

Michio MASUDA* & Masataka OHTA** : **The life history
of *Rhodophysema georgii* Batters
(Rhodophyta, Cryptonemiales)**

増田道夫*・太田雅隆** : 紅藻モツキフトリベニの生活史

Recent advances in culture techniques of algae have made it possible to trace a complete sequence of morphological phases in algal life histories. Recent studies of several members of the Cryptonemiales have demonstrated the existence of two types of life history in this order which differ from each other in that the gametangial and tetrasporangial phases are morphologically similar or dissimilar (Dixon *et al.*, 1972; Umezaki, 1972; Masuda, 1973b, 1974). It has been suggested that the crustose species for which only the tetrasporophyte had been detected might represent the tetrasporophytic phase of those algae for which only the gametophytes had been reported (Dixon, 1963). This suggestion has proved true in several species of the Cryptonemiales and the Gigartinales, in which the macroscopic gametophyte alternates with the small crustose tetrasporophyte (Dixon, *et al.*, 1972; South *et al.*, 1972; West, 1972). However, the life history of some crustose algae in Cryptonemiales, such as *Rhododiscus*, *Contarinia*, and marine species of *Hildenbrandia*, is still unknown. In these genera, only the tetrasporophytic phase is detected in the field. The situation regarding the life history of *Rhodophysema*, a genus of the Cryptonemiales with minute thalli, may be more complex.

Rhodophysema has been recorded from various localities in the North Atlantic, Arctic and North Pacific Oceans by many phycologists. It comprises three species: *Rhodophysema georgii* Batters, *R. elegans* (Crouan frat. ex J. Agardh) Dixon and *R. minus* Hollenberg et Abbott. The latter two species are apparently crustose, whereas the first one includes a globose form, which is characterized by the enlargement of the erect filament cells,

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in addition to a crustose form. The tetrasporophytic phase of these species has been frequently encountered in the field, but the gametophytic phases have not been reported except in *R. elegans*. In the last mentioned species from Greenland, the male gametangial plant has been described (Rosenvinge, 1910). The female gametangial plants of *Rhodophysema* have not been reported. This paper reports our observations on the life history of *Rhodophysema georgii* from Hokkaido, Japan, carried out in the laboratory as well as in the field.

Materials and Methods The specimens used in this study were collected in Oshoro Bay and at Rausu in the Shiretoko Peninsula, Hokkaido, from 1973 to 1974. The material for culture experiments was collected in Oshoro Bay on April 21, 1974, and cultured in the laboratory at the Institute of Algological Research, Muroran, according to the same methods as used for *Neodilsea crispata* (Masuda, 1973a). Unialgal cultures established from isolated tetraspores were maintained in freezer-incubators at 10 C and 14 C, both in 14-hr photoperiods. Voucher specimens and slides are preserved in the above-mentioned institute and also in the Herbarium of Faculty of Science, Hokkaido University, Sapporo (SAP).

Results *Observation on the plants collected in the field:* Plants collected agree well with the description and illustration given by Tokida (1934). The plants grow epiphytically on other red algae such as *Gymnogongrus flabelliformis*, *Chondrus yendoi*, *C. pinnulatus*, *Rhodoglossum japonicum* and *Laurencia nipponica* (Fig. 1, A). The tetrasporangial plants of *Rhodophysema georgii* were found abundantly on the hosts from April to June in Oshoro Bay where monthly collections had been undertaken from April to September, 1973, by one of us, Ohta. The tetrasporangia are borne on the terminal ends of the erect filaments and are surrounded by paraphyses (Fig. 1, D). The spores immediately after liberation are globular and light red in color, measuring 18.8–25.0 μ m in diameter (Fig. 2, A–B). The spermatangial plants were also found growing on the same host species. They are similar to the tetrasporangial plants in vegetative structure. The spermatangia are borne on spermatangial mother-cells formed from an outermost cell of the thallus, and they are not accompanied by paraphyses (Fig. 1, C) as in *Rhodophysema elegans* (Rosenvinge, 1910). The spermatangial mother-cells are pale yellow in color and easily distinguishable from the

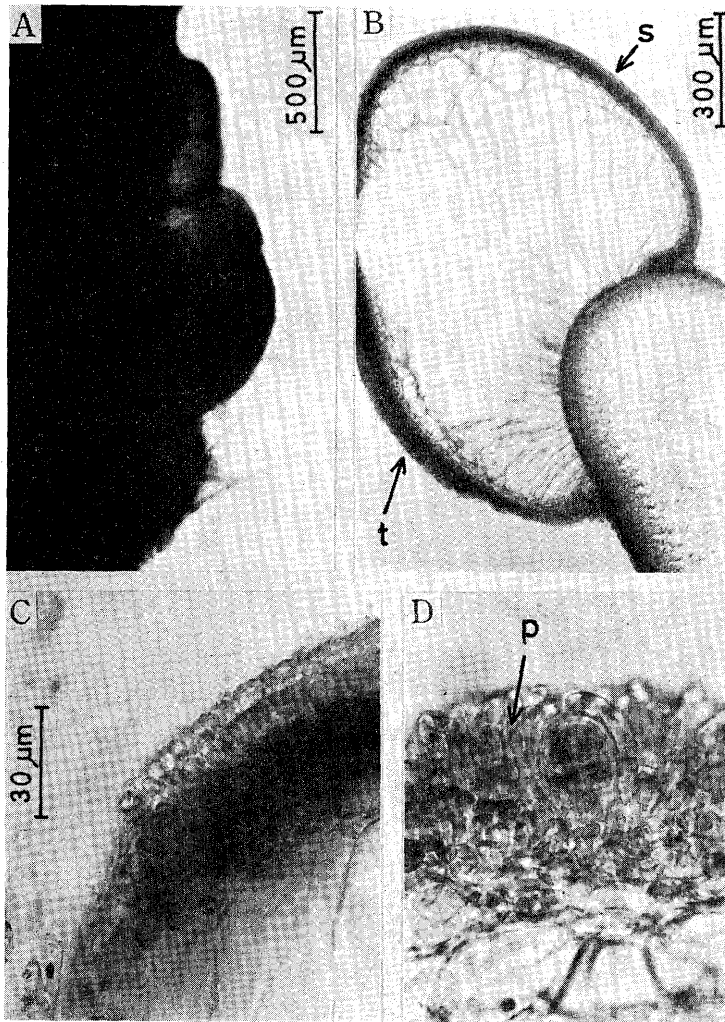


Fig. 1. *Rhodophysemia georgii* collected in the field. A. Habit of a fertile plant growing on *Gymnogongrus flabelliformis*. B. Longitudinal section of a plant bearing both spermatangia (s) and tetrasporangia (t). C. Longitudinal section of a mature spermatangial sorus. D. Longitudinal section of a mature tetrasporangial sorus, showing a tetrasporangium and paraphyses (p). (Photographed from living material). Use scale in A for A; scale in B for B; scale in C for C-D.

Table 1. Relative abundance of the three kinds of fertile plants and of the sterile plants in *Rhodophysemma georgii* from Oshoro Bay, examined from April to June, 1973.

Month	Total number of plants examined	Spermatangial plants	Tetrasporangial plants	Plants bearing both spermatangia & tetrasporangia	Sterile plants
April	56	26.8%	55.3%	12.5%	5.4%
May	88	31.8	48.9	14.8	4.5
June	183	26.2	53.6	20.2	—

sterile cells. Liberated spermatia are of a globular shape and measure 5.5–7.5 μ m in diameter (Fig. 2, B). The spermatia are colorless and their chloroplasts are not obvious under the light microscope. The colorless aspect and small size by comparison with tetraspores are similar to the situation in other Florideophycidean algae. Germination of spermatia was attempted but was unsuccessful, so they cannot be interpreted as monospores. Sometimes both the spermatangia and tetrasporangia are found on the same plant, forming their respective sori (Fig. 1, B). No differences were observed in these sori by comparison with those of pure spermatangial or pure tetrasporangial plants. Table 1 shows the relative abundance of the three kinds of fertile plants and of the sterile plants in our specimens from Oshoro Bay from April to June, 1973 (Apparently young small plants were eliminated from this examination). It is known from the Table that the percentage of plants bearing both spermatangia and tetrasporangia is fairly high. The three kinds of fertile plants were also met with among the specimens from Shiretoko. Female gametangial plants, however, have not been detected among a considerable number of collections examined.

Culture experiments: Tetraspores liberated from a pure tetrasporophyte were used for culture experiments. The mode of tetraspore germination was of the immediate discal type as shown in Fig. 2, C–G. The tetraspore divided into two cells by a plane running at right angles to the glass surface to which the spore had stuck with mucilage within one day after liberation (Fig. 2, C). Successive cell divisions resulted in the

formation of a monostromatic disc (Fig. 2, D-E). The disc grew concentrically by the marginal meristem which was paler in color than the central portion (Fig. 2, F-G). Concurrently with this marginal growth, the cells at the central portion of the disc divided by a plane parallel to the substratum and this portion became distromatic. Some of the cultured discs became furnished with unicellular colorless hairs issued from the surface cells (Fig. 2, G). Further cell divisions parallel to the substratum took place at the central portion which became several cell layers thick. Divisions then took place also in cells of the periphery. This produced

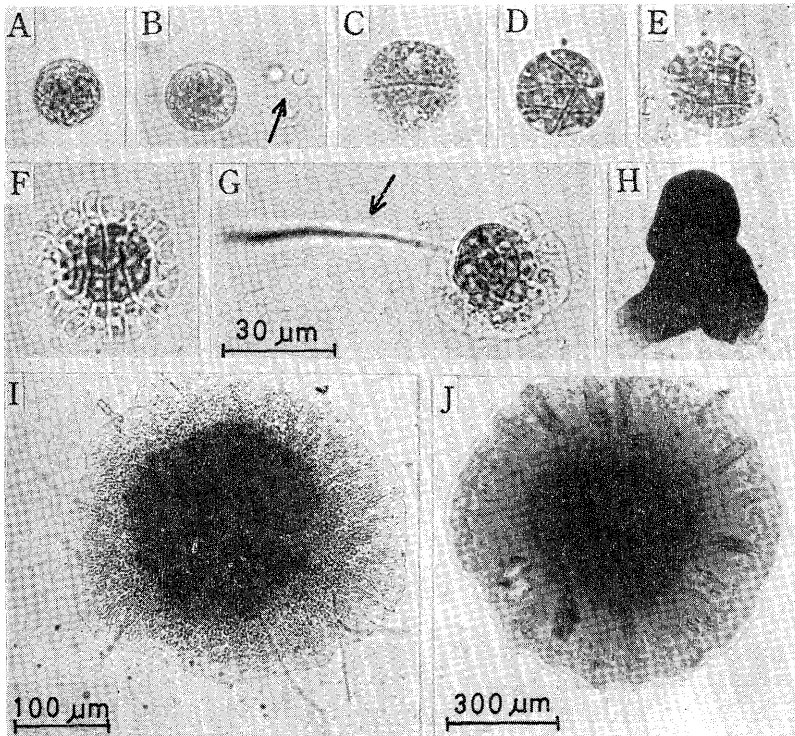


Fig. 2. *Rhodophysema georgii*. A. Tetraspore just after liberation from a plant collected in the field. B. Tetraspore and spermatia (arrow) from a plant collected in the field. C-J. Tetraspore germlings grown at 14 C (D, G, & H) and 10 C (C, E-F, & I-J), both in 14-hr photoperiods: C-D, one-day old; E, three-day old; F-G, five-day old, with a colorless hair (arrow); H-J, one-month old (H, side view; I & J, surface view). (Photographed from living material). Use scale in G for A-G; scale in I for I; scale in J for H & J.

discs identical with young plants found in the field in being polystromatic except at the margin. The discoid plants became larger and the following three types of thalli were produced after one month: (1) the pulvinate disc (Fig. 2, J), (2) the globose thallus (Fig. 2, H), and (3) the thallus of a form intermediate between the former two types (Fig. 2, I). About this time several plants grown at 10 C and 14 C liberated spermatia which were formed in the same way as in plants collected in the field (Fig. 3, A-B). No germination of the spermatia was observed. Two months after the start of the culture, the plants, which had either liberated spermatia or not, produced a considerable number of tetrasporangia at 10 C and 14 C (Fig. 3, C). The tetrasporangia were borne on the terminal cell of the erect filaments and provided with paraphyses as in plants collected in the field (Fig. 3, D). The tetraspores were liberated from the plants grown at 10 C

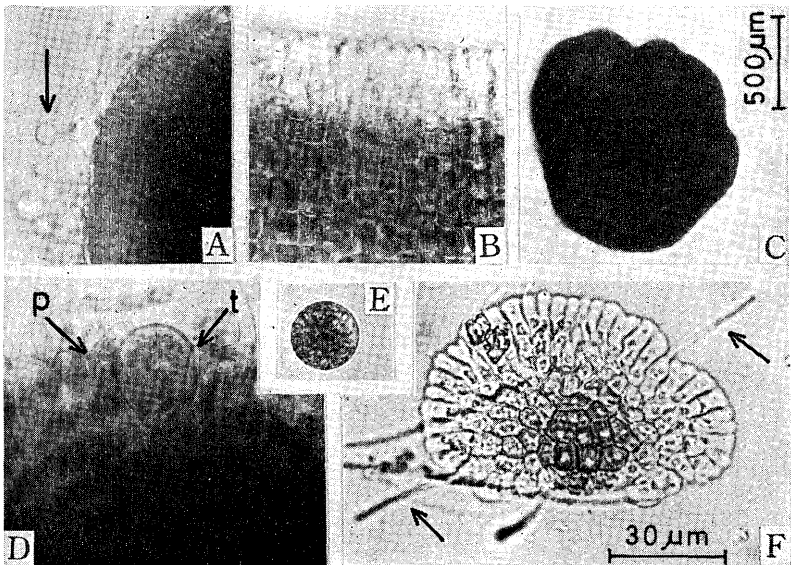


Fig. 3. *Rhodophysema georgii* cultured from tetraspores and grown at 10 C in a 14-hr photo-period. A. Portion of a mature spermatangial plant (one-month old) in surface view, showing a spermatium (arrow). B. Longitudinal section of the plant shown in A. C. Mature tetrasporangial plant (two-month old) in surface view. D. Cross section of the plant shown in C, showing a young tetrasporangium (t) and paraphyses (p). E. Tetraspore liberated from a cultured plant. F. Young tetraspore germling derived from a cultured plant, showing colorless hairs (arrows). (Photographed from living material). Use scale in C for C; scale in F for A-B, & D-F.

and germinated in the same way as those of the initial plant (Fig. 3, E-F). However, when cultured at 14 C, the tetraspore liberation was not observed and the tetrasporangia degenerated. The female gametangial plants were not detected at all in the present cultures, although the cultured plants all attained reproductive maturity. When 55 fertile individuals of two-month old cultured plants were examined, the number of plants bearing tetrasporangia, spermatangia, and both tetrasporangia and spermatangia, were in 3:1.5:1 ratio.

Discussion The majority of the Florideophycidae may possess a tri-phasic life history consisting of a sequence of gametophytic, carposporophytic and tetrasporophytic phases in which the first phase is haploid and the second and third phases are diploid. Several deviations from this pattern have been demonstrated with direct evidence as to the sequence of cytological or morphological phases in the life histories (Dixon, 1970). They are too extensive and complex to be considered, here. West and Norris (1966) cultured eleven species of the Florideophycidae obtained from Washington and California, and observed several variations of life histories among them. They reported that the tetraspore germlings in an unidentified species of *Callithamnion* developed solely into male gametophytes and tetrasporophytes in a ratio slightly greater than 1:3, and that no female gametophyte was found, and that the tetraspores of subsequent generations exhibited the same phenomenon.

The life history of *Rhodophysema georgii* described above is similar to that of the just-mentioned *Callithamnion* sp. The full-grown plants of *R. georgii* collected in the field bore spermatangia alone, or tetrasporangia alone, or spermatangia and tetrasporangia jointly, without exception. The possibility that this alga could possess a female gametophyte differing morphologically from the tetrasporophyte and male gametophyte seems to be precluded by the results of the present culture experiments. It is certain that this alga is devoid of a female gametophyte and the spermatia are functionally useless. Thus, this alga has a life history with only the tetrasporophyte and male gametophyte which are morphologically identical.

The occurrence of both tetrasporangia and gametangia on the same individual has been reported in a number of Florideophycidean algae in culture as well as in the field (Knaggs, 1969). This phenomenon has been

recorded rather infrequently in the members of the Cryptonemiales, but more commonly in those of the Ceramiales. Here we add a new example to Knaggs's list (1969). Relatively frequent occurrence of the plants bearing both tetrasporangia and spermatangia in *Rhodophysema georgii* suggests that this phenomenon is not to be interpreted as merely abnormal. No reliable cytological data have been obtained yet to know whether the nuclear division in the tetrasporangium of this alga is meiotic or apomeiotic. Any factors responsible for the absence of its female gametophyte are still unknown.

The present investigation revealed that the Japanese *Rhodophysema georgii* is an independent taxon, not representing a phase in the life history of another alga. However, the taxonomic position of the genus *Rhodophysema* is uncertain because of the absence of the female gametophyte. Although it had customarily been placed in the family Squamariaceae (Kylin, 1956), Denizot (1968) excluded it from the Squamariaceae, replacing this family name by the Peyssoneliaceae, and treated it as one of the entities of uncertain position together with *Coriophyllum*, *Erythrodermis*, *Ethelia*, *Rhododiscus*, etc. *Rhodophysema* differs from *Peyssonelia* in the absence of rhizoidal filaments and in the pattern of spermatangial formation, but they are allied to each other in the mode of thallus development and in the nature of tetrasporangia and paraphyses (Kylin, 1956). *Rhodophysema* is considered to be a member of the Cryptonemiales, and at least a genus holding a close relation to the Peyssoneliaceae.

The alga investigated in this study was first described as *Rhododermis georgii* (Batters) Collins var. *fucicola* Tokida on the basis of material collected in Oshoro Bay, Hokkaido, by Tokida (1934). Dixon (1964) retained that variety name on account of the absence of his personal data when he revived the genus name *Rhodophysema* for *Rhododermis*, citing it incorrectly as a variety of *Rhodophysema elegans*. Later, Denizot (1968) did not recognize the Tokida's variety as a distinct taxon but merged it into *Rhodophysema georgii* Batters. However, the Japanese plant does not fully agree with the typical *R. georgii* in several respects (Tokida, 1934, 1954). The taxonomic details of this alga will be reported together with other taxa of *Rhodophysema* in the near future by one of us, Masuda.

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Literature cited

- Denizot, M. 1968. Les Algues Floridees encrustantes (à l'exclusion des Corallinacées). Thesis, Paris. Dixon, P.S. 1963. The Rhodophyta: some aspects of their biology. *Oceanogr. Mar. Biol. Ann. Rev.* 1: 177-196. — 1964. Taxonomic and nomenclatural notes on the Florideae. IV. *Bot. Notiser.* 117: 56-78. — 1970. The Rhodophyta: some aspects of their biology. II. *Oceanogr. Mar. Biol. Ann. Rev.* 8: 307-352. —, S.N. Murray, W.N. Richardson and J.L. Scott. 1972. Life history studies in genera of the Cryptonemiales. *Soc. bot. Fr. Mémoires* 1972: 323-332. Knaggs, F.W. 1969. A review of Florideophycidean life histories and of culture techniques employed in their investigation. *Nova Hedwigia* 18: 293-330. Kylin, H. 1956. Die Gattungen der Rhodophyceen. Gleerup. Lund. Masuda, M. 1973a. *Neodilsea crispata*, a new species of red algae (Cryptonemiales, Rhodophyta). *Journ. Jap. Bot.* 48: 36-48. — 1973b. Taxonomy and life history of *Neodilsea integra* (Kjellm.) A. Zinova var. *longissima* var. nov. (Rhodophyta, Cryptonemiales). *Bul. Natn. Sci. Mus. Tokyo.* 16: 459-472. — 1974. Taxonomic notes on *Neodilsea tenuipes* Yamada et Mikami. *Bull. Jap. Soc. Phycol.* 22: 63-68. Rosenvinge, L.K. 1910. On the marine algae from north-east Greenland. *Medd. om Grønland.* 43: 93-133. South, G.R., R.G. Hooper and L.M. Irvine. 1972. The life history of *Turnerella pennyi* (Harv.) Schmitz. *Br. phycol. J.* 7: 221-233. Tokida, J. 1934. Phycological observation I. *Trans. Sapporo Nat. Hist. Soc.* 13: 196-202. — 1954. The marine algae of Southern Saghalien. *Mem. Fac. Fish., Hokkaido Univ.* 2: 1-264. Umezaki, I. 1972. The life history of *Hyalosiphonia caespitosa* (Dumontiaceae, Rhodophyta). *Journ. Jap. Bot.* 47: 278-288. West, J.A. 1972. The life history of *Petrocelis franciscana*. *Br. phycol. J.* 7: 299-308. — and R.E. Norris. 1966. Unusual phenomena in the life histories of Florideae in culture. *J. Phycol.* 2: 54-57.

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四分孢子体だけが報告されていた紅藻モツキフトリベニ (*Rhodophysemia georgii*) の生活史を培養実験と天然産の個体の観察により調査した。天然には四分孢子体のほかにそれと同形の雄性配偶体及び四分孢子嚢と精子嚢を同時に形成する個体が出現するが、雌性配偶体はみられない。培養実験において四分孢子体より放出された孢子の発芽体は、約 2 ヶ月後に全て成熟し、四分孢子嚢と精子嚢を別々に、また同時にそれらを形成する 3 種類の個体の出現数が 3:1.5:1 の割合であった。以上の結果から、本種的生活史には四分孢子体及びそれと同形の雄性配偶体は存在するが、雌性配偶体は欠けていることが明らかとなった。

□吉村 庸：原色日本地衣植物図鑑 A5 版 16+349 頁，カラー図版 48。保育社 (1974. 8)。¥3,400。地衣類では初めての本格的図鑑の出現である。植物群のなかで、専門外の人々にもっとも親しみにくく、わかりにくいこのグループを身近かなものと感じさせる功は大きい。主な属では種の検索表があり、各種の特徴も要領よくまとめてあり、日本産の大形地衣類はともかく、中・小形とくに固着地衣の研究がほとんど進んでいない現状で、ここまでまとめあげられた著者の労をねぎらいたい。カラー図版も一部のを除いてよくできているが、白黒の拡大図には倍率が示してあるのに、カラー拡大図に倍率が明示していないのは惜しい。日本の地衣類を扱う専門家にも、アマチュアにも、本書は当分の間スタンダードとして利用されることになると思うので、あえて 2・3 の苦言を呈する。本書に登載された地衣類全種に和名がつけられていて、新しく和名のつけられたものも多い。和名が必要か否かについては意見のわかれるところだが、著者自らが地衣類にこれほど徹底して和名をつけることが必要と考えたのであろうか。また、かりにそうとしても、和名のつけ方にもうひと工夫ほしかった。かな書きの植物用語や地衣成分の名称のいくつかに首をかしげるものがある。とくに地衣成分の場合には、ドイツ語に書き替えたものの発音からかな書きにする従来の習慣を守る方がよかった。学名の選択については、新しい研究によるものをできる限り採用した著者の努力は認めるが、図鑑という本書の性格と、2~3 年もすれば相当数学名を書きかえねばならぬ地衣学の現況から考えると、もっと定着した学名を使ってもよかったのではなからうか。かなりの数の誤植の訂正と併せて、版を重ねるとともにさらに立派な図鑑になることを祈る。(黒川 道)