

Taxonomic notes on the Halymeniaceae (Rhodophyta) from Japan. I. *Halymenia acuminata* (Holmes) J. Agardh.

Shigeo Kawaguchi

Department of Fisheries, Faculty of Agriculture, Kyushu University, Fukuoka, 812 Japan

Kawaguchi, S. 1991. Taxonomic notes on the Halymeniaceae (Rhodophyta) from Japan. I. *Halymenia acuminata* (Holmes) J. Agardh. Jpn. J. Phycol. 39: 329–336.

The vegetative and reproductive morphology of *Halymenia acuminata* (Holmes) J. Agardh is described and illustrated from materials collected near the type locality. This species lacks distinctive anticlinal medullary filaments a critical feature of *Halymenia*. The structure of its auxiliary cell ampullae and the developmental pattern of its pericarps are most like *Grateloupia* within the family Halymeniaceae. A mediate discal type of spore germination pattern also differs from that of *Halymenia* and is typical of *Grateloupia*. The resurrection of *Grateloupia acuminata* Holmes is therefore proposed.

Key Index Words: Grateloupia—Grateloupia acuminata—Halymenia—Halymenia acuminata—Halymeniaceae—Rhodophyta—taxonomy.

In 1896, Holmes described *Grateloupia acuminata* based on a specimen collected at Enoshima, on the central Pacific coast of Japan. Subsequently, J. Agardh (1901) transferred the species to *Halymenia*. Since then, the binomial *H. acuminata* has been accepted by Okamura (1908) and other workers (Segawa 1956, Lee and Kang 1986).

Recent authors consider genera within the family Halymeniaceae defined on vegetative features, and *Halymenia* is often characterized by the presence of conspicuous anticlinal filaments in the medulla (Abbott 1967, Kraft 1977, Maggs and Guiry 1982, Gargiulo *et al.* 1986). However, my recent study of a new species of *Grateloupia* (Kawaguchi 1990) has suggested that the anticlinal medullary filaments may not be as strong a generic characteristic as previously thought. The distinction between the two genera could rather alternatively be made on a combination of reproductive features and a spore germination pattern. The ultimate characterization of these genera thus remains to be resolved.

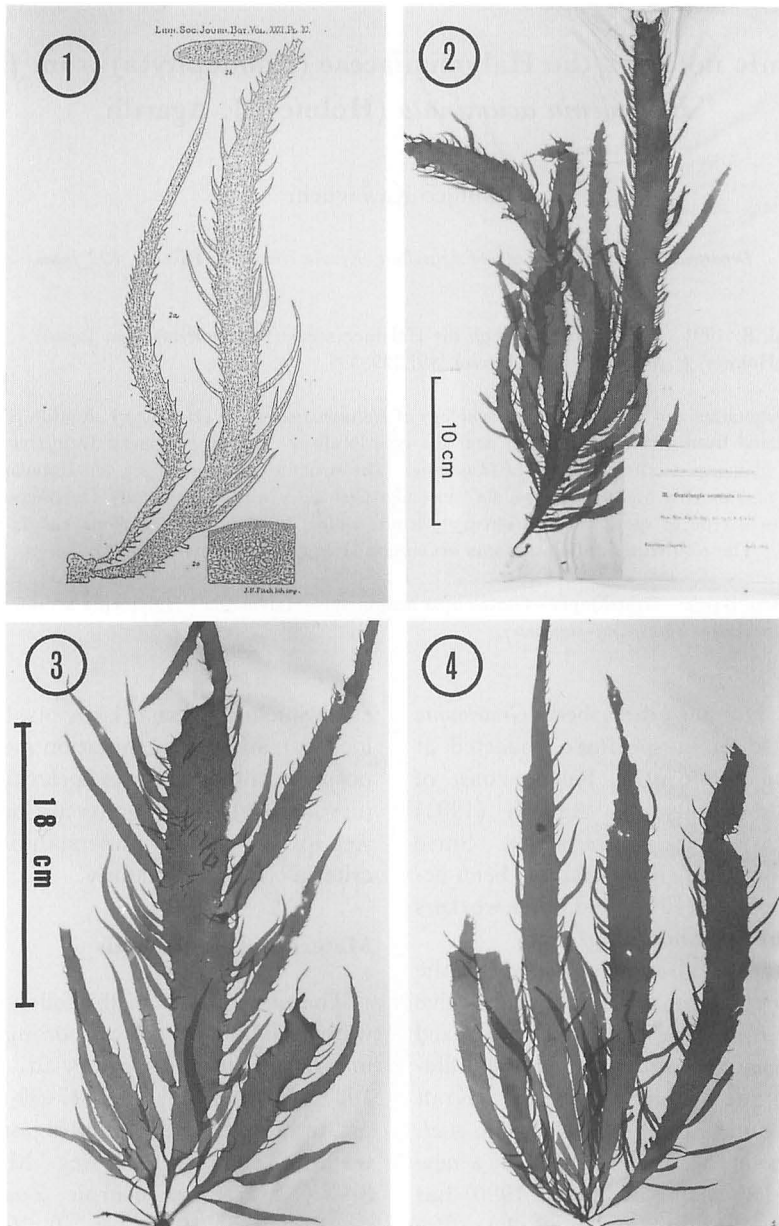
In the present study, vegetative and reproductive details of *Halymenia acuminata* are described principally from specimens collect-

ed at Shichirigahama (1 km east from the type locality), and the germination mode of its carpospores and tetraspores is clarified in laboratory culture. The results are presented as a step toward a better understanding of generic criteria within this family.

Materials and Methods

The materials from the following localities were used for study: tetrasporangial, Shirahama, Wakayama Pref., 30. iii. 1957, 5. iv. 1957, leg. Y. Tsuji, SAP 047499-50; cystocarpic, tetrasporangial, Inamuragasaki, Kanagawa Pref., 26. ii. 1967, leg. M. Yoshizaki, SAP 031317-8; cystocarpic, Zushi, Kanagawa Pref., iii. 1940, leg. T. Tanaka, SAP 021553; cystocarpic, Shichirigahama, Kanagawa Pref., 14. v. 1955, leg. Y. Tsuji, SAP 047504; cystocarpic, tetrasporangial, Shichirigahama, Kanagawa Pref., 2. iv. 1984, leg. S. Kawaguchi, *Kawaguchi* 1037-8 (cast up ashore); cystocarpic, tetrasporangial, Shichirigahama, Kanagawa Pref., 28. iii. 1990, leg. S. Kawaguchi, *Kawaguchi* 1017-9 (cast up ashore).

Although the type specimen (probably in



Figs. 1-4. *Halymenia acuminata* (Holmes) J. Agardh. Fig. 1. Holmes' original illustration. Fig. 2. Okamura's specimen used in *Algae Japonicae Exsiccatae* (no. 31, SAP Okamura herb. as *Grateloupia acuminata* Holmes). Figs. 3, 4. Cystocarpic plants (Kawaguchi 1038, 1037). Scale in Fig. 3 applies also to Fig. 4.

BM) has not been examined, the above specimens agree well with Holmes' illustrations (Fig. 1) and Okamura's specimen collected at the type locality in April 1897 and used in his *Algae Japonicae Exsiccatae* (as *Grateloupia acuminata* in SAP Okamura herb., Fig. 2).

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 and mounted in 50% glycerol-seawater mixture on microscope slides.

Carpores and tetraspores were obtained

from the drift specimens collected by the author at Shichirigahama on April 1 1989 and March 28 1990. Liberated spores were inoculated into small petri dishes (6 cm in diameter) containing full strength Provasoli's Enriched Seawater (PES). Plants were grown at 20°C, 12 : 12 light and dark cycle under white fluorescent light 1500–2000 lux.

Abbreviations of herbaria follow Holmgren *et al.* (1981).

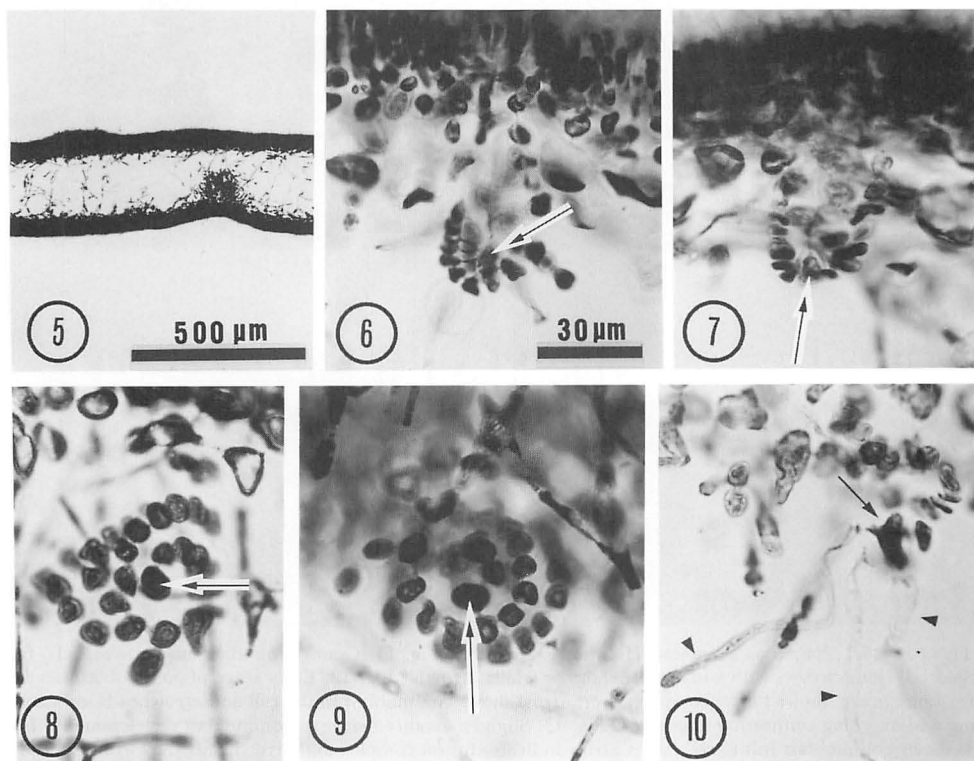
Observations

Vegetative morphology

The upright thalli arise caespitously from a discoid holdfast. The stipe, up to 3 cm long and 2 mm in diameter, gradually expands into a simple or a few times branched, flat, linear-lanceolate blade. Branching may occur also in the stipe. The margin of the blade

is beset with pinnate proliferations that are beset again with pinnate ramuli. Minute proliferations may also arise from the surfaces. Some of the marginal proliferations grow into bladelets with similar appearance to the main blade. The main blade reaches 50 cm high and 4 cm wide (Figs. 2–4). The texture is very gelatinous when young, but becomes somewhat firmer with age. The color is rose red to blood red.

The blade is up to 600 μm thick, composed of a rather thin cortex and lax medulla (Fig. 5). The cortex consists of about 6 cells, with an outer of 2–3 elliptical to rounded cells arranged in anticlinal rows and an inner of 3–4 larger, irregularly-shaped cells often laterally connected by secondary pit-connections. The medulla, about the three-fourths of the blade, consists of sparsely-intermeshed filaments, running in various directions (Fig. 5).

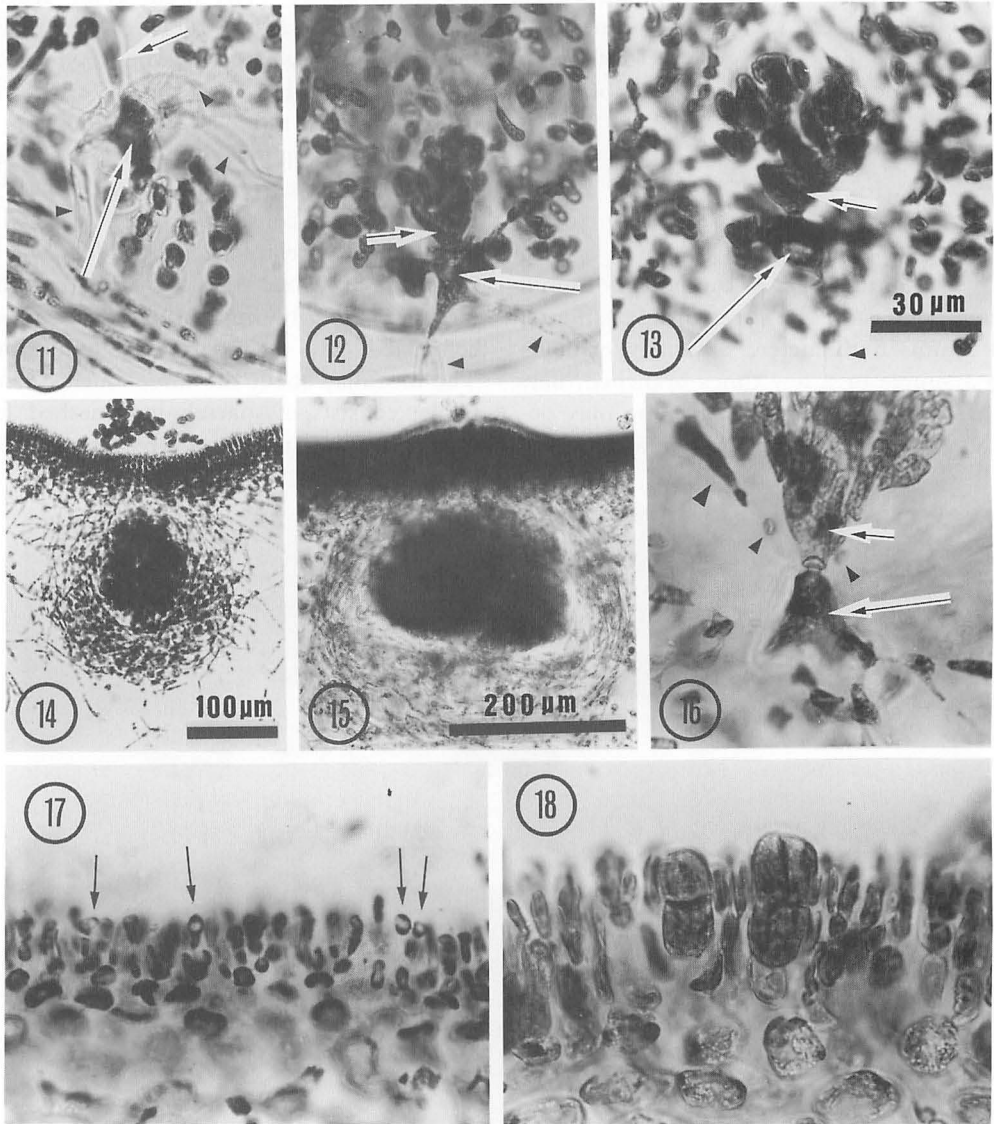


Figs. 5–10. *Halymenia acuminata* (Holmes) J. Agardh. Fig. 5. Transverse section of young branch showing sparse medulla. Figs. 6, 7. Carpoogonial ampullae. Arrow shows carpoogonium with trichogyne. Figs. 8, 9. Auxiliary cell ampullae branched to the second order. Arrow shows auxiliary cell. Fig. 10. Connecting filaments (arrowheads) produced from slightly enlarged cell (arrow). Scale in Fig. 6 applies also to Figs. 7–10.

Reproduction

Carpogonial branches and auxiliary cells are formed in separate flask-shaped ampullae of filaments branched to the second order.

The carpogonial branch is two-celled and positions in the center of the ampulla (Figs. 6, 7). The auxiliary cell ampulla is somewhat larger in size and usually the fifth cell of the



Figs. 11-18. *Halymenia acuminata* (Holmes) J. Agardh. Fig. 11. Connecting filaments (arrowheads) from enlarged cell (long arrow) with withered trichogyne (short arrow). Fig. 12. Early stage of gonimoblast development. Long arrow shows fusion complex, short arrow shows gonimoblast initial cell and arrowheads indicate incoming and outgoing connecting filaments. Fig. 13. Slightly advanced stage of gonimoblast development. Long arrow shows gonimoblast initial cell, short arrow indicates fusion complex and arrowheads show connecting filament. Fig. 14. More advanced stage. Note that pericarpial filaments are well developed. Fig. 15. Mature cystocarp with pericarp. Fig. 16. Basal portion of mature cystocarp. Long arrow shows fusion complex, short arrow indicates elongated gonimoblast initial. Note that ring-like structures (small arrowhead) and foliar radiating processes (large arrowhead) are seen along the initial. Fig. 17. Spermatangia formation. Fig. 18. Tetrasporangia formation. Scale in Fig. 13 applies also to Figs. 11, 12 and 16-18.

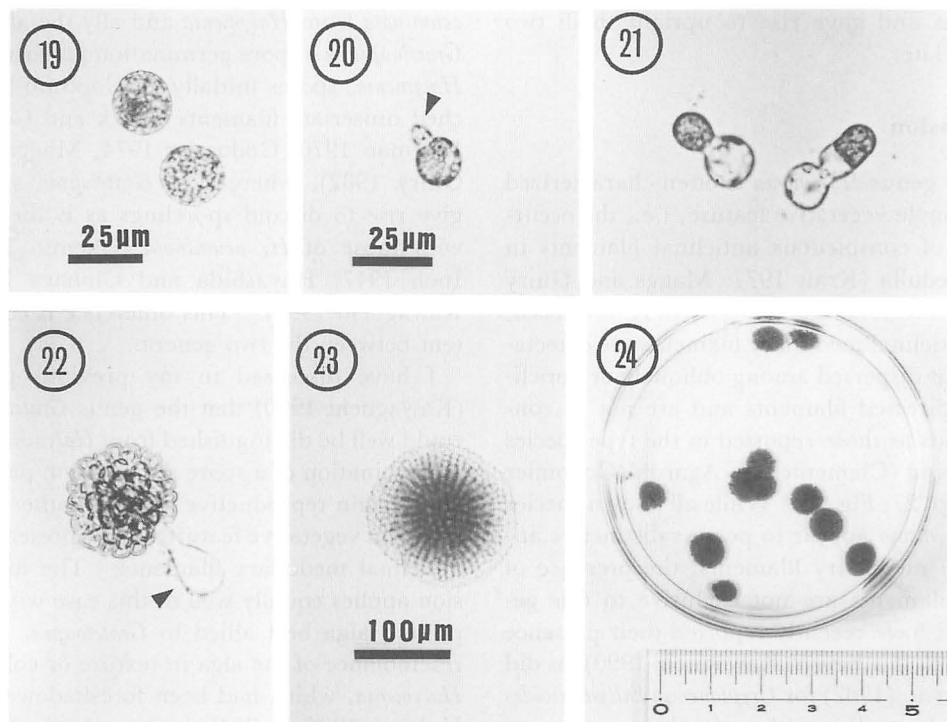
primary filament functions as an auxiliary cell (Figs. 8, 9).

The early stages of fertilization were not traced with certainty. However, several connecting filaments were observed to be cut off from a slightly enlarged, irregularly-shaped cell with a withered trichogyne (Figs. 10, 11). The connecting filament fuses with an auxiliary cell. The filament may terminate here, but often an outgoing filament is produced from the other side of the auxiliary cell (Fig. 12). After fusion a gonimoblast initial cell is cut off from the auxiliary cell toward the surface, and the ampullary cells then begin to produce lateral branchlets. The initial cell successively cuts off several gonimoblast cells and these in turn divide to form carposporangia (Figs. 12, 13). As the gonimoblast develops further, the ampullary filaments and the derivative branchlets become elongated to form a thick involucre

(=pericarp). Neighboring vegetative cells and their derivatives also contribute to the pericarp formation (Fig. 14). The pericarp remains distinct around the fully developed carposporophyte (Fig. 15). The mature cystocarp is spherical in outline, 300-400 μm in diameter, deeply immersed in the thallus and opens by a pore (an ostiole) in the cortex (Fig. 15). In old specimens, foliar radiating processes and small ring-like structures were observed along the side of the elongated gonimoblast initial (Fig. 16).

Male reproductive structures were found scattered on the plants bearing cystocarps. Spermatangia are cut off singly or in pairs from the outermost cortical cells (Fig. 17).

Tetrasporangia are dispersed over the blade as are the sexual organs. Tetrasporangial initials are cut off laterally from the cortical cells in the third layer from the surface. Mature sporangia are broadly ellipsoidal, 15-



Figs. 19-24. *Halymenia acuminata* (Holmes) J. Agardh. Fig. 19. Liberated carpospores. Fig. 20. Germ-tube formation (arrowhead) two days after inoculation. Fig. 21. 6-day-old germling. Note that spore content evacuated into germtube. Fig. 22. 10-day-old sporeling developing into crust with marginal meristem and empty spore wall (arrowhead). Fig. 23. 14-day-old crust. Fig. 24. Two-month-old crusts beginning to develop erect thalli. Scale in Fig. 20 applies also to Figs. 21, 22.

18 μm wide by 33–40 μm long, submerged in the cortex, and cruciately or decussately divided (Fig. 18).

Development of spores

Liberated carpospores are 18–22 μm in diameter (Fig. 19). One or two days after settling, the spore developed a germ tube (Fig. 20) into which the spore content migrated (Fig. 21). A septum was then formed, leaving only the original spore wall behind. Irregular divisions of the germ tube cell gave rise to a multicellular, discoid sporeling (Fig. 22). The disc grew by divisions of the marginal meristem and after one week reached 50 μm in diameter. In two weeks, the disc reached 100 μm in diameter (Fig. 23), and in five months, 3–5 mm (Fig. 24). Upright thalli arose from near the center of the disc after two months. Tetraspores developed in a similar manner to carpospores. The developed discs reached 2 mm in diameter in two months and gave rise to upright thalli two weeks later.

Discussion

The genus *Halymenia* is often characterized by a single vegetative feature, i.e., the occurrence of conspicuous anticlinal filaments in the medulla (Kraft 1977, Maggs and Guiry 1982, Gargiulo, *et al.* 1986). In *H. acuminata*, the anticlinal medullary filaments are detectable, but dispersed among obliquely or periclinally directed filaments and are not as conspicuous as those reported in the type species *H. floresia* (Clemente) C. Agardh (Codomier 1974, p. 27, Fig. 4). While all known species of *Halymenia* appear to possess distinctive anticlinal medullary filaments, the presence of such filaments are not exclusive to this genus. I have recently reported their presence in *Grateloupia kurogii* (Kawaguchi 1990), as did Scott *et al.* (1982) for *Cryptonemia kallymenioides* from Australia, although they were not present as regularly nor predominantly as is usual in the genus *Halymenia*.

Chiang (1970) proposed that the morphology of auxiliary cell ampullae is generically di-

agnostic within this family. The ampulla of *Halymenia acuminata* is sparingly branched up to the second order and conical in outline. This type of ampulla corresponds well with the *Grateloupia*-type in Chiang's scheme, and in contrast to the *Halymenia*-type which is profusely branched to the fourth order and tends to be wide across the top (Chiang 1970). Although Kraft (1977) and Guiry and Maggs (1982) have shown that the ampullar types are not invariably a consistent generic characteristic, the present alga is allied more to the genus *Grateloupia* than to *Halymenia* in this regard.

The similarity of this alga to *Grateloupia* is also found in its comparatively thick pericarp constructed not only of ampullary filaments but also of neighboring vegetative cells. This differs to *Halymenia* where the pericarp is reported to be derived only from ampullary filaments (Balakrishnan 1961, Chiang 1970, Maggs and Guiry 1982, Gargiulo *et al.* 1986).

The most decisive feature to separate *H. acuminata* from *Halymenia* and ally the alga to *Grateloupia* is a spore germination pattern. In *Halymenia*, spores initially develop into branched uniseriate filaments (Hoek and Cortel-Breeman 1970, Codomier 1974, Maggs and Guiry 1982), whereas in *Grateloupia* spores give rise to discoid sporelings as is the case with those of *H. acuminata* (Chemin 1937, Inoh 1947, Hayashida and Chihara 1967, Kawaguchi 1990). This difference is consistent between the two genera.

I have discussed in my previous paper (Kawaguchi 1990) that the genus *Grateloupia* could well be distinguished from *Halymenia* on a combination of a spore germination pattern and certain reproductive features rather than solely on vegetative features as the presence of anticlinal medullary filaments. The discussion applies equally well in this case with the present alga best allied to *Grateloupia*. The resemblance of the alga in texture or color to *Halymenia*, which had been foreshadowed by Holmes (1896, p. 254), is considered superficial. *Grateloupia turuturu* Yamada is a good example that supports this consideration. *G. turuturu* has lubricous texture and bright red color, but its reproductive features and spore

germination pattern are typical of *Grateloupia* (Kawabata 1962, Hayashida and Chihara 1967).

On these grounds, I conclude that *H. acuminata* does not belong in the genus *Halymenia* but in *Grateloupia*. I therefore propose the resurrection of the following binomial:

Grateloupia acuminata Holmes, Linn. Soc. J. Bot. 31: 254, fig. 2a-c. 1896.

Synonym: *Halymenia acuminata* (Holmes) J. Agardh, Sp. Alg. III(4): 130-131. 1901.

Acknowledgments

This study was undertaken mainly in the laboratory of Department of Botany, Faculty of Science, Hokkaido University. I wish to express my special thanks to Professor T. Yoshida, Hokkaido University, for his continual support and valuable comments on the manuscript. I also wish to thank Professor Y. M. Chiang, Taiwan National University, for critically reading the manuscript and instructive suggestions. My thanks are extended to Mr. J. A. Lewis, The University of Melbourne, for his assistance in improving the manuscript, to Mr. K. Kogame, Hokkaido University, for providing me the photograph of Okamura's specimen and finally to the anonymous reviewers for critical comments on the manuscript.

References

- Abbott, I. A. 1967. Studies in some red algae of the Pacific coast. I. Cryptonemiaceae. J. Phycol. 3: 139-149.
- Agardh, J. G. 1901. Species genera et ordines algarum, ... III (4). Lund.
- Balakrishnan, M. S. 1961. Studies on Indian Cryptonemiales. III. *Halymenia* C. A. Ag. J. Madras Univ. 31B: 183-217.
- Chemin, E. 1937. Le développement des spores chez les Rhodophycées. Rev. Gen. Bot. 49: 205-234, 300-327, 353-374, 424-448, 478-536.
- Chiang, Y. M. 1970. Morphological studies of red algae of the family Cryptonemiaceae. Univ. Calif. Pubs. Bot. 58: 1-95.
- Codomier, L. 1974. Recherches sur la structure et le développement des *Halymenia* C. Agardh (Rhodophycées, Cryptonémiales) des côtes de France et de la Méditerranée. Vie Millieu 24A: 1-24.
- Gargiulo, G. M., De Masi, F. and Tripodi, G. 1986. Structure and reproduction of *Halymenia asymmetrica* sp. nov. (Rhodophyta) from the Mediterranean sea. Phycologia 25: 144-151.
- Guiry, M. D. and Maggs, C. A. 1982. The morphology and life history of *Dermocorynus montagnei* Crouan frat. (Halymeniaceae, Rhodophyta) from Ireland. Br. Phycol. J. 17: 215-228.
- Hayashida, F. and Chihara, M. 1967. Studies on the germination of spores in the members of the Cryptonemiaceae. II. Germination of carpospores in certain species of *Grateloupia*. Bull. Nat. Sci. Mus. Tokyo 19: 19-30.
- Hoek, C. van den and Cortel-Breeman, A. M. 1970. Life-history studies on Rhodophyceae. II. *Halymenia floresia* (Clem.) Ag. Acta Bot. Neerl. 19: 341-362.
- Holmes, E. M. 1896. New marine algae from Japan. Linn. Soc. J. Bot. 31: 248-260.
- Holmgren, P. K., Keuken, W. and Schofield, E. K. 1981. Index herbariorum. Part 1. The herbaria of the world. Ed. 7. Regnum Veg. 106.
- Inoh, S. 1947. Kaiso no hassei (Development of marine algae) (in Japanese). Hokuryukan, Tokyo.
- Kawabata, S. 1962. A contribution to the systematic study of Grateloupiaceae from Japan (1). J. of Hokkaido Gakugei Univ. 13: 22-51.
- Kawaguchi, S. 1990. *Grateloupia kurogii*, a new species of the Halymeniaceae (Rhodophyta) from Japan. Jpn. J. Phycol. 38: 135-146.
- Kraft, G. T. 1977. The morphology of *Grateloupia intestinalis* from New Zealand, with some thoughts on generic criteria within the family Cryptonemiaceae (Rhodophyta). Phycologia 16: 43-51.
- Lee, I. K. and Kang, J. W. 1986. A check list of marine algae in Korea. Korean J. Phycol. 1: 311-325.
- Maggs, C. A. and Guiry, M. D. 1982. Morphology, phenology and photoperiodism in *Halymenia latifolia* Kütz. (Rhodophyta) from Ireland. Botanica Marina 25: 589-599.
- Okamura, K. 1908. Icones of Japanese Algae, Vol. I (7). Tokyo.
- Scott, F. J., Wetherbee, R. and Kraft, G. T. 1982. The morphology and development of some prominently stalked southern Australian Halymeniaceae (Cryptonemiales, Rhodophyta). I. *Cryptonemia kallymenioides* (Harvey) Kraft comb. nov. and *C. undulata* Sonder. J. Phycol. 18: 245-257.
- Segawa, S. 1956. Colored illustrations of the seaweeds of Japan (in Japanese). Hoikusha, Osaka.

川口栄男：日本産紅藻ムカデノリ科に関する分類ノート

I. *Halymenia acuminata* (Holmes) J. Agardh.

Holmes (1896) が江ノ島から *Grateloupia acuminata* の名で記載し、J. Agardh (1901) によってイソノハナ属 *Halymenia* に移されたオオムカデノリ *H. acuminata* の栄養体、生殖器官を精査した。本藻にはイソノハナ属に特徴的とされる垂直な髄糸が顕著には認められず、その助細胞 ampulla, 嚢果を包む pericarp の構造はむしろムカデノリ属 *Grateloupia* に最も近い特徴を示した。さらに、間接盤状型の胞子発芽様式はこれまでイソノハナ属で報告された様式とは明らかに異なり、ムカデノリ属に典型的である。従って、本藻はイソノハナ属ではなくムカデノリ属の種として扱うのが妥当であると結論した。元の名である *Grateloupia acuminata* Holmes を復活することを提案した。(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)