament near its point of attachment to the auxiliary cell (Fig. 8) although at times they appear to develop from the auxiliary cell itself. As many as 8–10 branched gonimoblast filaments 4–7 cells in length are produced in a single cystocarp. As the carposporophyte develops, the cells of the auxiliary cell branch and their connections broaden to form a pedicel (Fig. 8), the term originally used by SETCHELL (1906) in describing the structure in *C. simplex*.

As previously noted, the inner cortical cells beneath the upper surface of the blade elongate as the auxiliary cell branches mature. By late summer, these cells are densely filled with starch grains. The connections between the inner cortical cells surrounding each developing carposporophyte widen to form a nutritive network (Fig. 9). Connections between the carposporophyte and the nutritive tissue of the female gametophyte could not be detected at the level of resolution of freezing microtome sections and light microscopy.

Carpospores are released through a carpostome 58–88 μm in diameter (ave. 74 μm) on the upper surface of the blade during November and December. Carpospores liber-
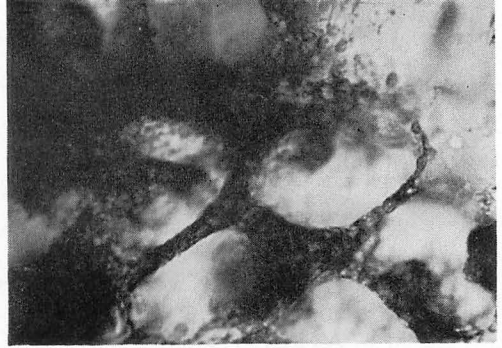

Fig. 9. Nutritive network of inner cortical cells which surrounded the maturing carpospores prior to their release. ×442.

ated at the end of November averaged 49.4 ±3.2 μm in diameter. Following their release, one to three sterile cells remain at the base of each gonimoblast filament. Based on an average carpostome density of 444/cm^2 and an estimate of 75 viable carpospores per cystocarp, a blade 90 mm in diameter produces about 1.5 million carpospores and one 150 mm in diameter produces about 5.2 million carpospores.

Senescence of blades is an integral part of reproductive maturity in *Constantinea*. As the carposporangia develop and release their spores, the blade loses its pigmentation and soon erodes, leaving a remnant of sterile blade about 60 mm in diameter. (PUESCHEL and COLE (1981) have recently shown that phytoferritin is produced as part of the senescence process in *C. subulifera* and *C. simplex* blades.)

Female reproductive structures in *C. subulifera* and *C. simplex* from British Columbia (kindly loaned by Dr. R. F. SCAGEL) were found to be similar to those in *C. rosamarina* including the structure and location of the carpogonial and auxiliary cell branches and the initiation of the gonimoblast filaments. Release of mature carpospores seems to vary somewhat in time between species as well as between geographic locations, generally occurring earlier in *C. subulifera* and later in *C. simplex* than in *C. rosamarina*.

Observations on male reproductive struc-

tures will appear in a subsequent paper.

Discussion

Both POWELL (1964) and ABBOTT (1968) have stated that the auxiliary cell branches in *Constantinea* are non-functional. In contrast, I found functional auxiliary cell branches in all three species. It is possible that both authors interpreted the lobed cells of the carpogonial branch to be young stages in gonimoblast initiation. ABBOTT (1968) did footnote an observation by Dr. R. E. NORRIS of gonimoblast filaments arising from an auxiliary cell in *C. rosa-marina* from Alaska. Dr. NORRIS has since kindly sent me his drawings of female reproductive structures and post-fertilization development in *C. rosa-marina* from the Aleutian Islands, and his observations appear to corroborate my own. The function of the lobed cells of the carpogonial branch is not immediately obvious; it may be related to the delayed initiation of connecting filaments since this feature also distinguishes *Constantinea* from other Dumontiaceae.

The occurrence of a nutritive tissue in *Constantinea* has not been previously recognized. Further careful microscopic examination of this structure is necessary to elucidate the mechanism by which developing carpospores obtain nutrition from it.

ABBOTT (1968) erected the family Weeksiaceae for members of the Dumontiaceae in which the auxiliary cell branches are without function, the nutritive cell of the carpogonial branch also serving as the generative auxiliary cell. The results of this study show that all three species of *Constantinea* possess functional auxiliary cell branches and therefore the transfer of the genus to the Weeksiaceae is unjustified.

In the species of the Dumontiaceae where the information is available, it appears that production of carposporangia follows fertilization almost immediately, as is the case in most Florideophyceae. In New England, male plants of *Dumontia contorta* are found in March and April and mature carposporo-

phytes in May and June (DUNN 1917, KILAR and MATHIESON 1978). In Japan, species of *Neodilsea* mature and produce carpospores in late summer and fall (MASUDA 1973a, 1973b, 1974, TAZAWA 1975).

In contrast to most of these species, in which the upright thalli are annual or even ephemeral, *Constantinea* has a perennial upright thallus (LINDSTROM 1980). In addition, many Dumontiaceae are intertidal or occur at the infralittoral fringe whereas *Constantinea* is mainly subtidal. These facts may be important in understanding the apparent differences in reproductive structures and strategy (namely, the lobed structure of cells of the carpogonial branch, delayed transfer of the fertilization nucleus to an auxiliary cell, and production of a nutritive tissue around the developing carposporophyte) between *Constantinea* and other Dumontiaceae.

Constantinea exhibits certain features of a climax dominant species: It is relatively slow growing but long-lived (plants to 18 years of age, based on the number of annual blades or blade scars visible on the perennial stipe, were found in this study), and it takes several years to reach sexual maturity (POWELL 1964). Like perennial species of *Laminaria* (MANN 1973), it takes advantage of stored food reserves and the small amount of available light during the winter months to produce a new blade which then has an advantage over annual subtidal plants which do not produce macroscopic upright thalli until late winter or early spring. The new blade of *Constantinea*, however, lacks starch reserves, but these are rapidly accumulated during the summer months. *Constantinea* also produces relatively large spores, which by their size (and food reserves) may have a competitive advantage over spores of other algae in the upper subtidal zone where sessile organisms compete for limited space.

Constantinea plants frequently occur in groups. Because the blades of *Constantinea* lie flat like saucers, shading occurs among the blades of individual plants and their nearest neighbors, a factor which undoubtedly affects the photosynthetic capacity of the

entire population.

Spermatia are produced by *Constantinea* blades in the spring. Although spring blades lack stored food reserves, the spermatia do not need this source of energy since they are non-motile. Following release of spermatia in *Constantinea*, the blades rapidly disintegrate leaving only the stipe and a small residual blade. Therefore, male plants do not appreciably shade female and tetrasporic plants during the summer months when these plants are accumulating starch for spore production. This argument may help explain the evolutionary advantage of delayed development of the carposporophyte in *Constantinea*.

Acknowledgments

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S. リンドストローム: 紅藻オキツバラの雌性生殖器官の構造と戦略

紅藻オキツバラ属の基本種である オキツバラ (*Constantinea rosa-marina*) の雌性生殖装置の構造を研究した。この藻はリュウモンソウ科に所属するが，次に述べる幾つかの特徴的な構造をもつことがわかった。なかでも，受精毛が伸長するにつれて，造果枝の弧のように出ばった部分の細胞群，特に後に栄養細胞になる細胞が耳たぶ状になる点は顕著な特徴である。春に受精がおこなわれ，受精核が栄養細胞に移ると，雌性生殖装置は休眠に入る。この休眠は，秋になって受精核が連絡糸を通り，離れたところにある助細胞糸の一つの細胞に完全に移動し，そして造胞糸が発達する秋の時季まで続く。成熟した果胞子体の周囲にできる栄養に富む網目状の細胞糸は内方の皮層細胞からつくられたものである。雄性の藻体は春に精子を放出するとほとんどの葉状部を脱落させてしまう。このことは，夏の間に葉状部にでんぷんを蓄積する雌性の藻体や四分胞子をつくる藻体に日蔭をつくらない結果をもたらし，比較的大きい胞子をつくる藻類の栄養分の供給に有利と思われる。この事実を考えると，夏に雌性生殖装置が休眠することは，この藻の進化的有利性であると仮定してよいであろう。