A taxonomic study of *Rhodophysea elegans* (Rhodophyta) from Japan

Michio Masuda* and Masataka Ohta**

增田道夫・太田雅隆：紅藻 *Rhodophysea elegans* の分類学的研究

*Rhodophysea elegans* (Crouan et Crouan ex J. Ag.) Dixon has been recorded from various localities in temperate to cold zones of the Northern Hemisphere (Kylin, 1956). Ganesan and West (1975) reported that the life history of the Californian population involves a simple recycling of the tetraptrophenytic phase without intervention of gametangial plants. This was corroborated later by South and Whittick (1976) in the Newfoundland population and by Fletcher (1977) in the British population. However, spermatangial plants have been reported from Greenland by Rosenvinge (1910), from the northeast coast of North America by Taylor (1957) and from Attu Island in the Aleutian Archipelago by Masuda (1978). These reports suggest that different populations with two different life history patterns may exist in this species.

In order to clarify this problem we had conducted laboratory culture experiments. Furthermore, the variability of the number of cell layers of the crust and the cell form as observed in section, both of which had been used for criteria of infraspecific entities of this species by several investigators (Batters, 1891; Newton, 1931; Dixon, 1964; Denizot, 1968; Hollenberg and Abbott, 1966), was analyzed, compared field materials with cultured plants.

**Materials and Methods**

The materials examined were collected at the following localities along the Pacific coast of Hokkaido in Japan from 1974 to 1979 (Fig. 1): Erimo (v-27, 1975, ⊕; vi-11, 1975, ⊖, including culture material; viii-26, 1976, ⊕); Muroran (iv-24, 1974, ⊕; vi-24, 1974, ⊖, including culture material; viii-20, 1974, ⊖; x-13, 1974, ⊕ & ⊖, including culture material; xii-12, 1974, ⊕ & ⊖; ii-28, 1975, ⊕ & ⊖, ii-2, 1976, ⊖, including culture material); Shirikishinai (vii-30, 1977, ⊖, including culture material); Hakodate (iv-28, 1979, ⊕ & ⊖). Most of the specimens were used for microscopic observations.

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in the living state. A portion of them was preserved in 10% formalin in seawater.

Unialgal cultures were established as follows. Fertile crusts were cleaned and washed in sterile seawater. Liberated tetraspores were rinsed quickly in PES culture medium (PROVASOLI, 1968) using finely-drawn glass capillary pipettes under a dissecting microscope and then inoculated into several drops of culture medium on slide glasses placed on the bottom of Petri dishes (9 cm × 2 cm). The Petri dishes were then placed under culture conditions tested. The tetraspores attached to slide glasses after 1 day from inoculation and then about 50 ml of medium were introduced into the Petri dishes. The slides were transferred to culture vessels (6.5 cm × 8.0 cm) containing 200 ml of medium one week later. The cultures were placed in freezer-incubators at 10°C, 16:8 (light-dark cycle) and 15°C, 16:8. Furthermore, culture experiments with the Muroran isolate were partly conducted at the laboratory of the Institute of Algological Research, Hokkaido University, Muroran, from June 1974 to January 1975. These results are indicated in the text as follows: 10°C, 14:10 and 14°C, 14:10. Lighting in all regimes was supplied by cool-white fluorescent lamps (2500–3500 lux). The culture medium was changed monthly.

Voucher specimens examined are deposited in the Herbarium of Faculty of Science, Hokkaido University, Sapporo (SAP 032133-032144).

**Observations and Discussion**

**Morphology**

*Rhodophysema elegans* grows on rocks, pebbles or pieces of glasses in sheltered places in the middle to lower intertidal zone at localities examined. Several plants combine usually to form a crust which reaches up to 2–3 cm in diameter and it is not easy to define the exact limits of a single plant. The crust is deep red in color and resembles that of *Hildenbrandia prototypus*. It consists of a monostromatic hypothallus, which is composed of radiating filaments (Fig. 7), and a polystromatic perithallus which is composed of tightly packed erect filaments (Fig. 2). The erect filaments are usually simple or sometimes dichotomous (Fig. 2). Lateral fusions between cells of adjacent hypothallus filaments are frequently found (Fig. 7, G, H). More than two cells sometimes fuse together (Fig. 7, H) as reported by ROSENVINGE (1917). Lateral fusions of erect filament cells are rare (Fig. 2, A, I). Unicellular colorless hairs develop from the terminal cells of the erect filaments and are sporadically present in the vegetative portion (Fig. 2, E) or

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Fig. 1. Map of Hokkaido, showing four localities where materials of *Rhodophysema elegans* were collected.
Fig. 2. Tangential sections of *R. elegans*. A–F. Field-collected plants of the Muroran population: A, young sorus, showing tetrasporangium initials (tsi) and paraphyses; B, lower portion of a crust; C, mature sorus; D, secondary tetrasporangium; E, unicellular colorless hair issuing in vegetative portion; F, mature spermatangial sorus, showing spermatangial mother-cells (spm) and spermatangia (sp.). G–J. Field-collected plants of the Erimo population: G, unicellular colorless hair between the paraphyses; H–J, mature sori, note H showing a secondary tetrasporangium (sts). K. Three-month-old cultured plant grown at 15°C, 16:8 in the Erimo population, showing a mature sorus.
Fig. 3. Variation polygraphs in vegetative structures for three populations of *R. elegans*. Tangential sections were made through the tetrasporangial sori. A–B. Muroran (A, field; B, culture). C–D. Shirikishinai (C, field; D, culture). E–F. Erimo (E, field; F, culture). Key: A, cell number of vertical cell-row; B, whole length of vertical cell-row (μm); C, diameter of hypothallus cell (μm); D, maximum length of erect filament cells (μm); E, minimum length of erect filament cells (μm); F, length of hypothallus cell (μm); G, maximum diameter of erect filament cells (μm); H, minimum diameter of erect filament cells (μm).
Table 1. The dimensions of vegetative and reproductive structures as observed in section (except tetraspores) for four populations.

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The data in the upper half of each rectangle is for field-collected plants and that in the lower half for cultured plants. Dashed line indicates that no information is available.

1) The tetrasporangia developed but did not release spores (see text).
between the paraphyses (Fig. 2, G). This situation is similar to the earlier Rosevninge's (1917) observation. Tetrasporangia are formed in a distinct sorus provided with paraphyses (Fig. 2). The majority of tetrasporangia arise directly from the ordinary terminal cells of the erect filaments, but some sporangia arise from stalk cells which appear to be pushing up into the sporangial sheath (Fig. 2, C, G, K). After discharge of the spores the sub-terminal cell of a tetrasporangium-bearing filament (including a stalk cell) grows into the vacated primary tetrasporangial sheath to form a secondary tetrasporangium (Fig. 2, D, H). The occurrence of the secondary tetrasporangia was reported by Rosevninge (1917) and Lund (1959). The paraphyses are borne on the terminal ends of the erect filaments concurrently with tetrasporangial formation (Fig. 2, A). Fully-grown paraphyses are simple and slightly paler in color than the vegetative cells. They are slightly attenuated toward the apices (Fig. 2).

The plants collected at the four localities have the above-mentioned vegetative and reproductive structures in common, but by dimensions of the vegetative and reproductive cells, and number of the cell layers consisting of the crusts two distinct groups are distinguished (Figs. 3, 5, 6; Table 1). The plants belonging to the first group are found at Muroran, Shirikishinai and Hakodate, and those of the second group are found at Erimo. The measurements are shown in Table 1 together with those of cultured plants. In surface view and in sections cell form and dimensions were variable in the different regions of a single plant. Especially in section cell form and dimensions vary according to the direction of sections. This suggests that the cell form in section is not a reliable criterion

Fig. 4. Scatter diagram showing variations of tetrasporangium dimensions for two populations of *R. elegans*. ○, Muroran, note those of cultured plants did not release spores (see text); ▲, Erimo. Rectangle I showing the range of tetrasporangium dimension for the British *R. elegans* reported by Fletcher (1977); II showing that for the Californian *R. elegans* reported by Ganesan and West (1975); III showing that for the Californian *R. elegans* given by Hollenberg and Abbott (1966).
by which infraspecific entities are distinguished. In the present study tangential sections through the sori were done and the cell rows near the center of the crusts were measured. The second group differs from the first group in having larger vegetative cells (hypothallus and erect filaments), fewer erect-filament cells, larger tetraspores and longer paraphysis cells (Table 1). Figs. 3, 5 and 6 clearly show differences between the two groups. The polygraphs in Fig. 3 show variation ranges and frequency of the vegetative cell dimension and cell number of vertical cell-rows in section. The polygraphs for field and cultured materials of each population are similar and indicate that these features are genetic. Further, the polygraphs for the Shirikishinai population demonstrate their similarity to the Muroran population. In other features, tetraspore dimension, length of paraphysis cells and life-history pattern the Shirikishinai population is similar to the Muroran population (Table 1).

Fig. 4 shows variation ranges of the mature tetrasporangium dimensions of the Muroran and Erimo populations. The dimensions of both the populations are similar to each other in field-collected plants, but those in cultured plants are different. This depends on insufficient development of the tetrasporangia in the Muroran isolate as will be stated later. In the Erimo population well-developed sporangia probably reaching maturity remained a two-spored stage (Fig. 2, H, J, K). On the contrary, in the

![Figure 5](image_url)

**Fig. 5.** Frequency curve in tetraspore diameters of four populations of *R. elegans*. ○—○, Muroran (field); □—□, Hokadate (field); Δ—Δ, Shirikishinai (field); ○—○, Erimo (field); ●—●, Erimo (culture).

![Figure 6](image_url)

**Fig. 6.** Variation polygraphs in paraphyses for two populations. A—B, Muroran (A, field; B, culture). C—D, Erimo (E, field; F, culture).

Key: A, whole length (μm); B, cell number; C, mean length of each paraphysis cell (μm); D, diameter in the proximal portion (μm).
Muroran, Shirikishina and Hakodate populations cruciate tetrasporangia predominated (Fig. 2, C). These suggest that the Erimo population usually possesses bisporangia instead of cruciate tetrasporangia and larger spores than those of other populations (Fig. 5). The predominant occurrence of bisporangia in *R. elegans* was also reported by South and Whittick (1976) and Fletcher (1977).

Fig. 6 shows variation ranges and frequency of the paraphyses of the Muroran and Erimo populations; whole length, number of cells, mean length of each paraphysis cell and diameter in the proximal portion. As these polygraphs show, the paraphysis cells of the Erimo population are longer than those of the Muroran population.

Fig. 7. Development of the hypothallus. A–D. Cultured plants of the Muroran population: A–B, seven-day-old germlings (A, grown at 10°C, 14:10, B, grown at 14°C, 14:10); C–D, fourteen-day-old germlings (C, grown at 14°C, 14:10, D, grown at 10°C, 14:10). E–G. Cultured plants of the Erimo population grown at 15°C, 16:8: E, three-day old; F, seven-day old; G, fourteen-day old. H. Marginal portion of a field-collected plant of the Erimo population.
Spermatangia were formed only on the plants collected at Muroran and Hakodate. They are borne in pairs or solitarily on spermatangial mother-cells which originate from the terminal cells of the erect filaments (Fig. 2, F). The spermatangial mother-cells and the spermatangia are pale yellow in color by which they are distinguishable from sterile cells. Liberated spermatia are globular in shape and almost colorless, measuring 6.3–7.5 μm in diameter.

Life history

Isolated tetraspores of both the groups germinated and developed in a manner similar to that reported previously for R. elegans (Ganesan and West, 1975; South and Whittick,

Fig. 8. Tetraspore and its development of the Muroran population. A. Tetraspore. B–J. Tetraspore germings grown at 14°C, 14:10; B–D, one day old; E, three-day old; F–I, seven-day old; J, fourteen-day old. K–L. One-month-old crusts (K, grown at 10°C, 14:10; L, grown at 14°C, 14:10).

Scale in H applies also to A–G and I; scale in K applies also to L.
1976; Fletcher, 1977) and R. georgii (Fletcher, 1975; Masuda and Ohta, 1975), resulting in the encrusting discs (Fig. 7, A–G; 8; 10, A–I). Especially, the development of radiating filaments constituting the hypothallus in the Muroran isolate is similar to that of the British population of R. elegans (Fletcher, 1977). The radiating filaments of most germlings develop while whirling (Fig. 7, A–C; 8, E, G–I), although some plants develop almost straight-forwardly (Fig. 7, D; 8, F, J).

The encrusting discs of the Muroran isolate reached 3–8 mm in diameter and became fertile at 14°C, 14:10 and 10°C, 14:10 by 3 months after culture initiation. They bore spermatangial and tetrasporangial sori on separate individuals in a manner similar to those of field-collected plants, respectively (Fig. 9). No plants bore carpogonia or cystocarps. This pattern of life history is similar to that reported for the Japanese R. georgii (Masuda and Ohta, 1975). The tetrasporangia divided usually once and sometimes twice, but did not release spores. Culture experiments started from field tetraspores were undertaken four times; thrice for the Muroran isolate (twice at 14°C, 14:10 and 10°C, 14:10, and once at 15°C, 16:8 and 10°C, 16:8) and once for the Shirikishinai isolate at 15°C, 16:8 and 10°C, 16:8. All the tetrasporangial plants did not release spores and the cytoplasm of the sporangia became paler in color and degenerated.


Scale in B applies also to A and C; scale in D applies also to E–G.
Fig. 10. Tetraspore and its development of the Erimo population. A–C and F–L, grown at 15°C, 16:8; D–E, grown at 10°C, 16:8. A. Tetraspore. B–H. Young tetraspore germlings: B–C, one-day old; D–E, three-day old; F–G, five-day old; H, fourteen-day old. I. One-month-old crust. J. Fertile tetrasporangial crust (2-month old). K–L. Tangential sections of fertile tetrasporangial crusts. Scale in F applies also to A–E, G and K; scale in L applies also to H.

although some of them were transferred to short-day conditions (14°C, 10:14; 10°C, 10:14; 15°C, 8:16; and 10°C, 8:16) or low temperature conditions (5°C, 16:8 and 5°C, 8:16).

The crusts of the Erimo isolate grew to 3–6 mm in diameter and reached reproductive maturity at 15°C, 16:8 and 10°C, 16:8 by 2 months after culture initiation (Fig. 10, J). They bore only tetrasporangia as did field plants (Fig. 2, K; 10, K, L). The tetrasporangia released viable spores contrary to those of the first group. The successive generations repeated the same pattern of life history at both the conditions. This pattern of life history is in agreement with that reported previously for R. elegans (Ganesan and

**Taxonomic remarks**

*Rhodophysema elegans* was originally characterized by having a distromatic crust based on the specimens from Brest, France (J. Agardh, 1852; Crouan and Crouan, 1867). Later investigators reported this species from various localities in the North Atlantic, Arctic and North Pacific Oceans (Batters, 1891; Kuckuck, 1897; Rosenvinge, 1898, 1910, 1917, 1926; Yendo, 1915; Newton, 1931; Kylin, 1944; Taylor, 1957; Lund, 1959; Norris and West, 1966; Hollenberg and Abbott, 1967; Chihara, 1972; Ganesan and West, 1975; Pedersen, 1976; South and Whittick, 1976; Fletcher, 1977; Kornmann and Sahling, 1977; Masuda, 1978). The plants with polystromatic crusts have been distinguished from the typical form and called var. *polystromatica* (Batters) Dixon (1964) or f. *polystromatica* (Batters) Denizot (1968). As pointed out by Ganesan and West (1975), circumscription of *R. elegans* varies among different investigators. This suggests that this species includes different several genetic races, or infraspecific entities or has been confused with other taxa. The original description and illustration (J. Agardh, 1852; Crouan and Crouan, 1867) are insufficient to understand this species and we have not examined the type material or the specimens from the type locality of this species. Hence, the typical *R. elegans* is not circumscribed here. On the basis of present knowledge we give a brief review of the noumenon of *R. elegans*.

Based on laboratory culture studies Ganesan and West (1975) and South and Whittick (1976) pointed out that the number of cell layers in the crusts is not a reliable criterion distinguishing var. *polystromatica* from the typical *R. elegans*. This supports the earlier Rosenvinge's (1917) opinion. On the other hand, our observations revealed that two groups of the local populations can be distinguished by the number of cell layers in the crusts in addition to the dimensions of vegetative and reproductive cells and the life-history patterns. These differences between the two groups are small in comparison with those distinguishing each species in the genus *Rhodophysema*. The varying circumscriptions of this species and insufficient informations of the type specimen are not enough to draw conclusions as to the infraspecific rank of the Japanese two groups. We consider them merely as infraspecific two groups of *R. elegans* at present. The determination of the rank awaits further detailed comparison with *R. elegans* from other geographic areas.

Regarding the life-history pattern, different two infraspecific groups may exist also in the North Atlantic *R. elegans*. The cultural evidence of the life history with tetrascalangial and spermatangial plants for one group of the Japanese *R. elegans* supports that the reported occurrence of the spermatangial plants from Greenland (Rosenvinge, 1910) and the northeast coast of North America (Taylor, 1957) is valid. South and Whittick (1976) who cultured two populations of *R. elegans* from Newfoundland reported that cultured plants of Bonne Bay developed tetrascalangial sori and the life history was
completed in culture through three generations but those of Alexander Bay did not reach reproductive maturity even after 3 years. This may depend on a physiological difference between the two populations, although South and Whittick did not state morphological differences. If this is true, two different groups are also present in the Newfoundland populations.

The Californian plants on which Ganesan and West’s (1975) culture studies are based differ from R. elegans reported by other investigators in having broad tetrasporangia (Fig. 4). The reported tetrasporangium dimensions of R. elegans varied according to investigators, ranging from 24 µm to 53 µm in length and from 12 µm to 30 µm in diameter. However, the tetrasporangium shape is narrowly ellipsoid in common, length/diameter ratio of 1.5–2.5 (Fig. 4). R. elegans var. polystromatica reported from Monterey, California by Hollenberg and Abbott (1966) seems to comprise two plants; one growing on rocks (p. 56, Fig. 18) and the other growing on stipes of Cystoseira (p. 56, Fig. 19). The latter is different from the former in having long and slender paraphyses and broad tetrasporangia. Judging from the magnification given in their illustrations, the tetrasporangium dimension of the plant growing on Cystoseira does not agree with their description. This suggests that the measurement of the tetrasporangium dimension is based on the plant growing on rocks. The given dimension is rather similar to the British and Japanese populations (Fig. 4). Thus, R. elegans includes different several infraspecific groups. Further detailed studies of this species from different geographic localities are obviously needed in order to analyze variation ranges of morphological features.

There is also a possibility that R. elegans has been confused with other taxa by some investigators. The Greenland plants reported by Pedersen (1976) are similar to R. nagaii Masuda (1978) in having long paraphyses and tetrasporangial pedicels. Previous records of R. elegans in Japan are uncertain. Yendo (1915) reported this species from Oshoro, Hokkaido growing on Rhodymenia palmata (=Palmaria palmata). According to our field observations on the alga in Oshoro Bay, Yendo’s report may be based on specimens of the other species, R. georgii, although we have not examined Yendo’s voucher specimens. Chihara (1972) recorded R. elegans var. polystromatica from Hidaka, Hokkaido but without description of his material. According to Chihara (pers. comm.), that plant grows abundantly on stipes of Cystoseira and resembles specimens from the west coast of North America. We collected many specimens of that plant from the same locality as Chihara’s collection was made. Its morphological features did not correspond with those of R. elegans. It is allied to R. nagaii Masuda (1978). The taxonomic details of the alga will be presented in the near future.

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Summary

Rhodophysema elegans (Crouan et Crouan ex J. Ag.) Dixon as found in Hokkaido, Japan was investigated in order to clarify life-history pattern and morphological variability. Two groups among the four local populations could be distinguished by the dimensions of vegetative and reproductive cells, the number of cell layers in the crusts, and the life-history patterns. These differences seem to be genetic, though small in comparison with criteria on which to base specific distinction in the Rhodophysema. The two groups were recognized as different infraspecific groups at present. A brief review of the nomenon of R. elegans, which has not been well circumscribed, was given on the basis of present knowledge.

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June, 1981


Rhodophysea elegansは半球形の巨大力帯から帯状にかけて広く分布することが知られている紺状細胞である。生活史に2つの型がある可能性と、藻体を構成する細胞層の数と形が種内分類に寄与する。本研究は北海道太平洋帯で新たに生育が確認された4つの地方集団について、以上の問題点を明らかにする目的で行われた。

栄養細胞と生殖細胞の大きさ、細胞層の数及び生活史の差異によって明瞭に区別し得る2群が認められた。自然集団の個体と培養個体の形態的差異を比較して学会の知見で、2群間の差異は遺伝的であると認められる。本属の種を分けて形態よりも小さい。原記載が本種を把握するには不充分である現段階では、両群を単に種内の2群としてだけ区別しておく。今後、異なる地域的産地の材料の形態的差異が解釈されて、本種の実体はより詳細に明らかになると考える。

村田 源・寺尾 滉：ハグロソウの学名

ハグロソウは Dicliptera Juss. ではなく、Peristrophe Nees に所属させるべきであるということは、すでに Bremekamp (1943) や山崎 (1970) によって指摘されている。ところが、ハグロソウには苞の緑に長い緑毛のあるものと、そうでないものがあり、北村・村田 (1957) や大井 (1965) では、前者をフチナハグロソウ var. japonica，後者をハグロソウ var. subrotunda Matsuda として区別している。山崎 (1970) はこのことにふれている。苞の形にはかなり変異があるが、その緑毛の長さはかなり安定しており、日本産の多くは長い緑毛のものである。九州と中国大陸にはこの両者が分布している。Dianthera japonica THUNB. の Type は長崎のもので、Flora Japonica Tab. 4 に出てくる図にもはっきりと長い緑毛が書かれている。やはり両者は変種として区別するのが適当であると思うので、ハグロソウの学名を次のように改める。


(G. Murata & H. Terao)