Grateloupia kurogii, a new species of the Halymeniaceae (Rhodophyta) from Japan*

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The vegetative and reproductive morphology and spore germination pattern of a foliose Halymeniacean species from Japan are described. While the alga has the conspicuous anticlinal medullary filaments previously considered characteristic of *Halymenia*, the auxiliary cell ampullae, some other reproductive features and a mediate discal type of spore germination pattern suggest a strong affinity to *Grateloupia*. From comparison of these features to previous descriptions of *Halymenia* and *Grateloupia* I conclude that the anticlinal medullary filaments may not be as strong a generic characteristic as previously thought, and that the new alga is best placed in the genus *Grateloupia*. The circular blade, with highly refractive cells in the medulla, serves to distinguish the alga from any other species of the genus. The alga is described as *G. kurogii* KAWAGUCHI sp. nov.

Key Index Words: Grateloupia—Grateloupia kurogii—Halymenia—Halymeniaceae—reproduction— Rhodophyta—spore germination pattern—taxonomy.

In the course of my systematic studies on the red algal family Halymeniaceae from Japan, I encountered an alga unlike any previously recorded for the family. Specimens of this alga collected at Enoshima in 1924 (in the herbarium of Faculty of Science, Hokkaido University, Sapporo [SAP]) were recognized by YAMADA and labeled by him as a distinct species "Aeodes dilatata YAMADA", together with a Japanese name "Maruba-fudaraku". In 1947, INOH cited this alga as "Halymeniopsis dilatata YAMADA" with a comment that it was Yamada's unpublished name. Since then, this alga has not been mentioned in the literature and these names remained nomen nudum.

In the present study, the vegetative and reproductive morphology of the alga is described from observations of many specimens, including YAMADA's voucher specimens. The rather thin thallus, lubricous texture and scattered reproductive structures of this alga suggest an affinity with Grateloupia (KRAFT 1977, KAWAGUCHI 1989). However, although the reproductive details and spore germination pattern are also typical of Grateloupia, the alga has distinctive anticlinal medullary filaments, considered characteristic of Halymenia (Аввотт 1967, KRAFT 1977, MAGGS and GUIRY 1982, GARGIULO et al. 1986), and refractive cells within the medulla, a feature not previously reported in Grateloupia. A detailed comparison between the features of this alga and those of the hitherto described species of Halymenia and Grateloupia is therefore necessary.

Materials and Methods

Approximately 20 specimens from the following localities (Fig. 1) have been used for anatomical study:

Kyushu: (1) Nango, Miyazaki Pref., 25 v 1982, leg. T. Yoshida & M. Marui, cystocarpic, SAP 037538; (2) Nomozaki, Nagasaki Pref., 3 iv 1936, leg. Matsubayashi, sterile,

^{*} Dedicated to the memory of the late Dr. Munenao KUROGI (1921–1988), Professor Emeritus of Hokkaido University.

KAWAGUCHI, S.



Fig. 1. Type and collection localities of Grateloupia kurogii KAWAGUCHI sp. nov.

SAP 028654; (3) Matsushima, Nagasaki Pref., 26 iii 1986, leg. anonymous, cystocarpic, *Kawaguchi* 0829–32; (4) Saikaibashi, Nagasaki Pref., 2 v, 14 v, 15 vi 1988, leg. S. KAWAGUCHI, cystocarpic, tetrasporangial, *Kawaguchi* 1005–1014.

Shikoku: (5) Uwajima, Ehime Pref., 22 v 1982, leg. T. YOSHIDA & M. MARUI, cystocarpic, SAP 047534 (drift); (6) Imabari, Ehime Pref., 18 viii 1981, leg. S. ARAI, cystocarpic, SAP 047536-7 (5 m deep); (7) Tojima, Ehime Pref., 21 v 1982, leg. T. YOSHIDA, tetrasporangial, *Kawaguchi* 0833.

Honshu: (8) Sugashima, Mie Pref., 24 v 1955, leg. Y. Tsuji, cystocarpic, *Kawaguchi* 0834; (9) Enoshima, Kanagawa Pref., v 1924, leg. Y. YAMADA, cystocarpic, tetrasporangial, SAP 21118-20; (10) Koajirowan, Kanagawa Pref., 3 v 1955, leg. Y. Tsuji, cystocarpic, SAP 047535.

The plants grow attached to rocky substrates in the subtidal zone to 5 m deep, except for the Saikaibashi plants which grew in the lower intertidal zone. The plants occur seasonally from early spring (March) to mid summer (August).

Spore germination studies were undertaken by inoculating pasteurized glass slides or small petri dishes (6 cm in diameter) with carpospores and tetraspores released from the Saikaibashi plants, and then grown in full strength Provasoli's Enriched Seawater (PES). Penicillin G (ca. 30 mg/l) and germanium dioxide (3-5 mg/l) were used as necessary to eliminate blue-green algae and diatoms. Plants were grown at 20°C, 12:12 LD (light and dark) cycle under white fluorescent light 2000-4000 lux.

Slides for the microscopic examination of vegetative and reproductive structures were prepared from either fresh, ca. 5% formalinseawater preserved, or dried specimens. The dried specimens were resoaked in seawater before sectioning. Sections were made by hand using a razor blade, stained with 0.5%(w/v) Cotton blue in a lactic acid/ phenol/glycerol/water (1:1:1:1) solution, then mounted on a glass slide with a glycerolseawater mixture containing a small volume of formalin. The voucher specimens used in the present study are deposited in SAP.

Results

Vegetative morphology

The plant is attached by a submarginal or central discoid holdfast on the undersurface of the blade. The flat blade, which develops from the base through a short, sometimes indistinct stipe, is circular to elliptical in shape, and usually 20-30 cm in diameter. The slightly thickened margin is entire or irregularly lacerated, at times crenulate, and slightly bullate (Fig. 2). The texture is lubricous in young plants, but becomes firmer with age. The color is rose red to blood red, or sometimes yellowish.

In section the thallus is $(200-)350-450 \ \mu m$ thick, and consists of two layers, cortex and medulla. The outer cortex, about 4 cells deep, consists of dichotomously branched filaments of ellipsoid to round, isodiametric cells compactly arranged in anticlinal The outermost cells are somewhat rows. This layer grades to an inner elongated. cortex, 3-4 cells deep, composed of larger, angular to stellate cells laterally connected by secondary pit-connections. The inner cortex merges into a medulla of simple or branched filaments of slender cells (40-75 μ m long by 2-3(-7) μ m broad), rather sparsely intermeshed. These filaments may be periclinally or obliquely directed, but most run perpendicularly from cortex to cortex. Interspersed with these medullary filaments are large stellate (or ganglionic) cells with long interconnecting arms (often exceeding $800 \ \mu m \log p$) containing highly refractive contents, at places forming connections with the usual filaments (Fig. 3A).

Reproduction

Reproductive structures occur scattered over all but the basal part of the blade. Carpogonial branches and auxiliary cells are formed in separate, flask-shaped, subsidiary branch systems called ampullae (SIOESTEDT 1926), produced from the inner cortical cells (Figs. 3B-E, 4A, B). Fewer carpogonial ampullae are found than auxiliary cell ampullae. In the carpogonial ampullae, the primary filament is up to 11 cells long, composed of spherical to ellipsoidal cells distally decreasing in size. From a few cells of the filament, simple secondary filaments are produced toward the surface. The two-celled carpogonial branch, composed of a carpogonium and a hypogynous cell, develops on the primary filament. The carpogonium is conical in shape and projects a trichogyne toward The hypogynous cell has a the surface. short, lateral branch (Fig. 3C, D). In the auxiliary cell ampullae, the primary filament is up to 13 cells long, consisting of rounded cells. From the first, second and third cell of the filament, simple secondary filaments arise. The auxiliary cell is usually the fourth or fifth cell of the primary filament, or sometimes one of the basal cells of a secondary filament. The auxiliary cell is easily distinguished from the other ampullary cells by its larger size and darker color when stain-The mature auxiliary cell is oval in ed. shape, and is located in the center at the bottom of the ampulla (Figs. 3B, E, 4A, B).

After presumed fertilization, apparent fusion of the carpogonium and the hypogynous cell occurs. The fusion complex involves ampullary cells and becomes extremely large and irregular in shape, measuring 100 μ m in the widest portion (Fig. 3F, G). Connecting filaments issue directly from this complex and



Fig. 2. Grateloupia kurogii. A. Holotype (SAP 21118). B. Isotype (SAP 21119). C. Cystocarpic specimen collected at Saikaibashi (KAWAGUCHI 1007). D. Tetrasporangial specimen collected at Saikaibashi (KAWAGUCHI 1006).

also from cells borne on the complex (Fig. 3G). Many connecting filaments are thus produced from a single fertilization. The connecting filaments are usually aseptate, but sometimes branching occurs (Fig. 4D, E). A connecting filament, passing through the medulla, fuses with an auxiliary cell at a place facing the interior of the thallus (Fig. 4C).

After contact with an auxiliary cell the connecting filament may cease to grow further, but in many cases an outgoing connecting filament is seen to be cut off from the auxiliary cell. This outgoing connecting filament may also branch (Fig. 4D, E). Diploidization of the auxiliary cell via a connecting filament results in the cutting off of a gonimoblast ini-



Fig. 3. Grateloupia kurogii. A. Transverse section of middle part of thallus. B. Auxiliary cell ampulla seen from the undersurface. Arrowhead shows auxiliary cell. C. Young carpogonial ampulla, with long arrow showing hypogynous cell and short arrow carpogonium. D. Carpogonial ampulla, with trichogyne (arrowhead). E. Auxiliary cell ampulla, arrowhead showing auxiliary cell. F, G. Large fusion complex (arrow). Arrowheads in G show incipient connecting filaments. H. Early stage of gonimoblast development. Long arrow shows gonimoblast initial cell, short arrow auxiliary cell and arrowheads connecting filament. Scale in B applies also to D–H.

tial cell toward the surface by a transverse septum, and several gonimoblast cells are cut off successively from the initial cell (Figs. 3H, 4C, F). At this time the cells of the ampullary filaments initiate numerous side chains (Figs. 3H, 4D-F, 5A, B). The gonimoblast cells continue to divide, most developing into carposporangia (Fig. 5A–D). With the growth of the carposporophyte, the auxiliary cell fuses with adjacent ampullary cells to form an irregularly-shaped fusion complex (Fig. 5A, B). The mature cystocarp is spherical in shape, to 250–300 μ m in diameter, composed of several gonimolobes, and surrounded by a



Fig. 4. Grateloupia kurogii. A, B. Auxiliary cell ampullae. The cells of primary filament are numbered. C-F. Early stages of gonimoblast development. E is drawn from the undersurface. Lateral filaments from ampullary cells are shown in black. Abbreviations used in the figure: aux, auxiliary cell; cf, connecting filament; fc, fusion complex; gb, gonimoblast; gbi, gonimoblast initial cell; lf, lateral filaments. Arrowheads show branching position of connecting filaments.

rather dense involucre (or pericarp) derived from ampullary cells, their side chains and derivatives from neighboring vegetative cells (Fig. 5D). The cystocarp is deeply immersed in the thallus and has a distinct ostiole.

Spermatangia were observed scattering on the thallus bearing cystocarps, the species being thus monoecious. Spermatangia are



Fig. 5. Grateloupia kurogii. A, B. Advanced stages of gonimoblast development. Arrow shows fusion cell and arrowheads connecting filament. C. Transverse section of female thallus showing the position of carposporophyte. Note that involuce is rather densely seen. D. Semi-mature cystocarp. E, F. Spermatangia formation. Arrows in E show spermatia on the surface of the blade. G. Tetrasporangia formation. Arrow shows tetrasporangial initial. Scale in A applies to B and F, and C to D.

borne singly or in pairs on the outermost cortical cells, which function as mother cells (Fig. 5E, F). The spermatia are tear-shaped, to $4 \ \mu m$ broad by $6 \ \mu m$ long, and vacuolate (Fig. 5F).

Tetrasporangia occur scattered over all but the basal part of the thallus. Tetrasporangial initials are cut off laterally from the cortical cells in the third or fourth layer from the surface. The first cell division always occurs transversely, soon followed by vertical ones, to form cruciately or decussately divided sporangia. The mature sporangium is ellipsoidal, 18-25 μ m broad by 35-45 μ m long, and submerged in the outer cortex (Fig. 5G).

Development of spores

Carpospores released from materials collected at Saikaibashi (2 May, 14 May, 15 June 1988) measured 19–38 μ m in diameter (average 24.2 μ m, N=80) (Fig. 6A). These spores started to germinate one or two days



Fig. 6. Grateloupia kurogii. A. Liberated carpospores. B, C. Germtube (arrowhead) produced from the carpospore after 1-2 days. D. 5-day germling of tetraspore. Note that spore content evacuated into germtube leaving empty wall (arrow). E. 8-day germling of carpospores developing into crust. Arrow shows empty original spore wall. F. 8-day crust of tetraspore. G. 14-day crust of carpospore. Scale in D applies also to A-C.

after inoculation (Fig. 6B, C). Initially a germ tube was formed and the spore content evacuated into it. A septum was then formed, leaving only a spore wall behind. The content divided repeatedly to form a radially expanded disc with a meristematic marginal portion of one-cell layer thick. In two weeks, these discs were about 120 μ m in diameter (Fig. 6E, G). Tetraspores were also obtained from the Saikaibashi collections (14 May 1988). These were almost the same size as the carpospores, and the mode of germination was also similar (Fig. 6D, F).

Discussion

The development of carpogonial branches and auxiliary cells within ampullae, as seen in this study, is characteristic of the family Halymeniaceae (SCHMITZ and HAUPTFLEISH 1897, SJOESTEDT 1926, BALAKRISHNAN 1961a, b, KAWABATA 1962, 1963, CHIANG 1970). Furthermore, the foliose blade, gelatinous texture and scattered reproductive structures suggest that the alga has affinities with species belonging to Halymenia, Grateloupia, Phyllymenia, Aeodes, Pachymenia or Pachymeniopsis. CHIANG (1970) considered the morphology of auxiliary cell ampullae (overall shape, extent or pattern of branching) to be of value in at least separating related groups of genera within the family. In his scheme, CHIANG (1970, p. 71-72) characterized an auxiliary cell ampulla with filaments branched to the second order and an overall conical outline as typical of Grateloupia (in this category, Phyllymenia and Pachymeniopsis are also included). In contrast, the Halymeniatype ampulla is branched to the third or fourth order, flattish and expanded, and the Aeodes-type, which includes Pachymenia, is very bushy with up to four (rarely five) orders of filaments, and cupshaped. The auxiliary cell ampullae of the present alga are clearly of CHIANG's Grateloupia-type.

The taxonomic importance of ampulla

reported for species of *Grateloupia* (Снемін 1937, Інон 1947, Начазніда and Снінака 1967) and *Prionitis* (Начазніда 1965), but

structure in the generic recognition of this family, however, was questioned and downgraded by KRAFT (1977) in his study on Grateloupia intestinalis (HOOKER et HARVEY) SETCHELL ex PARKINSON from New Zealand. This species falls well within the range of other Grateloupia species in its vegetative and reproductive features, only differing in the ampullar type from that associated with the genus by CHIANG (1970). KRAFT (1977, p. 50) concluded that "ampullar types are thus construed as somewhat inconsistent features at least among species otherwise referable to Grateloupia, and are probably not a strong generic characteristic..." GUIRY and MAGGS (1982) similarly reported that in Dermocorynus montagnei CROUAN frat. from around Ireland ampulla structure also differed from the type associated with the genus by CHIANG. Recent authors (KRAFT 1977, MAGGS and GUIRY 1982, GARGIULO et al. 1986) agree that generic limits within this family are best founded on vegetative features. Kraft (1977)characterized Aeodes and Pachymenia by their dense medulla and cortex, and distinguished Phyllymenia from its allied genus Grateloupia by the relatively deep cortex and the more developed medulla*. The above authors also agree with ABBOTT (1967) that the presence of anticlinal medullary filaments, as found in the present alga, is diagnostic of the genus Halymenia.

However, there are good reasons for not placing the present alga in Halymenia. It is known from the literature (HOEK and CORTEL-Breeman 1970, Codomier 1974, Maggs and GUIRY 1982) that in Halymenia, including the type species H. floresia (CLEMENTE) C. AGARDH, the spores germinate into branched, uniseriate filaments (acrochaetioid phase). I have confirmed that H. dilatata ZANARDINI from Japan also has this type of spore germination pattern (KAWAGUCHI unpubl.). The carpospores and tetraspores of the present alga did not show acrochaetioid growth, but developed into crusts soon after settlement, a mediate discal pattern that verifies INOH'S (1947) observations. The latter type of spore germination has previously been 1967) and *Prionitis* (HAYASHIDA 1965), but never in *Halymenia*. This difference in spore germination mode appears consistent in the genera, and therefore makes the placement of this alga in *Halymenia* unacceptable. The exclusion of the present alga from *Halymenia* is also supported by the observation that the pairbhaving modullary formate and

that the neighboring medullary filaments and their derivatives contribute in some degree to the formation of an involucre around the carposporophyte. This is not the case in other species of *Halymenia*, where only remnants of the ampullar filaments form the involucre (BALAKRISHNAN 1961b, CHIANG 1970, GAR-GIULO *et al.* 1986).

In relation to involucral formation, another aspect of morphology is worthy of note. BALAKRISHNAN (1961a) reported that in three Indian species of Grateloupia the ampullar filaments produce lateral branches. My observations on several Grateloupia species from Japan, including G. filicina (LAMOU-ROUX) C. AGARDH (the type species), confirmed that during the early stages of gonimoblast development the ampullar filaments develop lateral cells that form branchlets to a similar extent as in the present plant (KAWAGUCHI unpubl.). In Halymenia, on the other hand, the lateral cells are produced to a much lesser extent from the ampullary filaments (BALAKRISHNAN 1961b, KAWAGUCHI unpubl.). The lateral branchlets are reported to be subsequently used up in later stages of development (BALAKRISHNAN 1961a) or to contribute partly to the involucre (CHIANG 1970). In any case, however, the extent of initiation of lateral branchlets appears to be pronounced between the two genera. The present plant is typical of Grateloupia in this regard.

The overall reproductive features and spore germination pattern, together with the rather shallow cortex and lax medulla, suggest that the present plant is most closely related to

^{*} The genus *Pachymeniopsis* is not well differentiated from *Grateloupia*. Critical examination of its taxonomic status is now in progress by the author.

Grateloupia, in spite of the possession of anticlinal medullary filaments. A similar situation is found in Grateloupia turuturu YAMADA from Japan. In this species, the anticlinal medullary filaments are conspicuous, but other vegetative and reproductive features and spore germination pattern clearly fall within the range seen in other Grateloupia species (KAWABATA 1962, HAYASHIDA and CHIHARA 1967, KAWAGUCHI unpubl.). It appears that the anticlinal medullary filaments may not be as strong a generic characteristic as previously thought.

The refractive cells, which have not previously been reported for species of *Grateloupia*, might appear to pose a problem as to the placement of the alga in this genus. However, this feature (uncertain in function) is probably not a strong generic characteristic. According to SIMONS and HEWITT (1976), the South African *Pachymenia* includes both species with and without such cells.

Taking into account the facts discussed above, the weight of evidence leads me to the conclusion that the genus *Grateloupia* is the best place for this alga. As the circular blade with refractive cells serves to distinguish it from any other recorded species of the genus, I propose to describe the plant as a new species of *Grateloupia*.

Grateloupia kurogii KAWAGUCHI sp. nov.

Description

Planta foliosa, gelatinosa, roseorubra-purpurascentirubra, interdum flavida in colore, ex haptero discoideo usque ad 8 mm in diametro in substrato saxoso exoriens; stipes brevis vel haud detectabilis in laminam planam et recumbentem usque ad 40 cm in diametro extendens; lamina simpliciter circularis vel elliptica, interdum irregulariter robata, margine undulato, leviter incrassato; lamina 200-450 μ m crassa (in planta matura plerumque 350-450 μ m); filamenta medullaria ex cellulis gracilibus 2-7 μ m latis et 40-75 μ m longis plerumque anticlinaliter oriundis constantia; cellulae stellatae (aut ganglionicae) cum brachio longitudine quam 800 μ m longiori et contentis valde refractivis inter filamenta medullaria ordinaria intersperfilamentorum anticlinalium sis: cortex cellularum rotundatarum (exteriorum) et earum stellatarum (interiorum) in partes interiores versus amplitudine crescens; rami carpogoniales et cellulae auxiliares in fasciculis (ampullis) cellularum producti, ramis carpogonialibus 2-cellulatis, filamentis ampullarum cellularum auxiliarium laxe ramosis (ad ordinem secundum), cellular quarta sive quinta filamenti primi in cellulam auxiliarum amplificanti; filamenta involucralia aliquantum densa, ostiolo distincto; planta monoica, spermatangiis ex cellulis corticalibus exterrimis crescentibus; tetrasporangia in cortice exteriori dispersa, ambitu ellipsoidea, 18- $25 \,\mu m$ lata et $35-45 \,\mu m$ longa, cruciatim decussatimve divisa.

Holotypus: SAP 21118, specimen cystocarpicum in Enoshima Praefacturae Kanagawa (35°18'N, 139°29'E) mense maio anno 1924 a Y. YAMADA lectum (Fig. 2A).

Plant foliose, gelatinous, rose red to purplish red or sometimes yellowish in color, developing from a discoid holdfast to 8 mm in diameter, on rocky substrata; short or scarcely detectable stipe expanding into a flat, recumbent lamina to 40 cm in diameter; lamina simply circular to elliptical, or at times irregularly lobed, with an undulate, slightly thickened margin; lamina varying from 200 μ m to 450 μ m thick (in mature plants mostly 350-450 μ m); medullary filaments composed of slender cells 2–7 μ m wide by 40– 75 μ m long, mainly anticlinally oriented; large stellate (or ganglionic) cells, with arms exceeding 800 μ m in length and highly refractive contents interspersed among the usual medullary filaments; cortex of anticlinal filaments of round (outer) and stellate (inner) cells increasing in size toward the interior; carpogonial branches and auxiliary cells produced within cell clusters (ampullae), carpogonial branches two-celled, auxiliary cell ampullae filaments sparingly branched (to second order), the fourth or fifith cell of the primary filament enlarging into the auxiliary

cell; involucral filaments rather dense, ostiole distinct; plant monoecious, spermatangia developed from outermost cortical cells; tetrasporangia scattered in the outer cortex, ellipsoid in shape, $18-25 \,\mu\text{m}$ wide by 35- $45 \,\mu\text{m}$ long, cruciately or decussately divided.

Holotype: SAP 21118, cystocarpic specimen collected at Enoshima, Kanagawa Prefecture (35°18'N, 139°29'E) in May 1924 by Y. YAMADA (Fig. 2A).

Distribution: Endemic

Japanese name: Maruba-fudaraku

(Yamada)

Etymology: This species is named in honor of the late Professor Emeritus Munenao KUROGI, Hokkaido University, for his many contributions to our knowledge of phycology. The present study was mainly undertaken under his guidance in the laboratory of Department of Botany, Faculty of Science, Hokkaido University. Yamada's epithet "dilatata" was not adopted here to avoid possible confusion with Halymenia dilatata ZANARDINI.

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川口栄男:紅藻ムカデノリ科の一新種 Grateloupia kurogii (マルバフダラク)

日本産紅藻ムカデノリ科の一種の栄養体,生殖器官の形態的特徴と胞子の発芽様式を図示した。本種には, Halymenia 属の特徴とされる垂直に走る髄糸が顕著であるが,助細胞 ampulla の構造, 嚢果発達過程にみられる 特徴及び間接盤状型の胞子発芽様式は Grateloupia 属との強い関連を示唆した。本種のもつ特徴を Halymenia 属と Grateloupia 属の種と比較した。その結果,垂直な髄糸はこの科の属を区別する強い特徴ではなく,本種は Grateloupia 属に含めるべきであると結論された。更に,髄中に光を屈折する細胞を含む円形に広がる薬体は,他 の Grateloupia 属の種から本種を明瞭に区別する。従って,本種を Grateloupia kurogii KAWAGUCHI sp. nov. (マルバ フダラク,山田)として記載を行った。(812 福岡市東区箱崎6-10-1 九州大学農学部水産学第二教室)