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A systematic study of the tribe Rhodomeleae (Rhodomelaceae, Rhodophyta)

Michio MASUDA

Contents

Abbreviations used in the figures. a: apical cell. bs: basal segment. c: central cell. cb: carpogonial branch. cbi: carpogonial branch initial. co: cortical cell. cp: carpogonium. cv: cover cell. fp: fertile pericental cell. hf: holdfast. lb: lateral branch. p: pericentral cell. pb: proliferous branch. sbs: suprabasal segment. sn: stolon. sp: spermatangium. spb: spermatangial branch. spc: secondary pit-connection. spm: spermatangial mother cell. st_1: first sterile group. st_2: second sterile group. st_1i: first sterile group initial. st_2i: second sterile group initial. su: supporting cell. t: tetrasporangium. tb: trichoblast. tr: trichogyne.

Introduction

The Rhodomelaceae is the largest family of Florideophyceae, containing more than one hundred genera (KYLIN, 1956; HOMMERSAND, 1963). The base of the current taxonomy of the family was established by FALKENBERG (1901) in his excellent monograph. It is well known that this family shows great diversity in vegetative construction. The taxonomy of the Rhodomelaceae is ultimately based on the morphology of the vegetative structure, because of the close uniformity in the development of reproductive organs and the postfertilization process as taxonomic criteria. Since FALKENBERG (1901), many investigators have contributed to our knowledge of the taxonomy of the Rhodomelaceae. The detailed review of the history is given by SCAGEL (1953) and HOMMERSAND (1963). However, Rhodomelaceae still includes groups of which data for taxonomy are imcomplete or superficial. The tribe Rhodomeleae is one of the groups in which the taxonomic investigation has been allowed to slumber for many years.

The tribe Rhodomeleae was first proposed as a subdivision of the family Rhodomelaceae by FALKENBERG (in SCHMITZ, 1889) as a *nomen nudum*. At that time, it comprised five genera: *Bostrychia*, *Trigenea*, *Rhodomela*, *Odonthalia* and *Heterocladia*. Later, the full description of the Rhodomeleae was given by SCHMITZ and FALKENBERG (1897), and *Pollexfenia* was added to the tribe and *Bostrychia* was transferred to the Bostrychieae by FALKENBERG (1901). FALKENBERG (1901) recognized only two genera, *Rhodomela* and *Odonthalia*, in the Rhodomeleae, removing *Trigenea* and *Heterocladia* to the Heterocladieae and *Pollexfenia* to the Pterosiphonieae. According to him, the Rhodomeleae is characterized by two tetrasporangia borne in each fertile segment, sexual reproductive organs borne on polysiphonous branches and transverse division of pericentral cells. FALKENBERG's circumscription of Rhodomeleae has been accepted by later investigators.

The subdivisions of Rhodomelaceae referred by FALKENBERG (1901) were described as "Familie" and had been treated as subfamilies by later workers, although KYLIN (1956) treated these as groups. However, HOMMERSAND (1963) referred to them as tribes and erected three new subfamilies, Bostrychioideae, Rhodomeloideae including the tribe Rhodomeleae. and Polysiphonioideae. In agreement with HOMMERSAND I treat the Rhodomeleae as a tribe. Recently, WYNNE (1980) described a monotypic genus *Beringiella* as the third member of the Rhodomeleae. Thus, at present

three genera are acribed to this tribe. *Rhodomela* and *Odonthalia* are well known as widely distributed red algae in the colder seas of the Northern Hemisphere. The species of the genera have been confusing to previous workers because of their complicated morphology. Particularly, it was pointed out that the Japanese species of *Rhodomela* was complicated and heterogeneous (MASUDA, 1972).

The development of the thallus in the tribe Rhodomeleae has been described chiefly through studies of the apices of mature plants. However, the majority of the species in the tribe show a very complex morphology and it is difficult to analyze the ontogeny of the vegetative development by the apical morphology of mature plants. In the Rhodomeleae as well as other tribes of Rhodomelaceae, which have a complex morphology and where the vegetative structure of the thallus is the basic criterion used for taxonomic discrimination, a detailed investigation of the vegetative ontogeny is required based on all stages of morphological development.

Analyzing morphological variation requires a detailed knowledge of the range of variation in a taxon under all conditions of season, environment, and geographic location. Periodic observation of plants in the field and laboratory seems to be most useful for understanding environmental and geographic variation. Information also may be obtained from field transplantation experiments, but these may disrupt natural vegatation and distribution by introducing exotic species. In addition, transplantation is difficult for small plants, although it has been attempted for large plants such as various laminariaceous species. Thus, laboratory culture experiments are most suitable for this purpose. It is possible to culture several plants inhabiting different environments in the same environment, *i. e.*, in laboratory to understand the effect of environmental and geographic variations. Culture studies also facilitate tracing the pattern of development, observing ecological characters such as growth and maturation, and testing for cross-fertilization. To evaluate the stability of morphological characters both field-collected plants and cultured plants should be examined. Then, it is possible to assess the value of a potential taxonomic character. Culture studies in this tribe by previous workers have been restricted to observations on the early development of the spores (INOH, 1944, 1947).

The development of experimental taxonomy has led to the application of the biological species concept. From this point of view, the possibility of cross-fertilization is an important consideration in the recognition of species. This approach is possible in culture studies. This type of work in the tribe has not been reported so far.

Since 1970, I have been studying the species of the Rhodomeleae chiefly

occurring in Japan and adjacent waters in pursuit of aforementioned objectives. In this paper twelve species are reported. This paper is chiefly based on a dissertation in partial fulfilment of the degree of Doctor of Science, Hokkaido University, Sapporo (1974) to which further study of the tribe is added.

Materials and Methods

The present study was carried out on twelve species of three genera, *Rhodomela*, *Neorhodomela* gen. nov. and *Odonthalia* as follows : *Rhodomela confervoides* (HUDSON) SILVA, *R. lycopodioides* (LINNAEUS) C. AGARDH f. *tenuissima* (RUPRECHT) KJELLMAN, *R. sachalinensis* MASUDA, sp. nov., *R. teres* (PERESTENKO) MASUDA, comb. nov., *Neorhodomela munita* (PERESTENKO)

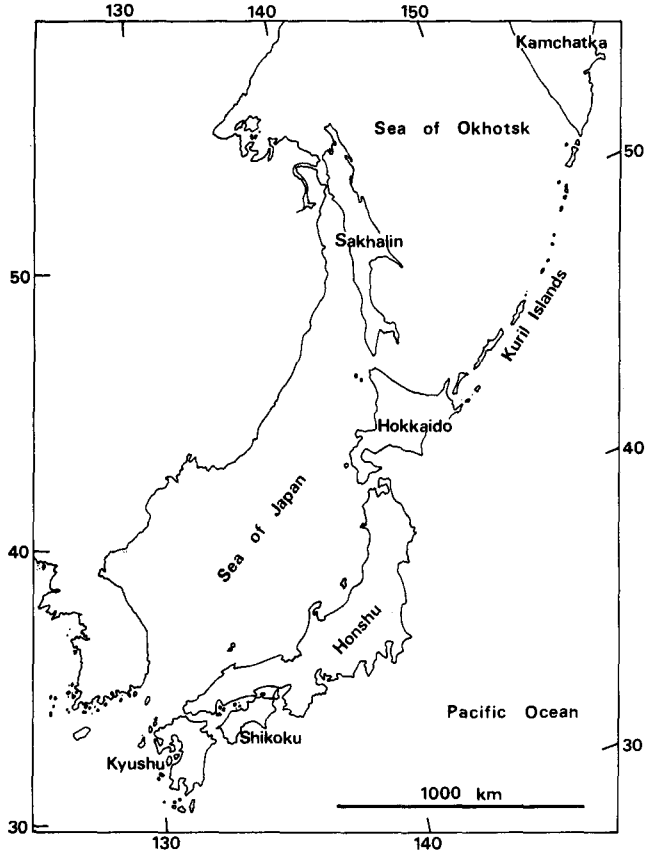

Fig. 1. Map showing the major islands and seas of Japan and adjacent waters.

MASUDA, comb. nov., *N. aculeata* (PERESTENKO) MASUDA, stat. et comb. nov., *N. larix* (TURNER) MASUDA, comb. nov., *N. oregona* (DOTY) MASUDA, comb. nov., *Odonthalia annae* PERESTENKO, *O. corymbifera* (GMELIN) GREVILLE, *O. macrocarpa* MASUDA, sp. nov. and *O. yamadae* MASUDA, sp. nov.

Most of the specimens used in this study were collected chiefly by me between 1967 and 1974 from various localities in Japan. The major islands are shown in Figure 1 together with other islands where herbarium specimens examined were collected. The seawater temperatures of three localities concerned are shown in Figure 2. A list of materials studied will be given in the chapter of the description of each species. Specimens fixed and preserved in 10% formalin in seawater or in 70% ethyl alcohol were examined. A portion of the formalin-fixed materials was dried on herbarium sheets. The herbarium specimens examined are deposited in the following herbaria: the Herbarium of Department of Botany, Faculty of Science, Hokkaido University, Sapporo (SAP); the OKAMURA Herbarium housed in SAP; the Herbarium of Plant Pathology, Botanical Institute, Faculty of Agriculture, Hokkaido University (SAPA); the TOKIDA Herbarium housed in the Herbarium of Faculty of Fisheries, Hokkaido University, Hakodate; the KAWABATA Herbarium housed in Iwamizawa Branch of Hokkaido Kyoiku University, Iwamizawa; the YENDO Herbarium housed in the Herbarium of Faculty of Science, University of Tokyo (TI); the Herbarium of National Science Museum, Tokyo (TNS); the Herbarium of School of Botany, Trinity College, Dublin (TCD); the Herbarium of University of California, Berkeley (UC); the Herbarium of the Komarov Botanical Institute of the Academy of Science, Leningrad (LE); and the Marine Algal Herbarium of Atlantic Regional Laboratory, Halifax. Liquid preserved materials provided by Drs. Takeo OHMORI, Louis D. DRUEHL, John A. WEST, Tadao YOSHIDA and Iemasa YAMADA were also used.

Unialgal cultures were established as follows: small pieces of fertile branches were cleaned and washed in autoclaved seawater with small painting brushes, and placed in Petri dishes (7.5 cm × 1.8 cm) with culture medium, liberated spores were rinsed two or three times in culture medium using finely-drawn glass capillary pipettes under a dissecting microscope, then inoculated onto several drops of culture medium on slide glasses placed on the bottom of Petri dishes (9 cm × 2 cm). One day later 40–50 *ml* of culture medium was added to each Petri dish. The sporelings were cultured in Petri dishes for 10 days, while the early developmental stages were examined, and then transferred to a glass vessel (6.5 cm × 8.0 cm) containing 200 *ml* of culture medium. When material was not fertile or failed to liberate the spores, excised and cleaned branches were placed in Petri dishes with culture

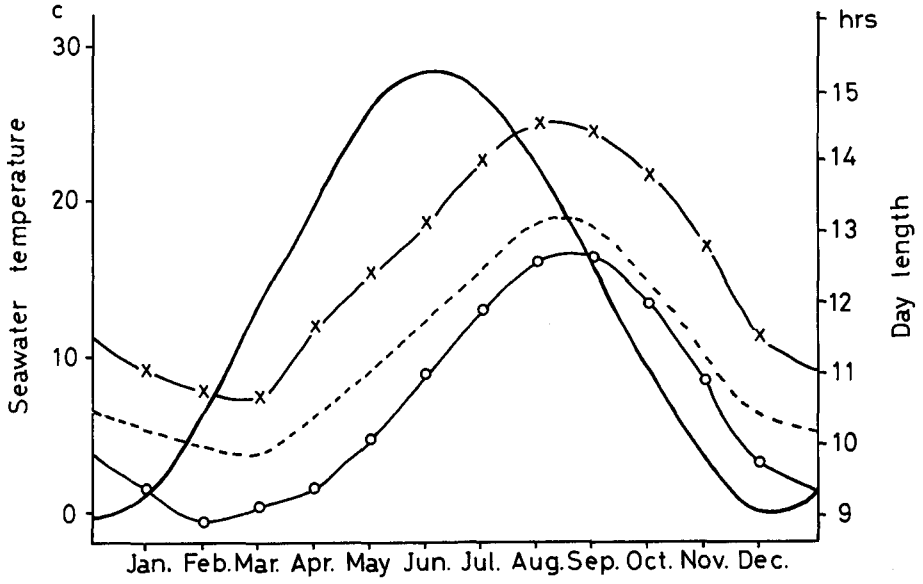

Fig. 2. Day length (——) at Muroran, surface seawater temperature (○——○) at Rausu (- - - -) at Muroran, and (×——×) at Shimotsui near Tamano, Okayama (average of two years, 1970-1971).

medium, the apices of indeterminate branches were excised with a glass capillary pipette under a dissecting microscope, then excised tips were rinsed and introduced individually into screw cap tubes (2 cm × 13 cm) each containing 10 *ml* of medium, and one month later transferred to a glass vessel (6.5 cm × 8.0 cm). To obtain both male and female gametophytes for crossing experiments, tetraspores were introduced individually into screw cap tubes containing 10 *ml* of medium, later a single germling was detached and transferred to a glass vessel containing 200 m*l* of medium.

All culture experiments were carried out in still culture employing ES medium (PROVASOLI, 1968). ES enrichment in screw cap tubes (10 *ml*) or Erlenmeyer flasks (500 *ml*) and filtered seawater were separately sterilized in a autoclave (ca. 120°C, 1 kg/cm²) for twenty minutes. The culture medium was changed monthly. Cultures were kept in freezer-incubators illuminated with cool white fluorescent lamps (ca. 1500–2500 lux). The different culture conditions were as follows: 5°C, 14 : 10 LD (light-dark cycle); 5°C, 10 : 14 LD; 10°C, 14 : 10 LD; 10°C, 10 : 14 LD; 14°C, 14 : 10 LD; 14°C, 10 : 14 LD; 18°C, 14 : 10 LD; 18°C, 10 : 14 LD; 22°C, 14 : 10 LD at the Institute of Algological Research, Hokkaido University, Muroran, and 5°C, 16 : 8 LD;

5°C, 8 : 16 LD ; 10°C, 16 : 8 LD ; 10°C, 8 : 16 LD ; 15°C, 16 : 8 LD ; 15°C, 8 : 16 LD ; 20°C, 16 : 8 LD ; 20°C, 8 : 16 LD at the laboratory of Department of Botany, Faculty of Science, Hokkaido University, Sapporo.

Microscopic examinations were done chiefly on liquid-preserved materials and also sometimes on living materials. Sections were made by hand using the straight-edge razor and pith stick and stained with cotton blue or erythrosin.

The description of geographic distribution of each species in Japan and adjacent waters was done by studying historic and contemporary specimens. A set of voucher specimens are preserved in SAP and the Institute of Algological Research, Muroran.

Results

Rhodomela C. AGARDH, 1822, nom. cons.

The genus *Rhodomela* was established by C. AGARDH (1822) including a number of species formerly assigned to *Fucus*, *Odonthalia* and *Ceramium*. However, most of them have been transferred to other genera such as *Odonthalia*, *Pterosiphonia* and *Halopithys* by later investigators. The genus name, *Rhodomela*, has been conserved against *Fuscaria* STACKHOUSE (1809) by the International Code of Botanical Nomenclature (STAFLEU *et al.*, 1978). According to SILVA (1952), the lectotype species is *Rhodomela confervoides* (HUDSON) SILVA, which is based on *Fucus confervoides* HUDSON (1762).

In addition to the characters of the tribe Rhodomeleae mentioned earlier, *Rhodomela* is characterized as follows : (1) terete erect thalli with the polysiphonous structure covered with a thick cortex and with several main axes arising from a common discoid holdfast, (2) the main axes with many spirally arranged branches divided into progressively shorter branches, (3) adventitious branches formed from outermost cortical cells, and (4) trichoblasts.

DE TONI (1924) recognized only two species in this genus : *Rhodomela lycopodioides* (LINNAEUS) C. AGARDH and *R. larix* (TURNER) C. AGARDH. He considered *Rhodomela confervoides* (=*R. subfusca* (WOODWARD) C. AGARDH) and *R. virgata* KJELLMAN to be synonymous with *R. lycopodioides*. However, his opinion has not been accepted by other phycologists (ROSENBERG, 1933 ; KYLIN, 1944 ; TAYLOR, 1957 ; KORNMANN and SAHLING, 1977). Atlantic and Arctic species of this genus, *R. confervoides*, *R. lycopodioides* and *R. virgata*, had been investigated by many phycologists (KJELLMAN, 1883 ; FALKENBERG, 1901 ; KYLIN 1914, 1923, 1944 ; ROSENVINGE, 1903, 1923-24 ; ROSENBERG, 1933 ; TAYLOR, 1957 ; KORNMANN and SAHLING, 1977), but they

have not been well defined. In addition to the four species mentioned above, following five species have been assigned to this genus: *Rhodomela macracantha* (KÜTZING) SETCHELL in TOKIDA (1934), *R. patagoniensis* TAYLOR (1939), *R. gracilis* YAMADA et NAKAMURA in YAMADA et TANAKA (1944 b), *R. sibirica* A. ZINOVA et VINOGRADOVA in VINOGRADOVA (1973 a) and *R. munita* PERESTENKO (1980). Thus, at present nine species are referred to this genus.

In Japan and adjacent waters, *Rhodomela confervoides* (as *R. subfusca*), *R. larix*, *R. macracantha*, *R. gracilis* and *R. lycopodioides* f. *tenuissima* have been reported by OKAMURA (1922, 1936), TOKIDA (1934, 1949, 1954), NAGAI (1941), YAMADA and TANAKA (1944 b), TAZAWA (1975), MASUDA and SHIMIZU (1980), and others. In this paper, the circumscription of the Japanese *Rhodomela* is discussed to transfer *R. larix* to a new genus *Neorhodomela* as *N. aculeata* based on *R. larix* subsp. *aculeata* PERESTENKO and to erect a new species, *R. sachalinensis*, based on *R. macracantha* SETCHELL (non *Lophura macracantha* KÜTZING). Furthermore, *R. gracilis* YAMADA et NAKAMURA (non HARVEY) is reduced to the synonymy with a new combined name, *R. teres* based on *Odonthalia teres* PERESTENKO. In addition, the result of morphological observations and culture studies of Atlantic *R. confervoides* is reported.

Rhodomela confervoides (HUDSON) SILVA

SILVA, 1952, p. 269; FELDMANN, 1954, p. 117; TAYLOR, 1957, p. 334, pl. 40, fig. 9; LAMB and ZIMMERMANN, 1964, p. 229; EDELSTEIN and MCLACHLAN, 1966, p. 1055; KORNMANN and SAHLING, 1977, p. 252.

Basionym: *Fucus confervoides* HUDSON, 1762, p. 474.

Synonyms: *Rhodomela subfusca* (WOODWARD) C. AGARDH, 1822, p. 378; HARVEY, 1846-51, pl. 100, 1853, p. 26; J. AGARDH, 1863, p. 883; FALKENBERG, 1901, p. 593, Taf. 11, figs. 2-17; ROSENVINGE, 1903, p. 459, figs. 9 (d-e)-13, 1923-24, p. 451, figs. 411 (b)-412 (a), 415-418 (d-e), 421 (as *R. subfusca* f. *genuina*); KYLIN, 1907, p. 145 (as *R. subfusca* f. *typica*), 1944, p. 86; NEWTON, 1931, p. 336, fig. 207; LEVRING, 1940, p. 109, figs. 34, 36 (as *R. subfusca* f. *typica*); WAERN, 1952, p. 225, figs. 14-15; ZINOVA, 1955, p. 199, fig. 164.

Fucus subfuscus WOODWARD, 1791, p. 131, fig. 12; TURNER, 1808, p. 20, pl. 10.

Materials

The specimens used were collected at Ile Verte, Roscoff, France, by Dr. Tadao YOSHIDA from November 1972 to July 1973.

YOSHIDA in SAP (iii-1973, spermatangial, cystocarpic & tetrasporangial; vii-1973, sterile; xi-1972, sterile; xii-1972, spermatangial, cystocarpic & tetrasporangial)

A parent plant with tetrasporangia for culture experiments was collected on March 21, 1973 by Dr. T. YOSHIDA at Roscoff and sent to me by air mail. Culture experiments were set up 9 days after collection.

Description

Plants perennial, terete, densely branched up to 4 to 5 times, with conspicuous main axes arising from a common discoid base, attaining up to 50 cm high, dark red in color, adhering readily to paper in drying; main axes branched in a spiral manner, bearing progressively shorter and more slender branches, 900-1150 μm in diameter just above the holdfast, becoming gradually thicker upward, reaching a maximum diameter of 1200-1600 μm in the lower third portion and gradually more slender upward, the branching intervals of main axes up to 3-5 mm in the middle portion; branches of all orders except determinate branches growing in a pattern similar to that of the main axis; pericentral cells six to seven, surrounded by several layers of cortical cells; vegetative trichoblasts borne on the apical portion of indeterminate branches, divided once or twice pseudodichotomously, sometimes simple, faintly pigmented when young, almost colorless when mature; plants dioecious; spermatangia borne on the apical portion of branches and covering the surface, sometimes on simple trichoblasts; procarps originating from the suprabasal segment of the fertile trichoblasts; mature cystocarps enveloped by well developed pericarps, urceolate or ovoid, measuring 550-670 μm $\times$ 440-600 μm; tetrasporangia formed in pairs in 6-10 successive segments in the upper portion of branches, measuring 140-170 μm $\times$ 140-160 μm when mature.

Observations

Habitat and Phenology: The habitat and phenological information for the French *R. confervoides* was reported by FELDMANN (1954) based on observations at Roscoff. Some additional data were provided by YOSHIDA (pers. comm.)

This species grows on rocks or pebbles on sandy bottom in sheltered areas of the lower littoral zone. According to FELDMANN (1954), this species is perennial and fertile from December to July. The plants collected by Dr. T. YOSHIDA from winter to spring were fertile and most developed plants were found at the end of March. Plants collected in December possessed many well developed proliferous branches which bore reproductive

organs. The proliferous branches most likely appeared in late summer or early autumn.

Morphology of field plants: Plants consist of several upright thalli issuing from a common basal disc. They are dark red in color, having soft texture, and adhere readily to paper in drying. The first year plants are up to 50 cm high, branched several times and are provided with the fifth or sixth order branches in the most developed ones. Each erect thallus has a conspicuous main axis which is terete and almost straight. Main axes are 900–1150 μm in diameter just above the basal disc and become gradually thicker upward, attaining a maximum diameter of 1200–1600 μm in the lower third portion, and gradually more slender upward. Branches of the first order are produced from central cells of the main axis and are arranged in a spiral manner. The branching intervals of the main axis is 0.5–2 mm at the lower portion, becoming longer upward and up to 3–5 mm in the middle portion, and gradually shorter upward. The first order branches except for the several lower ones, which are not divided and are short, develop in a pattern similar to that of the main axis and are divided into progressively shorter and more slender branches. Among them branches borne on the lower third portion of the main axis reach a maximum size of 30 cm long. Branches of all orders attenuate at the distal and proximal portions and reach a maximum diameter in the lower third portion.

The second year plants possess proliferous branches developing from old main axes as well as from branches of the first order and sometimes from those of the second order. In materials preserved in 10% formalin seawater, proliferous branches are distinguishable from old branches by a paler color. The old main axis of plants collected on December 21, 1972 had many stumps of fallen branches arranged spirally. Central cells of these fallen branches are directly connected with the central cells of the main axis. Thus, the fallen branches are ordinary branches produced from the central cells of the main axis in the preceding year, whereas the proliferous branches are formed adventitiously from the cortical cells. Old main axes are stout and 1200–1650 μm in diameter in the lower portion. The proliferous branches produce up to fourth or fifth order branches and attain up to 22 cm high. Main axes of the proliferous branches are 700–800 μm in diameter in the proximal portion and 1400–1500 μm in diameter in the lower third portion. The main axes are more densely covered with the first order branches than those of the first year plant. The intervals of the first order branches on the main axis are up to 2 mm in the middle portion.

Adventitious branches are produced from the outermost cortical cell.

They are borne usually at the axillary portion (ROSENVINGE, 1923-24) and sometimes at other places.

Vegetative trichoblasts are formed on the apical portion of indeterminate branches and divided once or twice pseudodichotomously, reaching up to

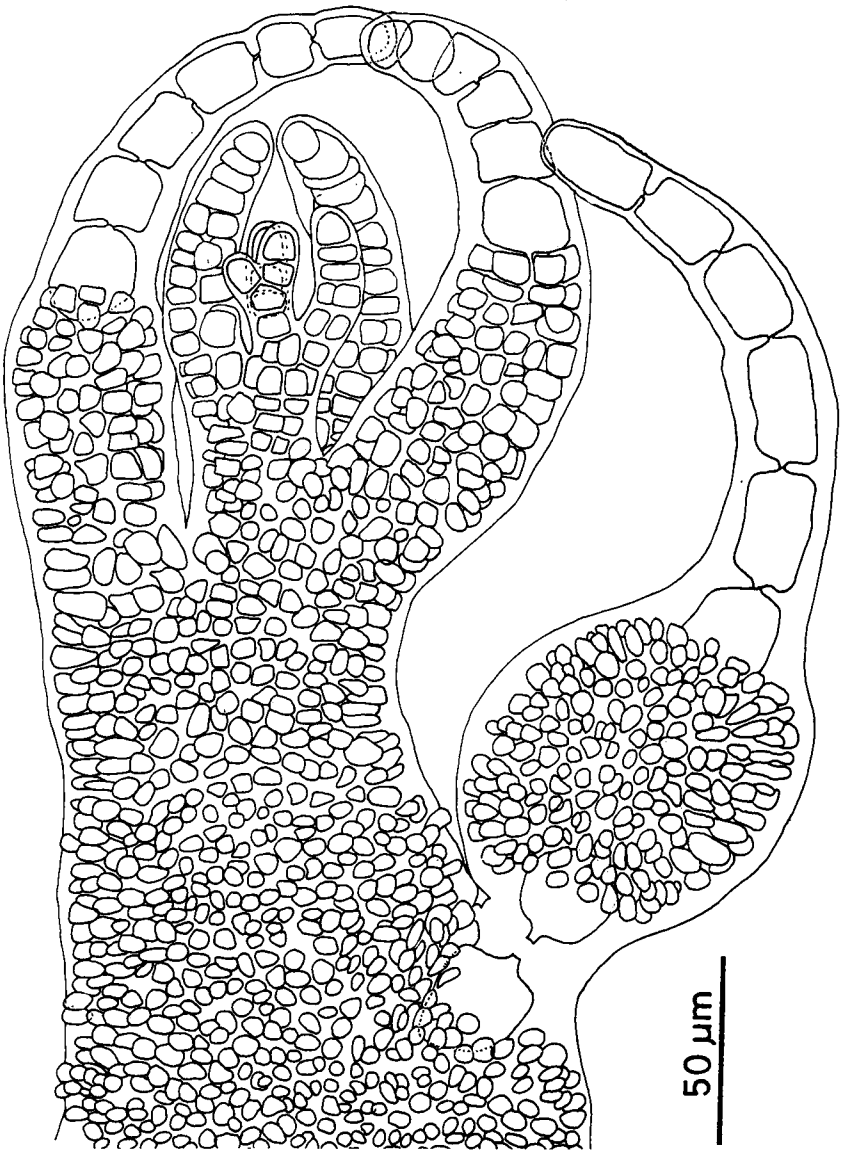

Fig. 3. *Rhodomela confervoides* (HUDSON) SILVA. Tip of a spermatangial branch.

500 μm long. The first branch occurs from the second or third segment (Pl. 7, A). Simple vegetative trichoblasts are also found. Young trichoblasts are faintly colored, but fully grown ones are almost colorless.

The main axes and branches are uniaxial and composed of a central axial cell, six to seven pericentral cells, usually six in determinate simple branchlets, and several layers of cortical cells (Pl. 8, A, B). Pericerntral cells are divided transversely into two cells (sometimes three cells). The upper cell of the two retains the pit-connection with the central axial cell, while the lower one becomes linked by secondary connection with a pericentral cell of the underlying segment. The pericentral cells cut off two or three cortical cells outward, each of which is again divided transversely (Pl. 8, C). The cortical cells also cut off one or two cortical cells outward. This process is repeated so that the cortex becomes 15-16 layered in the lower portion of the old main axis (Pl. 8, A) and 6-7 layered in the middle portion of the proliferous branches (Pl. 8, B). The central cells of the main axis are 150-200 μm long near the base and become gradually elongated upward. They reach a maximum length of 3-5 mm in the middle portion of the main axis. The length corresponds to the branching interval. The outer cortex of the lower portion of the main axis and the first order branches are composed of very tightly packed cortical cells (Pl. 8, C).

The spermatangia of *R. confervoides* have been described or illustrated by FALKENBERG (1901), ROSENVINGE (1903, 1923-24) and NEWTON (1931), but there is a discrepancy among their reports. ROSENVINGE described and illustrated spermatangia which were formed on both unspecialized ordinary branches and trichoblasts. On the other hand, FALKENBERG and NEWTON reported spermatangia only borne on ordinary branches. The spermatangia of plants collected from Roscoff are borne in the apical portion of the ordinary and axillary adventitious branches (Fig. 3). The spermatangial branches are divided spirally once or twice. The spermatngia cover the surface of the branches except for the upper monosiphonous segments. They are also produced on simple trichoblasts. Thus, the spermatangial branches are similar to those reported by ROSENVINGE (1903, 1923-24).

The procarps are produced from the suprabasal segment of the fertile trichoblast as in the majority of the Rhodomelaceae (Fig. 4, A, C). Likewise, they are rarely borne on the third segment of the trichoblast (Fig. 4, E). Morphologically, there is no observable difference between fertile trichoblasts and vegetative trichoblasts. The fertile trichoblasts are usually simple and composed of 6-9 segments (Fig. 4) and rarely divided once or twice. They are formed at the apical portion of ordinary branches of the first to sixth orders. The development of procarps, as seen in Fig. 4, is similar to that

of *R. virgata* (KYLIN, 1914, 1923). The initial of the first (lateral) group of sterile cell is cut off first from the fertile pericentral cell which functions as the supporting cell. Then, the carpogonial-branch initial is cut off from the supporting cell on the adaxial side. The second (basal) group of sterile cell is later formed below the first sterile group. The procarp before fertilization consists of a supporting cell, a 4-celled carpogonial branch, and two groups of sterile cells. The postfertilization development was not traced. Mature cystocarps show somewhat variable shapes. They are urceolate or rarely ovoid and measure 550-670 μm in height and 440-600 μm in diameter (Pl. 2, P).

The tetrasporangia are usually borne on the upper portion of ordinary branches of the second to sixth orders. The tetrasporangial branches are morphologically identical to sterile branches. Adventitious fertile branches were not so commonly observed in the Ile Verte material. Two tetrasporangia

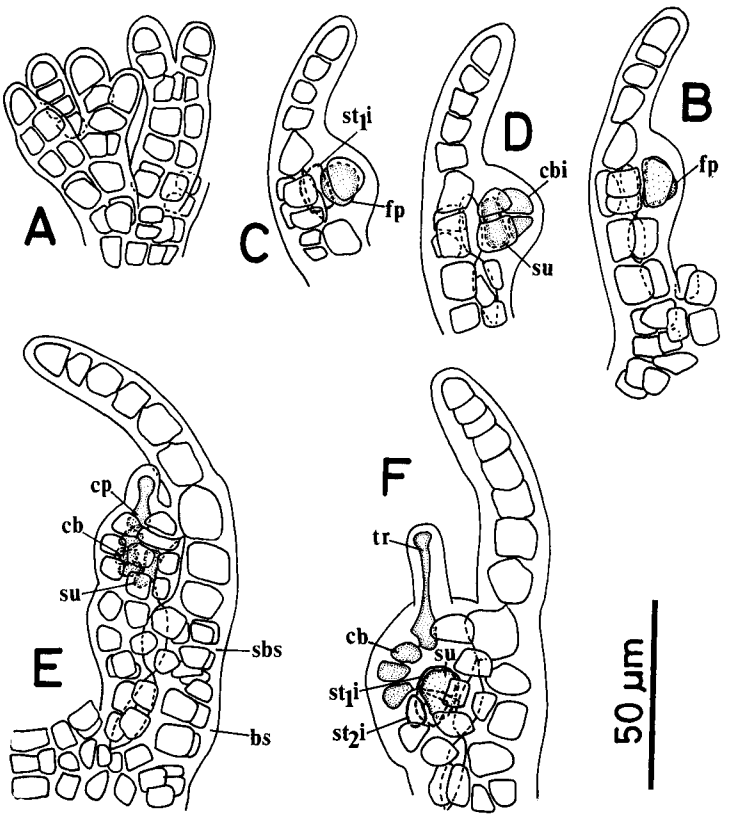

Fig. 4. *Rhodomela confervoides.* A-F. Stages in the development of procarps.

are produced in each of 6-10 successive segments of the fertile branches. Each sporangium is provided with two cover cells. Mature tetrasporangia measure 140-170 μm in height and 140-160 μm in diameter in surface view and are divided tetrahedrally

Culture study: Unialgal cultures were obtained from excised apical tips of indeterminate branches of a tetrasporangial plant (Pl. 1, A). The apical tips were cultured at 10°C, 14 : 10 LD and 14°C, 14 : 10 LD. They grew into plants with many tetrasporangia (Pl. 2, A) within 3 to 4 months. The plants subsequently released viable tetraspores. Liberated tetraspores were dark red in color and measured 81-95 μm in diameter (Pl. 2, B). They were cultured under the following conditions: 5°C, 14 : 10 LD; 5°C, 10 : 14 LD; 10°C, 14 : 10 LD; 10°C, 10 : 14 LD; 14°C, 14 : 10 LD; 14°C, 10 : 14 LD; 18°C, 14 : 10 LD and 18°C 10 : 14 LD. The following account is based on observations on plants kept under 10°C, 14 : 10 LD unless otherwise indicated.

Isolated tetraspores germinated into bipolar sporelings of several cells and differentiated into a colorless rhizoidal portion produced from one pole of the spore and a pigmented upright shoot portion from the other within one day (Pl. 2, C). The sporelings grew straight and produced an initial of the first branch from the subapical segment (Pl. 2, D; Fig. 5, A) that later grew into a vegetative trichoblast (Fig. 5, B). In the plants examined the first branch always developed into the trichoblast. The sporelings grew by means of a large apical cell from which pericentral cells subsequently were cut off. The pericentral cells simultaneously cut off cortical cells. Rhizoids were divided repeatedly to form the discoid holdfast (Pl. 2, D-G). Subsequently, three or four spirally arranged trichoblasts were produced successively from each segment of the apical portion of the sporelings. The trichoblasts were divided pseudodichotomously two or three times and reached a length of 1 mm. The first branching always took place in the second segment. They were faintly colored when young, and later became almost colorless. The trichoblasts began to shed successively in the lower portion of sporelings. Thus, the vegetative trichoblasts of this species were deciduous. After the formation of 3 to 4 trichoblasts ordinary branches were produced on the apical portion replacing the trichoblasts within 7 days (Pl. 2, G; Fig. 5, C). The ordinary branches were successively produced from each segment in a spiral manner (Pl. 2, H). After 30 days, the sporelings reached a height of 1.5 cm and produced 14-16 branches. The branches of the first order grew in the same manner as the main axis and produced vegetative trichoblasts and ordinary branches of the second order. New secondary main axes which issued from the basal disc were strongly recurved as

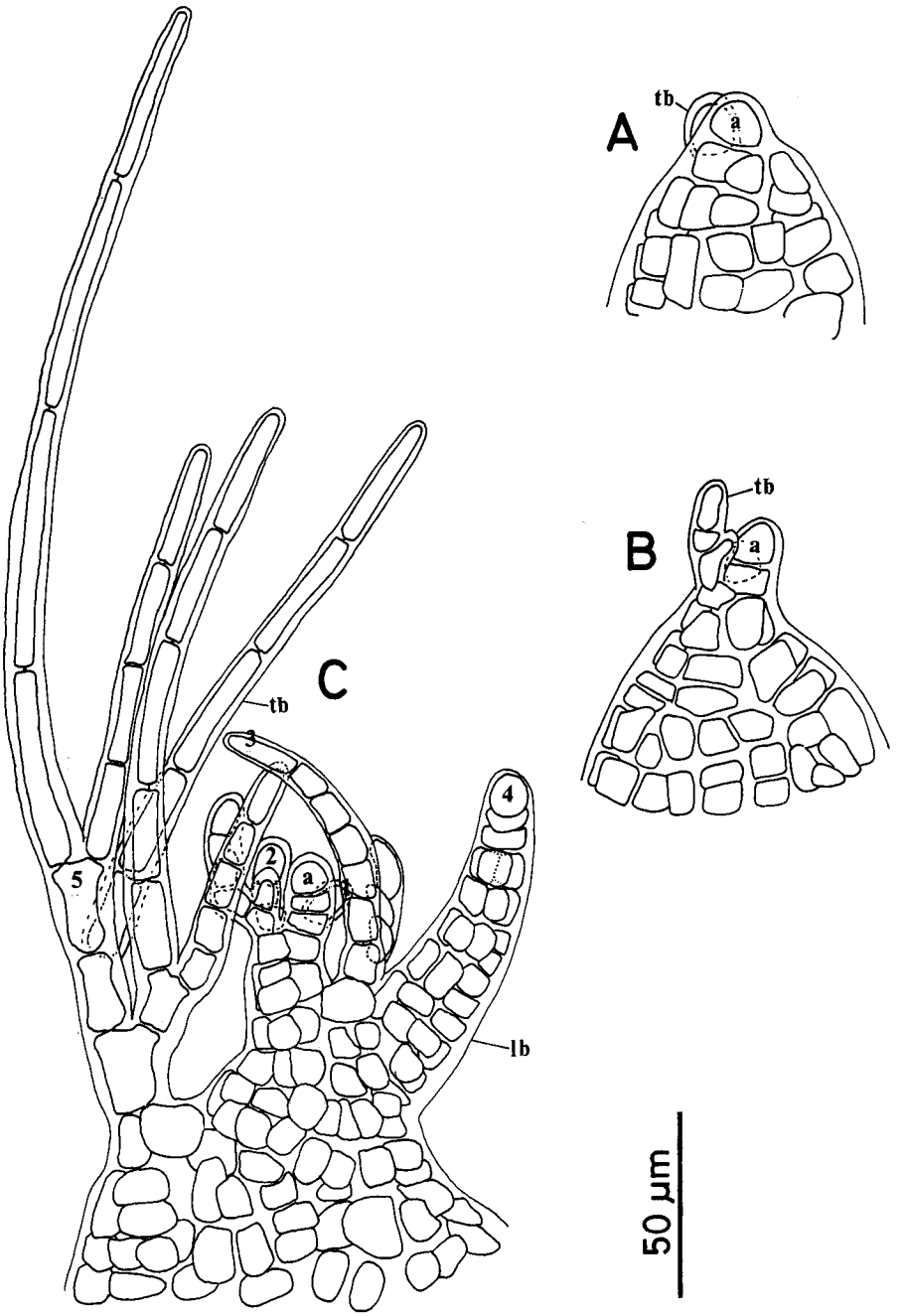

Fig. 5. *Rhodomela confervoides.* Stages in the development of the apical portion of sporelings. A. Three-day-old sporeling, issuing the first lateral. B. Five-day-old one, issuing a trichoblast and the second lateral. C. Seven-day-old one forming spirally arranged trichoblasts and ordinary branch numbered in their sequence of formation.

illustrated by ROSENVINGE (1923-24). The formation of adventitious branches was not observed at this stage.

After 2 months, the plants attained a height of 4 cm and produced the third or fourth order branches. Eight to 10 secondary erect shoots were also produced from the basal disc. The secondary shoots developed in the same manner as the primary shoot and reached up to 2 cm high. The plants bore male and female gametangia on separate individuals (Pl. 1, B, C).

The gametangia were produced on the apical portion of indeterminate branches of the first and second orders on the primary main axis. The development and structure were similar to those of field materials. The spermatangial branches were distinguishable with the unaided eye by the yellowish white color. They were usually branched once or twice in a spiral manner, but sometimes were simple (Pl. 2, J). The spermatangia were also borne on simple trichoblasts as well as on branched trichoblasts (Pl. 2, I). The procarps were produced on trichoblasts, which were usually simple (Pl. 2, K; Fig. 4, B, D, F) and rarely divided once or twice. Female gametangial plants cultured with male gemetangial plants developed ripe cystocarps within 30 days after the appearance of the gametangia (Pl. 1, D), but female plants cultured solitarily did not bear cystocarps. The sterile upper portion of fertile trichoblasts remained on the mature cystocarps (Pl. 2, L, M). Fully grown cystocarps were urceolate or rarely ovoid in shape and measured 530-700 μm $\times$ 420-650 μm. They were usually provided with rather wide ostioles (Pl. 2, L-N) through which viable carpospores were discharged (Pl. 2, M). Although carpospores were club-shaped within the cystocarps, liberated carpospores assumed a globular shape, as did the tetraspores, and resembled the latter in many respects other than in size (Pl. 2, O). They were slightly larger than the latter and measured 87.5-97.5 μm in diameter.

Plants derived from tetraspores grew more rapidly at 10-18°C than at 5°C and they grew best in long day conditions. The plants cultured at 14°C, 14 : 10 LD and 14°C, 10 : 14 LD reached reproductive maturity after 2 months, and the plants cultured at 5°C, 14 : 10 LD, 5°C, 10 : 14 LD and 10°C, 10 : 14 LD reached reproductive maturity 3 months after initiation. However, the plants cultured at 18°C, 14 : 10 LD and 18°C, 10 : 14 LD did not bear any reproductive organs even 5 months after initiation and then, the cultures were terminated.

Carpospores derived from the cystocarpic plants were cultured in the same eight kinds of conditions as tetraspores were. Germination of the carpospores and subsequent development of sporelings were the same as for the tetraspores described above. The sporelings reached reproductive maturity

and formed tetrasporangia at 10°C, 14 : 10 LD, 14°C, 14 : 10 LD and 14°C, 10 : 14 LD 3 months after initiation, at 10°C, 10 : 14 LD and 5°C, 14 : 10 LD and 5°C, 10 : 14 LD 4–5 months after initiation. The tetrasporangia were formed in the upper portion of the second to the fourth order branches. They were produced in pairs in 7–15 successive segments of the branches. Mature sporangia were 140–160 μm × 140–160 μm in surface view. However, the plants cultured at 18°C, 14 : 10 LD and 18°C, 10 : 14 LD did not reach reproductive maturity even 6 months after initiation and then, the cultures were terminated.

As already described, according to FELDMANN (1954) and YOSHIDA (pers. comm.), *Rhodomela confervoides* at Roscoff reaches reproductive maturity in winter and is fertile to spring or early summer, when the sea-water temperature ranges 9–14°C and the daylength is 8–15 hours (CABIOCH and YOSHIDA, pers. comm.). The results obtained from the present culture experiments agree fairly well in environmental conditions of reproductive maturation with field observations at Roscoff by FELDMANN (1954) and YOSHIDA (pers. comm.).

Comparison of cultured plants with field materials showed no apparent difference in thallus color, thallus structure (Pl. 8, D, E), and gross morphology (Pl. 1, B, C) with only minor exceptions. Lower branches of any order in field-collected plants do not branch, whereas those of cultured plants usually branch well. The first produced and lowest branch was the longest in 2-month-old plants, but later it was overtopped by branches situated on the lower third to the middle portion of the primary main axis.

Taxonomic discussion

This alga had been known under the name of *Rhodomela subfusca* (WOODWARD) C. AGARDH (1822) of which basionym is *Fucus subfuscus* WOODWARD (1791), until SILVA (1952) proposed a new combined name, *R. confervoides* (HUDSON) SILVA based on *Fucus confervoides* HUDSON (1762). SILVA's combined name has been accepted by later investigators. HUDSON's original description of *Fucus confervoides* is brief: "*caule tereti ramosissimo, ramulis alternis faciculatis brevissimis tuberculatis scabris*". This description is insufficient to recognize the HUDSON's species as a member of *Rhodomela*, hence, it is impossible to decide whether the HUDSON's species is identical with the WOODWARD's or not without examination of the voucher specimens. On the other hand, the description of *Fucus subfuscus* by WOODWARD is adequate to understand the entity. At present I follow SILVA's opinion adopting the WOODWARD's species concept of this alga.

Judging from the original description and illustration given by WOOD-

WARD (1791), the plant collected from Roscoff seems to be identical with *Fucus subfuscus* which have been treated as the typical form of *Rhodomela confervoides* by the previous workers quoted above. The typical form of this species is characterized by rather firm and thick main axes with numerous well developed branches divided densely and regularly in a spiral manner, and dark red color of thallus.

In addition to the typical form, according to TAYLOR (1957), *R. confervoides* comprises two forms, f. *gracilior* (J. AGARDH) TAYLOR based on *R. subfusca* f. *gracilior* J. AGARDH (1863) and f. *rochei* (HARVEY) TAYLOR based on *R. rochei* HARVEY (1853). *R. confervoides* f. *gracilior* is characterized by slender and elongate thalli with long branchlets in loose apical clusters, moniliform tetrasporangial branchlets, and racemose and stalked pericarps, whereas f. *rochei* is characterized by more slender thalli, loose branching with a bilateral tendency, capillary ultimate branchlets with abundant trichoblasts, long-stalked pericarps in long racemose series and bright rose color of thallus (HARVEY, 1853; TAYLOR, 1957). A specimen referable to f. *rochei* was encountered in the herbarium specimens sent to me by Dr. T. EDELSTEIN. This plant, collected at Chance Harbor, Pictou Co., Nove Scotia, on June 2, 1971 (No. 5373), agrees well in external features with the specimen of *Rhodomela rochei* in PBA No. 1296 which was collected from Wood's Hole, Massachusetts, on April 23, 1905 by F. S. COLLINS (COLLINS, *et al.*, 1905). Both the specimens are distinguishable from the French plant of *R. confervoides* described here by their very slender and soft thalli. Only one herbarium specimen belonging to f. *gracilior* was encounterd in PBA No. 890 as *R. subfusca* var. *gracilis* (HARVEY) FARLOW (COLLINS, *et al.*, 1901). As pointed out by HARVEY (1853), this specimen has slightly thicker branches than those of f. *rochei*. According to my preliminary examination of the aforementioned herbarium specimens, of three forms of *R. confervoides*, f. *gracilior* and f. *rochei* are closely related in having slender branches and very soft substance by which the two forms can be distinguished from the typical form. In addition, the following observation reported by LAMB and ZIMMERMANN (1964) should be worthy of attention. They studied the seasonal succession of the marine algae of Cape Ann, Massachusetts and stated as follows: the deep water form, f. *gracilior* occurring in the *Laminaria* and *Agarum* zones, remains in good condition at all seasons, and it is very dissimilar to the typical form, of robust growth with strongly penicillate end-branchlets in aspect, being more slender and not markedly penicillate at the tips. A further experimental study is necessary to confirm whether the difference between the typical form of *R. confervoides* and the two forms is based on a genetic character or not.

Rhodomela lycopodioides (LINNAEUS) C. AGARDH f. *tenuissima* (RUPRECHT) KJELLMAN

KJELLMAN, 1883, p. 109, 1889, p. 24; SETCHELL and GARDNER, 1903, p. 332; YENDO, 1909, p. 132; E. S. ZINOVA, 1954, p. 302; VOZZHINSKAJA, 1965, p. 77; MASUDA and SHIMIZU, 1980, p. 241, figs. 1-24.

Basionym: *Fuscaria tenuissima* RUPRECHET, 1850, p. 221, Taf. 10.

Synonym: *Rhodomela tenuissima* (RUPRECHT) KJELLMAN, 1875, p. 6; A. D. ZINOVA, 1970, p. 106; VINOGRADOVA, 1973 b, p. 44, 1978, p. 10; GRINTAL, 1974, p. 115; TOLSTIKAVA, 1974, p. 152; KLOCZCOVA, 1976, p. 24; KLOCZCOVA and BYVALINA, 1979, p. 15.

Japanese name: Miyabi-fujimatsumo (MASUDA and SHIMIZU, 1980)

Materials

The specimens examined were collected at Akkeshi, eastern coast of Hokkaido from 1976 to 1979. SAP 032151-032159 (iv-1976, cystocarpic & tetrasporangial; iv-1977, tetrasporangial; v-1977, spermatangial, cystocarpic & tetrasporangial; vi-1976, cystocarpic & tetrasporangial; vi-1979, ditto; vii-1977, ditto; viii-1977, old sterile; xii-1976, sterile).

The following herbarium specimens were also observed: (1) sterile specimens collected in Mamga Bay, western coast of the Sea of Okhotsk on July 28, 1844 and determined by F. J. RUPRECHT as *Fuscaria tenuissima* (LE); (2) cystocarpic specimen collected in Golofnin Bay, Alaska by R. C. MCGREGOR in 1900 (UC 96155); (3) cystocarpic specimen collected from Cape Nome, Alaska during July 25-26, 1899 (UC 96145); (4) sterile specimen collected from St. Lawrence in July 1931 *H. L. Mason* No. 243 (UC 466127); (5) spermatangial and tetrasporangial specimens collected from Port Clarence, Alaska on July 19, 1931 *H. L. Mason* No. 238 (UC 466147).

Parent cystocarpic and tetrasporangial plants for culture experiments were collected at Akkeshi on June 4, 1976 (Figs. 6, 7). The plants were transported to the laboratory of Department of Botany, Faculty of Science, Hokkaido University in a plastic chest on ice.

Description

Plants perennial, terete, densely branched up to 5 to 6 times in a spiral manner, with conspicuous main axes arising from a common basal disc, attaining up to 42.5 cm high, dark brownish red in color, soft, adhering closely to paper in drying; main axes 350-660 μm in diameter just above the basal disc, gradually becoming thicker upward, reaching a maximum diameter of 500-1000 μm about 0.8-1.5 cm above the base, tapering abruptly from a portion of 400-700 μm in diameter to that of 200-350 μm in diameter,

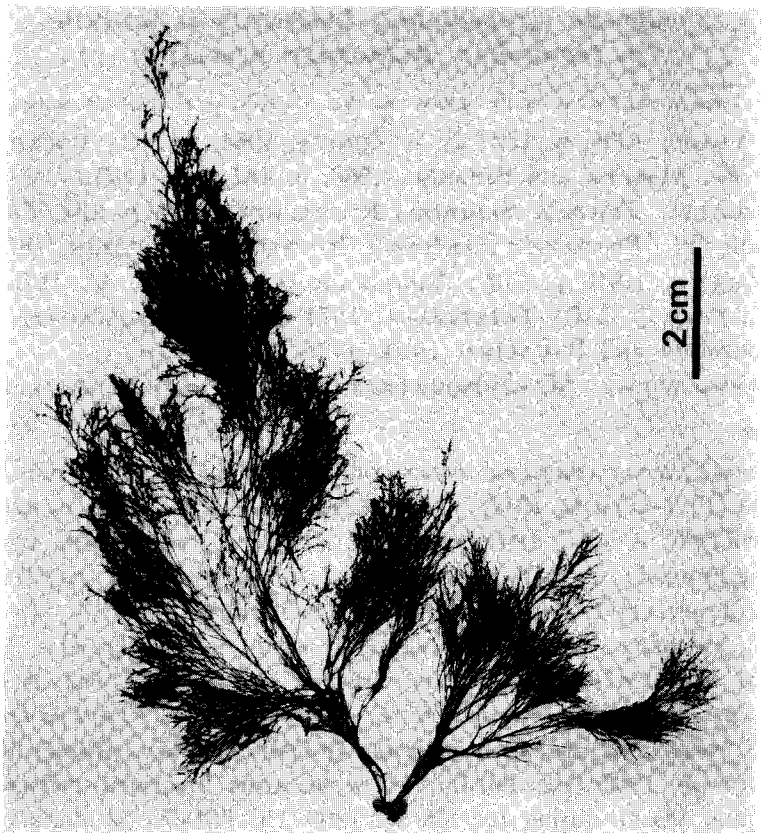

Fig. 6. *Rhodomela lycopodioides* (LINNAEUS) C. AGARDH f. *tenuissima* (RUPRECHT) KJELLMAN. Cystocarpic plant (parent for culture experiments) collected at Akkeshi on June 4, 1976 (SAP 032154).

and gradually becoming more slender upward; branches of the first order reaching a maximum length of 7–10 cm in the lower portion of the main axes, divided into progressively shorter and more slender branches; pericentral cells seven, sometimes six, surrounded by several layers of cortical cells; vegetative trichoblasts formed on the apical portion of the main axes and branches of any order, almost colorless, simple or divided once pseudodichotomously; plants dioecious; spermatangia borne on the apical portion of branches and covering the surface; procarps borne on the suprabasal segments of the fertile trichoblasts; mature cystpcarps enveloped by well developed pericarps, oblate to broadly ovoid, 230–300 μm × 320–450 μm; carpospores globular, dark red in color, 68.8–82.5 μm in diameter; tetrasporangia formed in pairs or solitarily in 3–16 successive segments in the up-

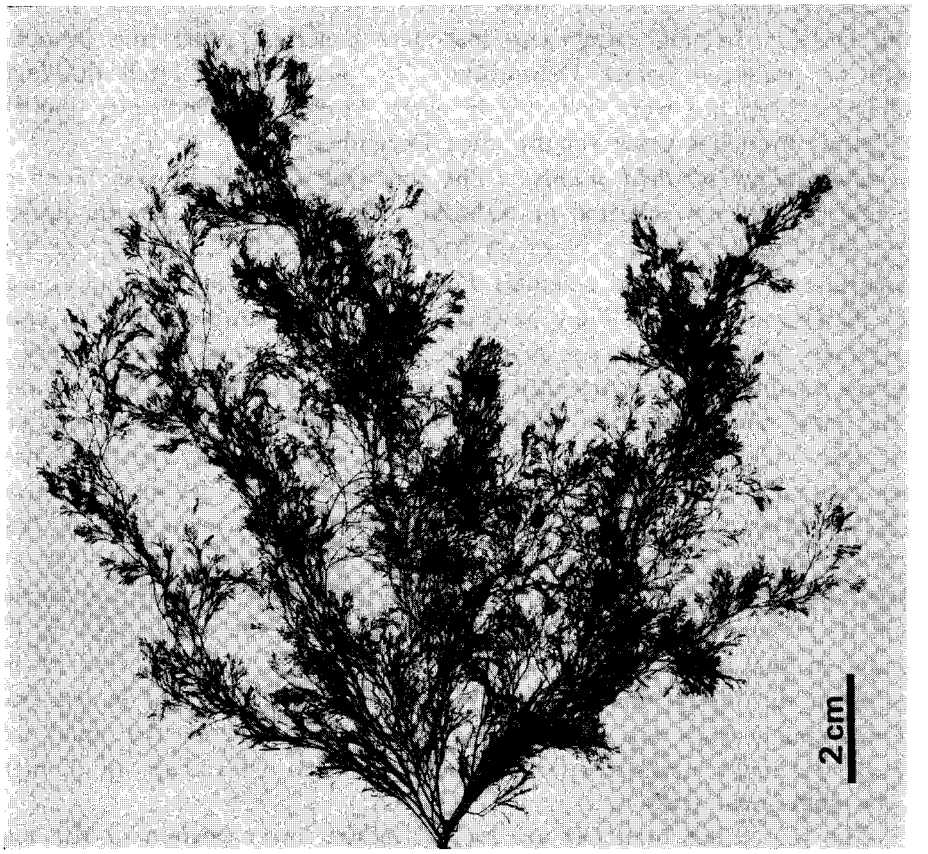

Fig. 7. *Rhodomela lycopodioides* f. *tenuissima*. Tetrasporangial plant (parent for culture experiments) collected at Akkeshi on June 4, 1976 (SAP 032155).

permost portion of branches; mature sporangia protruding from the branches, 107.5–125.0 μm × 95.0–112.5 μm; tetraspores 55.0–73.8 μm in diameter.

Observations

Habitat and Phenology: This alga grows on rocks or shells in depths between 3 and 5 m, judging from its frequent occurrence in the dredges at Akkeshi. Fertile plants were collected from early April to early July. The plants collected in early July were old and possessed a few cystocarps and tetrasporangia. The plants collected in August possessed only lower portions of the main axis and of the branches of the first and second orders (MASUDA and SHIMIZU, 1980, fig. 2). The plants collected in December had many short proliferous branches arising from the main axis and the first order

branches, although the second order branches fell off (MASUDA and SHIMIZU, 1980, fig. 3). Judging from these specimens collected, proliferous branches might be produced before December. The plants having well developed proliferous branches were collected in early April. This indicates that the proliferous branches grow rapidly after December.

Morphology of field plants: The following description was based on the first year plants collected at Akkeshi. Plants consist of several upright terete thalli arising from a common basal disc (Figs. 6, 7). They are dark brownish red in color and resemble *Polysiphonia* species in external appearance (RUPRECHT, 1850). They have soft texture and adhere closely to paper in drying. Fertile plants are 4.5–42.5 cm high, branched several times in a spiral manner and are provided with the sixth or seventh order branches in the most developed ones. Each upright thallus possesses a conspicuous main axis. The main axes are 350–660 μm in diameter just above the basal disc, becoming gradually thicker upward, and reach a maximum diameter of 500–1000 μm about 0.8–1.5 cm above the base. They taper abruptly from a portion of 400–700 μm in diameter to that of 200–350 μm (MASUDA and SHIMIZU, 1980, fig. 4). This depends on a sudden decrease of cortical layer development in this region. The cortex of the main axes is 2–3 layered in the upper slender portion (Fig. 8, A, B), whereas that is 6–7 layered in the lower thick portion (Fig. 8, C) and 4–5 layered in the transitional region from the thick to slender portions. Then, the main axes become gradually more slender upward and reach 90–150 μm in diameter in the uppermost portion.

The first order branches are longest in the lower portion of the main axes, reaching 7–10 cm in length and are divided into progressively shorter and more slender branches. The first order branches arising from the lower thick portion of the main axis grow in a manner similar to that of the main axes and become thicker in the proximal portion. The thicker portions of the main axes and the first order branches contrast strikingly with the upper filiform portions. These thicker portions are perennial and produce many proliferous branches probably in late autumn as stated above.

Adventitious branches arise sometimes from the lower portion of the main axis. They originate from the outermost cortical cells. This alga is devoid of axillary adventitious branches.

Vegetative trichoblasts are formed on the growing apex of the main axis and branches of any order. They are almost colorless, simple or divided once pseudodichotomously (MASUDA and SHIMIZU, 1980, figs. 9, 17, 18).

The fertile second year plants possess many well developed proliferous branches arising from the lower portions of old main axes and first order

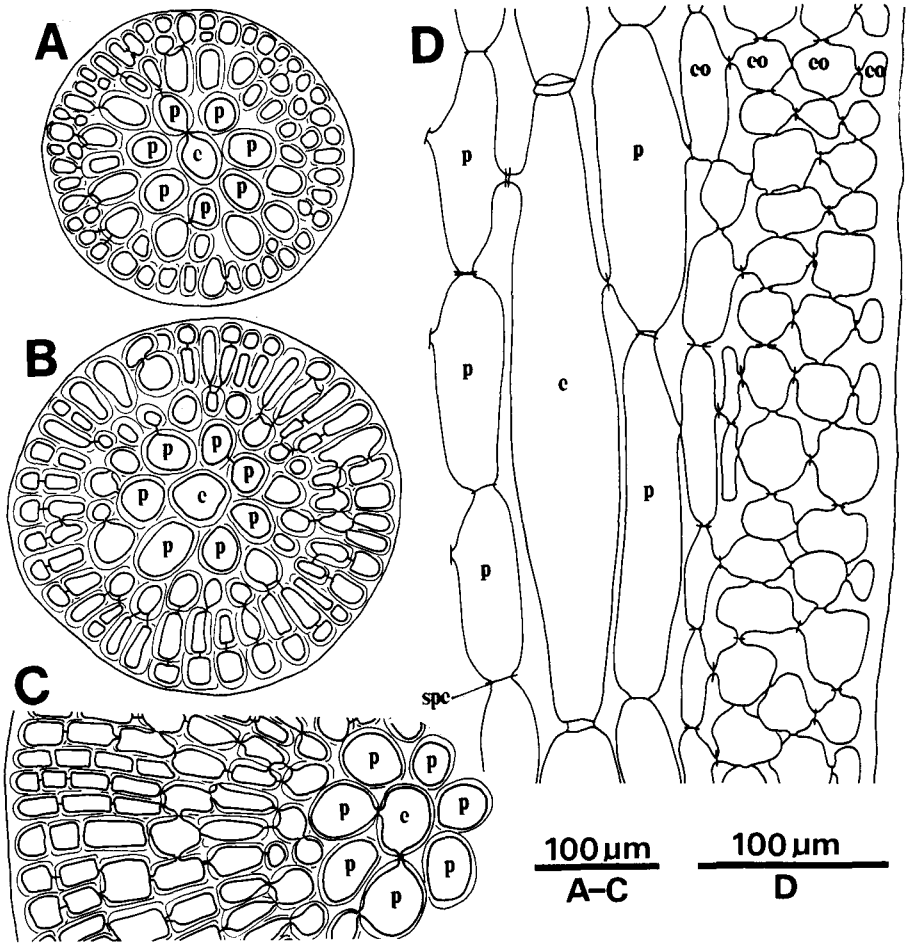

Fig. 8. *Rhodomela lycopodioides* f. *tenuissima*. A–C. Cross sections of a main axis: A, portion about 2.5 cm above the base; B, portion about 2.2 cm above the base; C, portion about 1.8 cm above the base. D. Longitudinal section of the lower portion of a main axis.

branches. These proliferous branches grow in a manner similar to that of the main axes of the first year plants. Thus, the second year plants show more complicated morphology than the first year plants.

The upright thalli are uniaxial and composed of a central axial cell, seven (sometimes six) pericentral cells and several layers of cortical cells (Fig. 8, A–C). Pericentral cells are divided transversely into two cells (sometimes three cells) (Fig. 8, D). The upper pericentral cell retains the pit-connection with the central axial cell, but the lower one becomes linked by

secondary pit-connection with a pericentral cell of the the underlying segment. The pericentral cells cut off two or three cortical cells outward. Each cortical cell is also divided transversely once or twice (Fig. 8, D). The cortical cells cut off one or two cortical cells outward. This process is repeated so that there is a 2-3 layered cortex in the upper portion of the main axes of the first year plant and a 8-10 layered cortex in their lower portion.

Spermatangia, procarps and tetrasporangia are formed on separate individuals. The spermatangia are borne superficially on the uppermost portion of ordinary branches (MASUDA and SHIMIZU, 1980, fig. 24). They cover the surface of the branches except for the apical monosiphonous segments (Fig. 9, A-C).

The procarps are produced from the suprabasal segments of fertile trichoblasts (Fig. 9, D, E) which issue from upper portion of branches. The fertile trichoblasts are simple or divided once pseudodichotomously. The mature procarp is enveloped with a pericarp and consists of a supporting cell, a 4-celled carpogonial branch and two groups of sterile cells. As the cystocarps develop, the monosiphonous portion of the fertile trichoblasts falls off. Ripe cystocarps are oblate to broadly ovoid and measure 230-300 μm in height and 320-450 μm in diameter (Fig. 9, F, G). Liberated carpospores are globular, dark red in color and measure 68.8-82.5 μm in diameter (Fig. 10, A).

The tetrasporangia are also borne on the uppermost portion of branches of ultimate and penultimate orders (MASUDA and SHIMIZU, 1980, fig. 19). They are formed usually in pairs or rarely solitarily in 3 to 16 successive segments of the branches. Each sporangium is provided with two cover cells (Fig. 9, H, I). Mature tetrasporangia protrude from the tetrasporangial branches and measure 107.5-125.0 μm $\times$ 96.0-112.5 μm in surface view. Thus, the mature tetrasporangial branches are moniliform (RUPRECHT, 1850). Liberated tetraspores are similar in morphology to carpospores except in the size (Fig. 10, B). They are smaller than the latter and 55.0-73.8 μm in diameter.

Culture study: Unialgal cultures were obtained from isolated tetraspores and carpospores, both of which were first cultured at 10°C, 16 : 8 LD and 15°C, 16 : 8 LD. No apparent difference was found in germination stage between both sporelings. The ontogeny of the carposporelings is described below. The carpospores attached to the substrate and differentiated a colorless rhizoid and pigmented upright shoot cells within one day (Fig. 10, C). The sporelings grew rapidly and straight at 10°C, 16 : 8 LD and 15°C. 16 : 8 LD (Fig. 10, D-F). Within 5 days, upright shoots formed the first

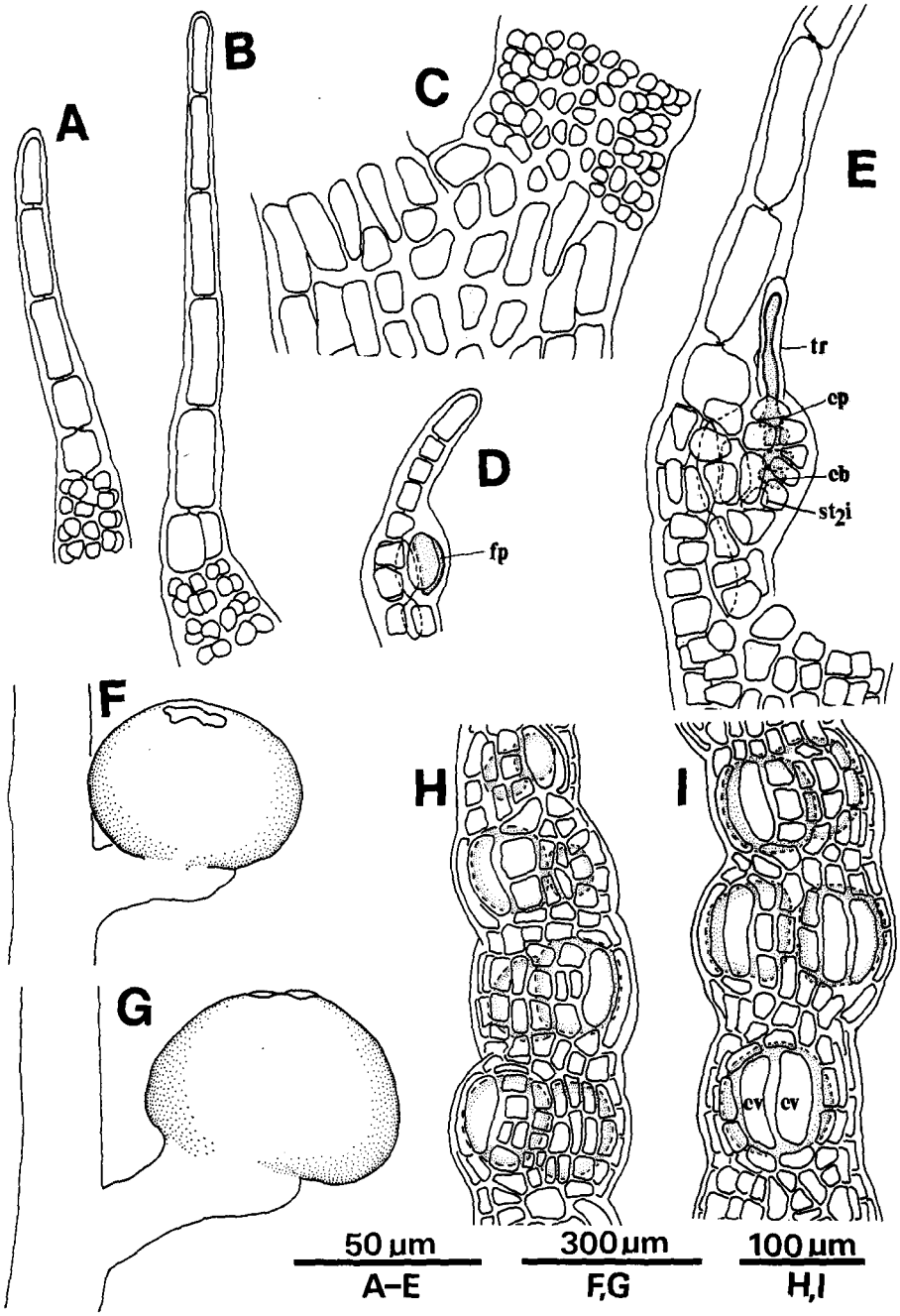

Fig. 9. *Rhodomela lycopodioides* f. *tenuissima*. A–C. Spermatangial branches, showing the apical portion in A and B, and the proximal portion in C. D–E. Female fertile trichoblasts bearing procarps. F, G. Mature cystocarps. H, I. Portion of tetrasporangial branches.

branch (Fig. 10, E; 11, A) which grew into a vegetative trichoblast later (Fig. 10, F; 11, B). Rhizoid cells were divided repeatedly to form the discoid holdfast (Fig. 10, F, J; 11, C–F). Subsequently, vegetative trichoblasts were produced successively from each segment of the primary axis of the sporelings in a spiral manner (Fig. 11, B). They were almost colorless (young ones being faintly pigmented) and grew up to 2 mm in length and

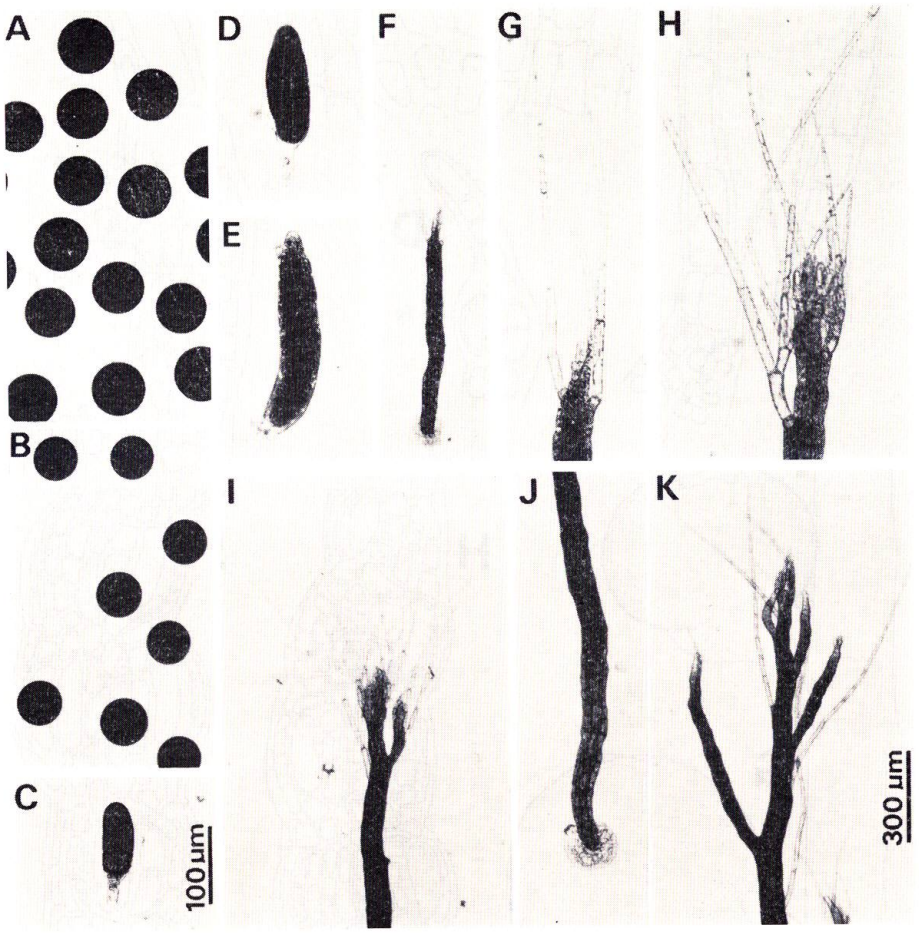

Fig. 10. *Rhodomela lycopodioides* f. *tenuissima*. A. Carpospores from a field-collected plant. B. Tetraspores from a field-collected plant. C–K. Development of carposporelings grown at 10°C, 16 : 8 LD (C–E) and 15°C, 16 : 8 LD (F–K): C, one day old; D, three days old; E, five days old; F, G, eight days old; H–J, fourteen days old; K, twenty-one days old.

Scale in C applies also to A, B, D, E, G, & H; scale in K applies also to F, I & J.

branch (Fig. 10, E; 11, A) which grew into a vegetative trichoblast later (Fig. 10, F; 11, B). Rhizoid cells were divided repeatedly to form the discoid holdfast (Fig. 10, F, J; 11, C–F). Subsequently, vegetative trichoblasts were produced successively from each segment of the primary axis of the sporelings in a spiral manner (Fig. 11, B). They were almost colorless (young ones being faintly pigmented) and grew up to 2 mm in length and

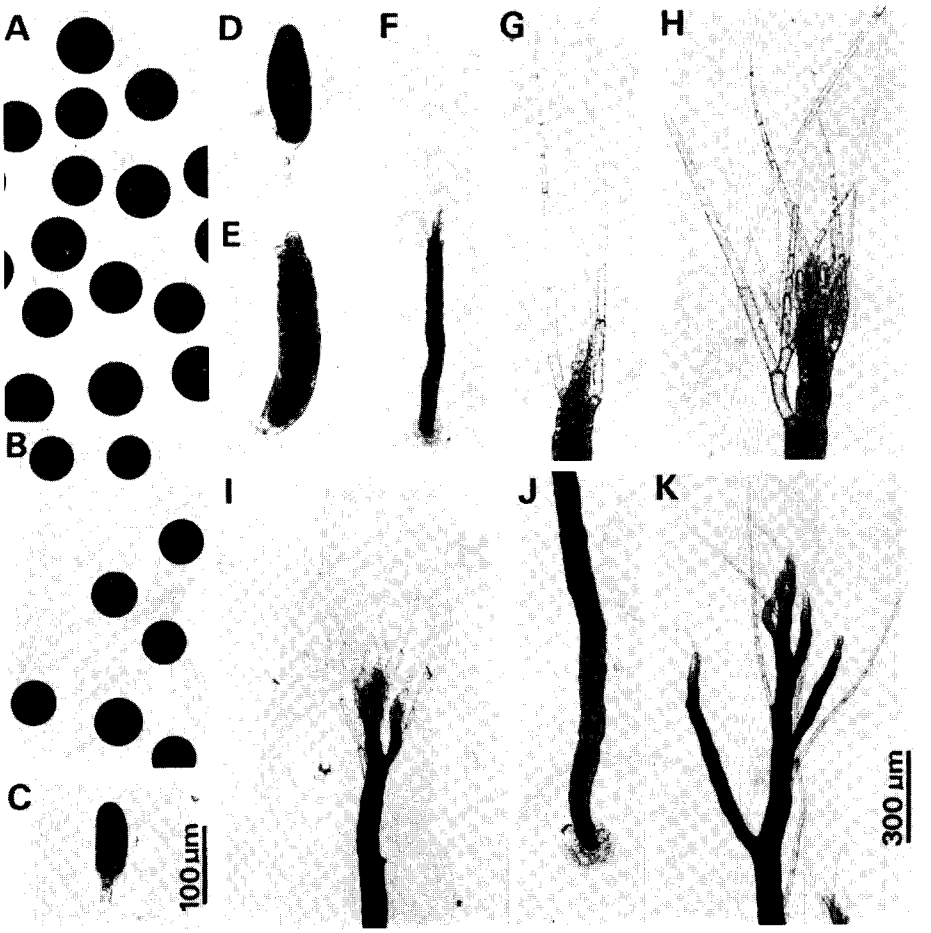

Fig. 10. *Rhodomela lycopodioides* f. *tenuissima*. A. Carpospores from a field-collected plant. B. Tetraspores from a field-collected plant. C–K. Development of carposporelings grown at 10°C, 16:8 LD (C–E) and 15°C, 16:8 LD (F–K): C, one day old; D, three days old; E, five days old; F, G, eight days old; H–J, fourteen days old; K, twenty-one days old.

Scale in C applies also to A, B, D, E, G, & H; scale in K applies also to F, I & J.

16 μm in diameter in the proximal portion. The majority of the trichoblasts were simple or branched once pseudodichotomously (Fig. 10, F-I; 11, B; 12, A, B) as were those of field-collected plants. A few of them were branched twice or thrice. The trichoblasts were deciduous and began to shed successively in the lower portion of sporelings.

After the formation of 10 or more trichoblasts from the primary axis an ordinary branch was produced replacing the trichoblasts within 14 days (Fig. 12, A, B). However, trichoblasts were produced again, two or three (sometimes five) successively replacing the ordinary lateral branch (Fig. 12, A, B) and then they were replaced by ordinary lateral branches (Fig. 10, K). This process was repeatedly several times within one month. Hence, vegetative trichoblasts were always present between the ordinary lateral branches on the primary axis. All the ordinary branches of the first order grew indeterminately as did the primary axis (Fig. 13). Adventitious branches were formed from surface cells of the lower portion of the primary axis (Fig. 11, G, H). They also grew indeterminately.

After one month, the plant reached up to 3 cm in length and produced 10-16 branches of the first order (Fig. 13). The branching intervals were irregular and ranged from 500 μm to 1.5 mm (sometimes to 3.5-5.0 mm). Secondary upright shoots were rarely formed from the surface of the discoid holdfasts. One-month-old cultures grown at 15°C, 16 : 8 LD were divided into five groups. The four groups were shifted to 5°C, 16 : 8 LD, 5°C, 8 : 16 LD, 10°C, 8 : 16 LD and 15°C, 8 : 16 LD, respectively. Another group was maintained at 15°C, 16 : 8 LD. The cultures grown at 10°C, 16 : 8 LD was maintained at the same condition. The primary axis of the plants cultured at each condition became thick in the lower portion as did field plants. This feature was especially conspicuous in the plants cultured at 15°C, 16 : 8 LD and 15°C, 8 : 16 LD (Fig. 14). Furthermore, the plants cultured at the two conditions bore fewer branches. On the contrary, the plants cultured at 5°C, 16 : 8 LD and 5°C, 8 : 16 LD bore many branches in a manner similar to that of field plants.

No reproductive structures were observed on cultured plants after one year. Then, apical tips of the main axes were cut 3-5 cm in length and continued to culture at each condition. The excised tips grew well as did the sporelings. After 3 months, the plants grown at 5°C, 16 : 8 LD and 5°C, 8 : 16 LD reached reproductive maturity (Fig. 15, A) and formed tetrasporangia (Fig. 15, C). The tetrasporangia were borne on the uppermost portion of the first to fourth order branches in two rows of 3-10 successive segments. Mature tetrasporangia were 85-100 μm × 83-93 μm in size. Moniliform branches bearing mature tetrasporangia (Fig. 15, C) are similar to

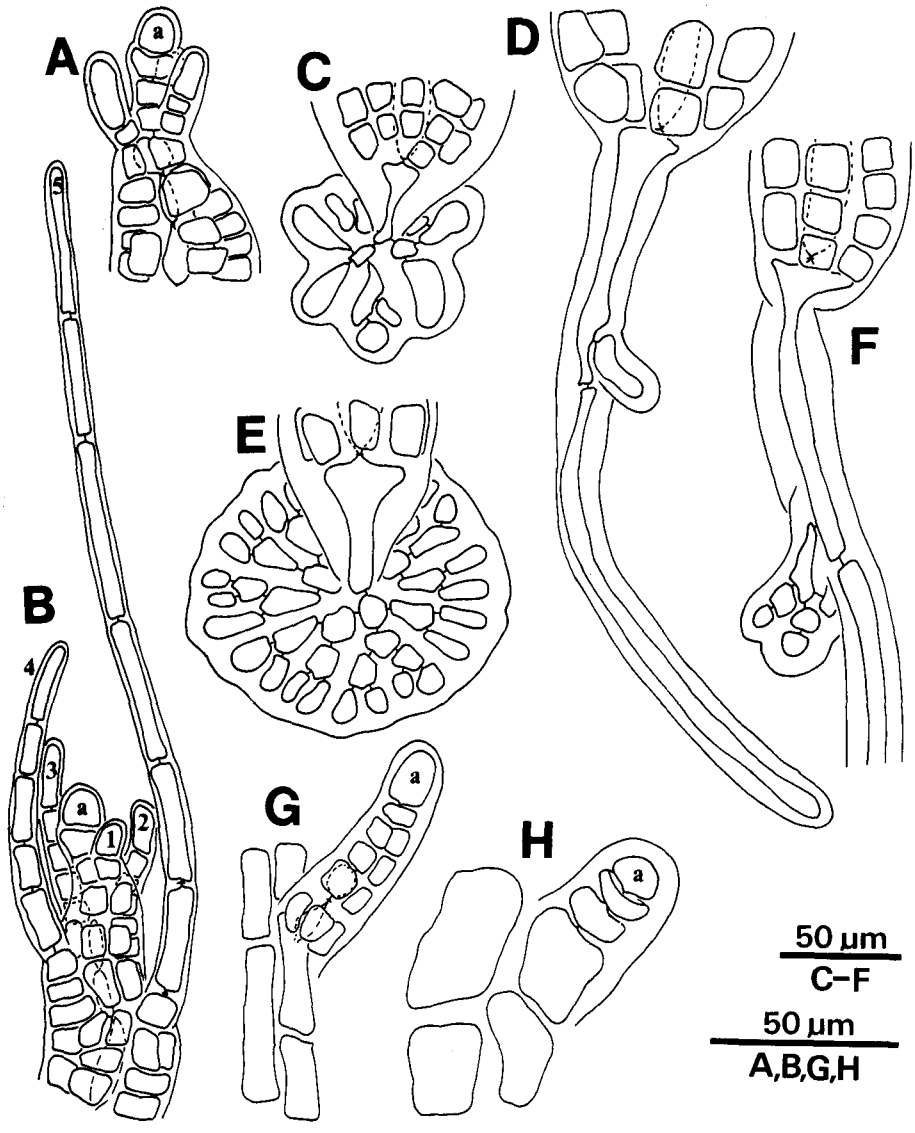

Fig. 11. *Rhodomela lycopodioides* f. *tenuissima*. A, B. Stages in the development of the apical portion of sporelings grown at 15°C, 16:8 LD: A, five-day-old sporeling; B, eight-day-old one forming spirally arranged trichoblasts numbered in their sequence of formation. C–F. Stages in the development of the basal disc grown at 15°C, 16:8 LD (C–E) and at 10°C, 16:8 LD (F): C, D, five days old; E, F, eight days old. G, H. Young adventitious branches formed from the surface cells of the main axis of the sporelings grown at 15°C, 16:8 LD (surface view): G, fourteen days old; H, twenty-one days old.

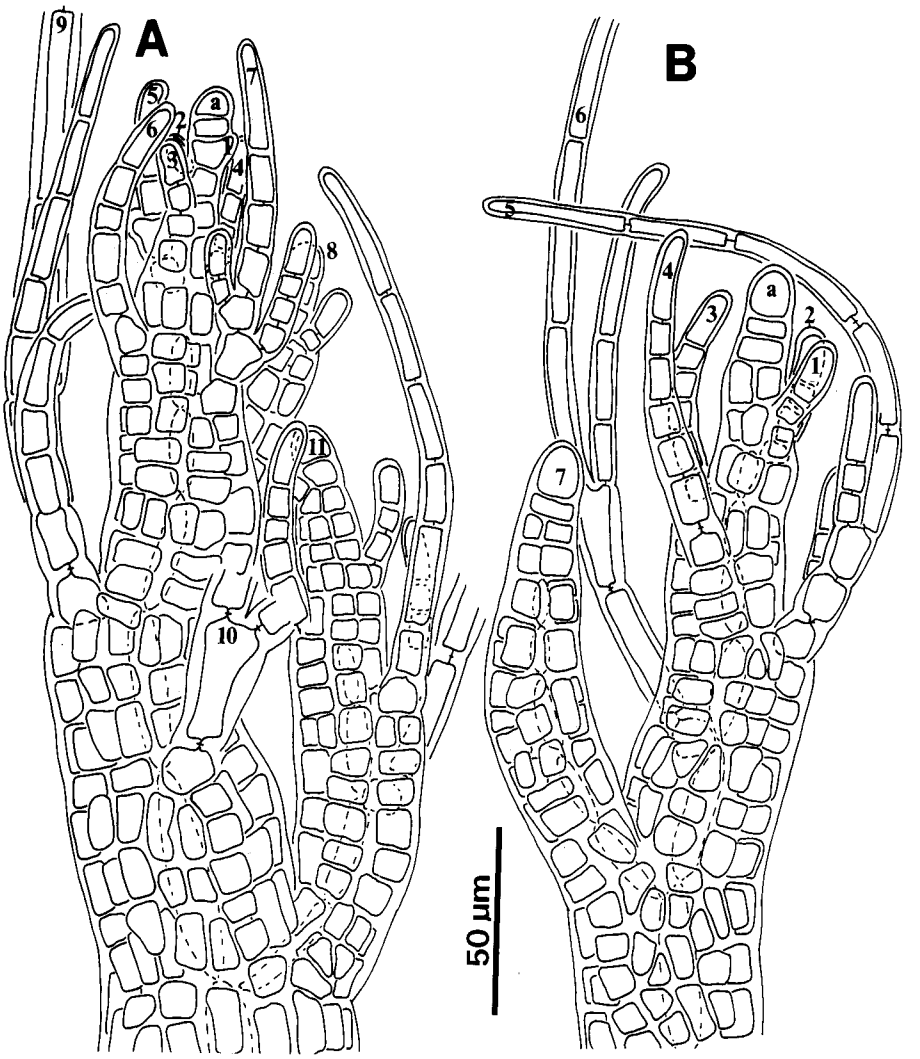

Fig. 12. *Rhodomela lycopodioides* f. *tenuissima*. A, B. Apical portion of 14-day-old sporelings grown at 15°C, 16 : 8 LD, showing the spiral arrangement of trichoblasts and ordinary branches numbered in their sequence of formation.

those of field-collected plants. Liberated tetraspores averaged 66 µm (55-75 µm) in diameter. No plants became reproductive in the other four conditions after 6 months and then, the cultures were terminated.

The tetraspores, which were liberated from the plants grown at 5°C, 16 : 8 LD and 5°C, 8 : 16 LD, germinated and grew into plants similar in

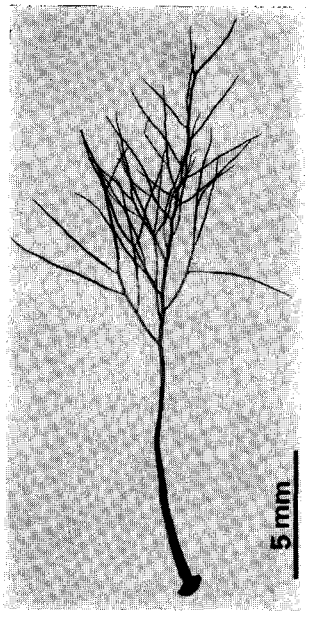

Fig. 13. *Rhodomela lycopodioides* f. *tenuissima*. One-month-old plant grown at 15°C, 16 : 8 LD.

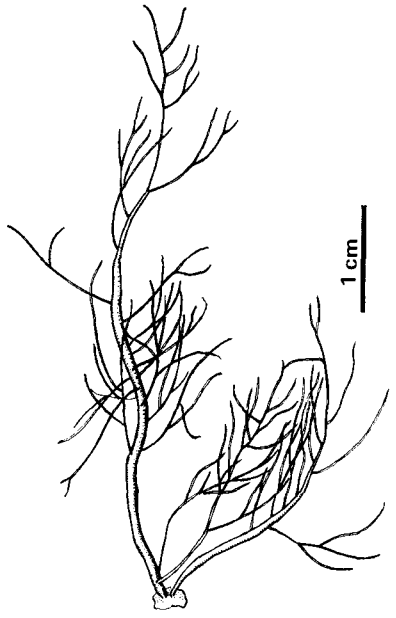

Fig. 14. *Rhodomela lycopodioides* f. *tenuissima*. Two and a half months old plant grown at 15°C, 16 : 8 LD.

morphology to parent tetrasporophytes. These plants reached reproductive maturity 6 months after germination at both conditions (Fig. 15, B). They produced spermatangia and procarps on separate individuals (Fig. 15, D, E) in a manner similar to that of field-collected plants. The spermatangia and procarps were borne on the uppermost portion of the first to fourth order branches (Fig. 15, D, E). Cystocarps appeared only when female plants were mixed with male plants bearing spermatangia, but they did not become mature. Well developed cystocarps on the female plant measured 250–260 μm in length and 200–210 μm in diameter.

Tetrasporelings derived from field-collected plants, which were cultured by the same conditions and procedure as in the aforementioned carposporelings, showed a morphological variation similar to that of the carposporelings according to culture conditions attempted. They bore spermatangia and procarps only at 5°C, 16 : 8 LD and 5°C, 8 : 16 LD. However, no cystocarp development was observed, although female and male plants were mixed in a single culture.

Thus, cultured plants of this alga bore reproductive structures only at 5°C, 16 : 8 LD and 5°C, 8 : 16 LD. Furthermore, cultured plants grown at

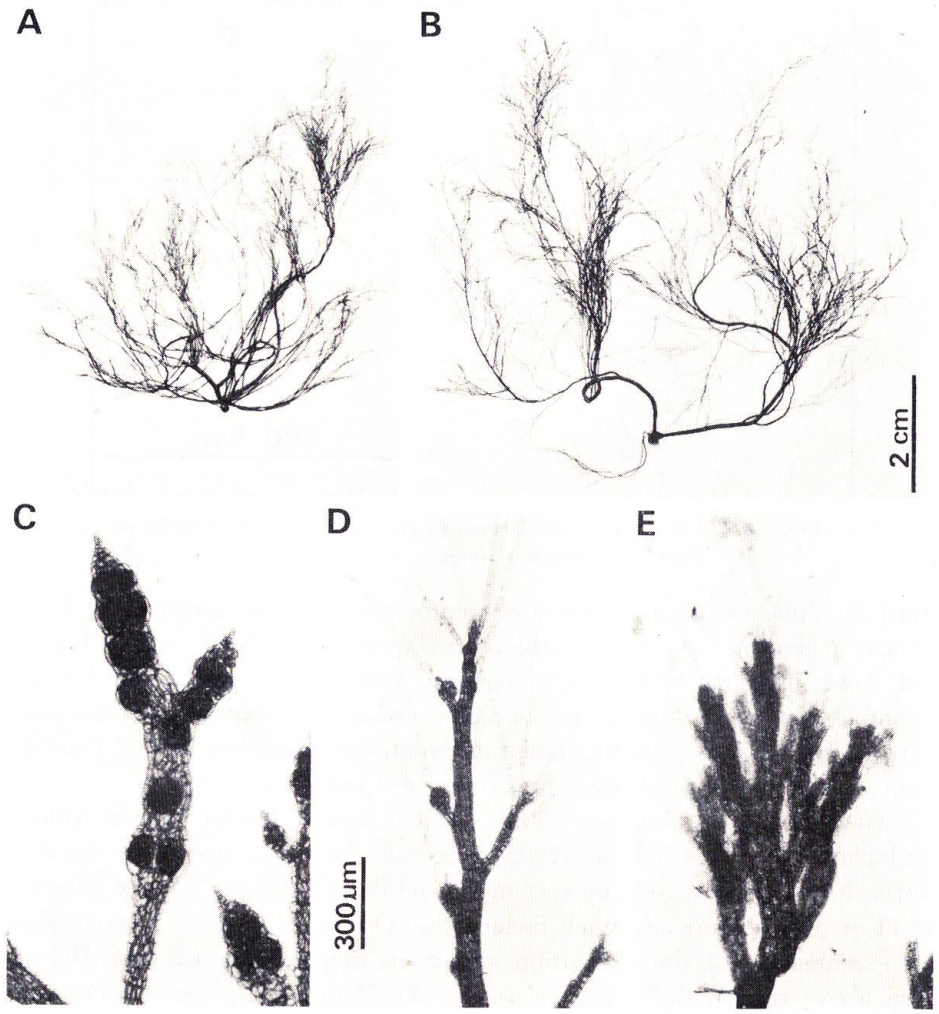

Fig. 15. *Rhodomela lycopodioides* f. *tenuissima*. A. Fertile tetrasporangial plant (fifteen months old) grown at 15°C, 16 : 8 LD for one month and then shifted to 5°C, 16 : 8 LD. B. Six-month-old fertile spermatangial (right) and procarpic plant (left), whose basal discs coalescing. C. Tetrasporangia formed on the plant shown in A. D. Procarps borne on the plant shown in B. E. Spermatangial branches borne on the plant shown in B.
Scale in B applies also to A ; scale in D applies also to C & E.

15°C showed irregular development as growth advanced, but the plants shifted to 5°C grew well and showed a morphology similar to field plants collected from December to June. In the field, this species became fertile

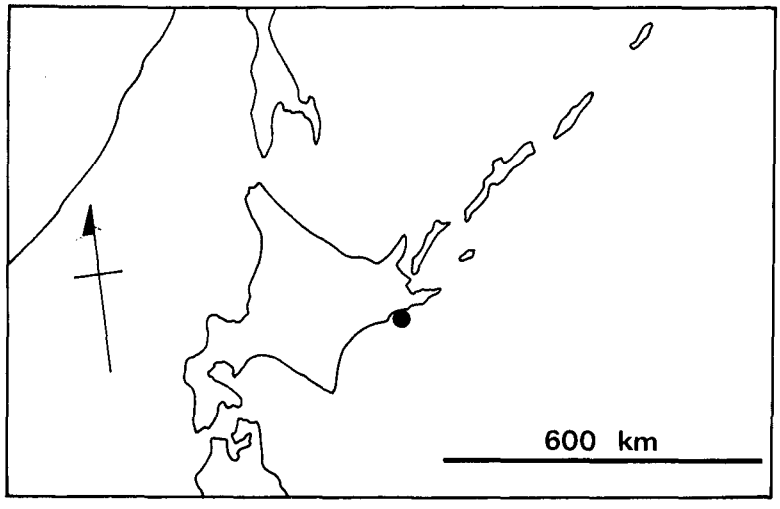

Fig. 16. Distriburion of *Rhodomela lycopodioides* f. *tenuissima* in Japan and adjacent waters.

April to June when the seawater temperatures were about 3-11°C. In August when the seawater temperatures were about 16°C only old plants with lower portions of the main axis and of the branches of the first and second orders were found. In December when the seawater temperatures were about 2°C, plants with numerous proliferous branches issuing from the main axes and the first order branches were collected.

Geographic distribution: This alga has been collected only at Akkeshi in Japan (Fig. 16). YENDO (1909) reported this alga from the northern Kurile Islands. However, no specimen referable to the alga is now deposited in TI or SAPA, both of which include the YENDO collection of marine algae. An examination of the herbarium specimens deposited in LE and UC and cited above reveals that this alga is also distributed along the western coast of the Sea of Okhotsk and the coast of Alaska.

Taxonomic discussion

The aforementioned alga found in Japan is identical with the alga described by RUPRECHT (1850) in every respect (MASUDA and SHIMIZU, 1980). This alga was originally described on the basis of materials collected from Larga Angra, Dshukshandran, Nichta and Mamga, western coast of the Sea of Okhotsk (RUPRECHT, 1850). It was transferred to *Rhodomela* by KJELLMAN (1875). Later, KJELLMAN (1883) treated it as one of infraspecific taxa of *Rhodomela lycopodioides* (LINNAEUS) C. AGARDH.

According to KJELLMAN (1883), *R. lycopodioides* includes five forms

and seven subforms. I could not obtain materials of other infraspecific taxa than f. *tenuissima* for detailed investigation. The illustrations given by TURNER (1808) and HARVEY (1846-51) show a habit of which the main axes are covered densely with short branches like the genus *Lycopodium* of the Lycophyta. This form is considered to be the typical form of *R. lycopodioides* (KJELLMAN, 1883). The alga under discussion is distinguished from the typical form by the absence of short branches covering densely the main axis. Recently, the phycologists of the Union of Soviet Socialist Republics have adopted a KJELLMAN's former combined name, *R. tenuissima* (RUPRECHT) KJELLMAN (1875) to the alga under discussion (A. D. ZINOVA, 1970; VINOGRADOVA, 1973 b, 1978; GRINTAL, 1974; TOLSTIKOVA, 1974; KLOCZCOVA, 1976; KLOCZCOVA and BYVALINA, 1979). However, according to JAASUND (1965) who studied on the marine algal vegetation of northern Norway, *R. lycopodioides* is a very variable and common alga in northern Norway. He stated as follows. (1) *R. lycopodioides* f. *typica* subf. *compacta* is the dominant type occurring in the lower intertidal zone on exposed rocks. (2) Sublittoral plants collected in an inlet on Sandvaer looked like *R. subfusca* (=*R. confervoides*) as encountered in South Scandinavea with plants up to 35 cm in length. (3) The forms *laxa*, *setacea*, *tenera*, and *cladostephus* were encoutered in pools in the fjords. Thus, variations in *R. lycopodioides* seem to depend, at least, partly on environmental conditions. At present I am unable to assess the influence of environmental factors on the variability of *R. lycopodioides*. Further experimental analysis of the variability of *R. lycopodioides* is necessary. Until sufficient data has been obtained, I treat the alga as one of infraspecific taxa of *R. lycopodioides*.

Rhodomela sachalinensis MASUDA, sp. nov.

Synonyms: *Rhodomela macracantha* SETCHELL in TOKIDA (non *Lophura macracantha* KÜTZING) 1934, p. 25, 1949, p. 69, 1954, p. 222; OKAMURA, 1936, p. 900; TAZAWA, 1957, p. 34, pl. 1 (4).

Rhodomela subfusca auct. non C. AGARDH; OKAMURA, 1922 (*pro parte*), p. 151, pl. 186, fig. 3; KAWABATA, 1936 (*pro parte*), p. 212; NAGAI, 1941 (*pro parte*), p. 235.

Japanese name: Karafuto-fujimatsumo (nom. nov.)

Materials

The specimens examined were collected at Utoro, Rausu, Hanasaki and Akkeshi in Hokkaido from 1968 to 1972. Utoro: *Masuda* 6563, 6564, 6573-84 & 12982-13008 (v-1968, young sterile; vi-1969, sterile & tetrasporangial;

vii-1968, spermatangial & tetrasporangial; viii-1968, old sterile & tetrasporangial). Rausu: *Masuda* 6565-72, 6585-6619, 6683, 9566-9568 & 13009 (v-1968, young sterile; vi-1969, sterile; vii-1968, sterile & procarpic; viii-1968, tetrasporangial; ix-1971, cystocarpic & tetrasporangial; x-1968, old tetrasporangial). Hanasaki: *Masuda* 9452-9565 (vii-1970, spermatangial & tetrasporangial, leg. I. YAMADA; ix-1970, tetrasporangial; x-1970, cystocarpic & tetrasporangial). Akkeshi: *Masuda* 9389-9451 (vi-1970, sterile; vi-1971, sterile).

Furthermore, the herbarium specimens deposited in several herbaria quoted below were examined. KURILES Etorof Island: NAGAI Herb. in SAPA (Bettobu, viii-1930, tetrasporangial; Toshirari, viii-1931; Shibetoro, viii-1931), YENDO Herb. in TI (Rubetsu, vi-1906). Kunashiri Island: SAP 22035 (Sokobetsu, viii-1931), NAGAI Herb. (Atoiya, viii-1929; Rebun-iso, vii-1929; Ponkotan, vii-1936, cystocarpic & tetrasporangial; Kotankeshi, viii-1936, tetrasporangial; Toshoro, viii-1931, tetrasporangial; Sokobetsu, viii-1931). SAKHALIN SAP 21290 (Kaihyo-to, vii-1930), TOKIDA Herb. (Yoman, vii-1935, spermatangial; viii-1935, tetrasporangial; Kitashiretoko, viii-1935, spermatangial; Higashisoya, viii-1929, tetrasporangial; Airo, vii-1906, tetrasporangial; Nakashiretoko, viii-1906, tetrasporangial). HOKKAIDO Abashiri: SAP 20033 (vi-1934). Nemuro: SAP 11342 & 12499 (viii-1929).

The following plants were used for culture experiments: cystocarpic plants collected at Rausu on September 21, 1971, at Hanasaki on October 17, 1970; tetrasporangial plants collected at Rausu on September 21, 1971, at Hanasaki on September 27, 1970 and October 17, 1970; sterile plants collected at Akkeshi on June 21, 1970.

Description

Plantae annuae, thallis rectis pluribus e disco basali et stolonibus effectis; thalli recti teres, spiratim ramosissimi usque ad ramos ordinis quarti, usque ad 28 cm in altitudine attingentes, in colore atrobrunneolo-rubri ubi vivi, in sicco denigrati, ad tactum molles, exsiccatione chartae adhaerentes; axis principalis rectus vel leviter flexuosus, 850-1000 μm in diametro ad partem infimam, diametrum maximum ad partem tertiam infernam 950-1600 μm attingens; ramuli determinati spiniformes breves abundantes ad partes infernas axium principalium et ramorum indeterminatorum; rami adventitii numerosi, apprime ad axillam; cellulae pericentrales 6, a stratis pluribus cellularum corticearum circumcinctae; trichoblasti vegetativi in parte apicali ramorum portati, abundantes, in colore roseoli, pseudodichotome 4-vel 5-ies ramosi; plantae dioeciae; spermatangia in ramulis determinatis simplicibus ramorum usitatorum et adventitiorum axillarium formata; cystocarpia in

ramis adventitiis axillaribus portata, globosa, 380–500 μm × 380–550 μm ; carposporae globulares, in colore atrorubrae, 60–70 μm in diametro ; tetrasporangia primo in ramulis determinatis simplicibus ramorum usitatorum et postea in ramulis dense aggregatis ramorum adventitiorum axillarium formata, in series duas ad 5–7 segmenta successiva ramulorum, omnino cellulis obtectis duabus instructa, 88–100 μm × 95–105 μm, tetraedrice divisa ; tetrasporae 50–65 μm in diametro.

Holotypus : Specimen tetrasporangiferum (SAP 031874)

Plants annual, with several upright thalli arising from a basal disc and stolons ; upright thalli terete, much branched spirally up to fourth order branches, attaining up to 28 cm in height, dark brownish-red in color when fresh, turning to black in drying, soft to the touch, adhering to paper in drying ; main axis straight or slightly flexuous, 850–1000 μm in diameter at the lowest portion, reaching a maximum diameter of 950–1600 μm in the lower third portion ; short thorn-like determinate branchlets abundant in the lower portion of main axes and indeterminate branches ; adventitious branches numerous, especially in the axil ; pericentral cells 6, surrounded by several layers of cortical cells ; vegetative trichoblasts borne on the apical portion of branches, abundant, light rose in color, divided 4–5 times pseudodichotomously ; plants dioecious ; spermatangia formed on simple determinate branchlets of ordinary and axillary adventitious branches ; cystocarps borne on axillary adventitious branches, globose, 380–500 μm × 380–550 μm ; carpospores globular, dark red in color, 60–70 μm in diameter ; tetrasporangia first formed on simple determinate branchlets of ordinary branches, and later on densely aggregate branchlets of adventitious branches, in two rows on 5–7 successive segments of the branchlets, each provided with two cover cells, 88–100 μm × 95–105 μm, divided tetrahedrally ; tetraspores 50–65 μm in diameter.

Holotype : SAP 031874 (*Masuda* 6590) tetrasporangial secimen collected at Rausu, Shiretoko Peninsula, Hokkaido, on August 22, 1968 by Y. YAMADA and M. MASUDA (Pl. 3, A).

Observations

Habitat and *Phenology* : This plant grows on rocks usually in the upper sublittoral zone and sometimes in the lower intertidal zone in the shade of rocks. It appears in late spring and reaches a maximum length of about 28 cm in August. The growing season continues to late autumn when the upright portion of the plant is lost. Mature spermatangial and procarpic plants are found at the beginning of July. Mature cystocarpic and tetrasporangial plants can be collected from the end of August to Octo-

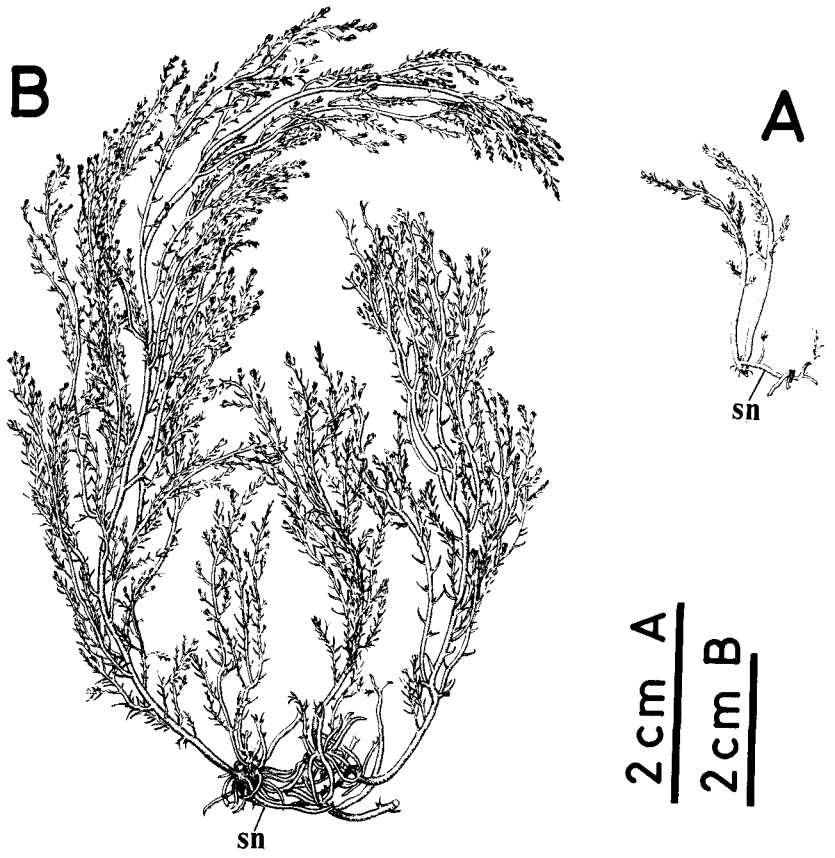

Fig. 17. *Rhodomela sachalinensis* MASUDA. A, B. Habit of young plants arising from a basal disc and stolons.

ber. Old eroded plants are found in the end of October and no plants are found during winter to mid-spring. No proliferous branches were observed in the material examined. Thus, this species seems to be a summer annual.

Morphology of field plants: The following account is based on plants collected at the type locality, Rausu, unless otherwise indicated. Plants consist of several upright thalli arising from a small disc and well developed stolons (Fig. 17). Several plants entangle with each other, assembling usually in clumps (Pl. 3, B–D). The stolons are produced adventitiously from the lower portion of the main axis of the upright thallus and are fastened to the substrate by small discs. They produce several upright axes adventitiously from the outermost cortical cells (Fig. 18, A). Plants are dark brownish red in color. They are soft in texture, adhering to paper in drying, but become harder as they grow old.

Each erect thallus of well developed plants is provided with fourth order branches. It has a conspicuous main axis which is straight or slightly flexuous (Pl. 3; Fig. 17). Main axes of young plants are denudate below (Fig. 17, A), but they become crowded in mature plants because stolons issue from the lower denudate portion. Main axes of mature plants are attenuate toward the base and 850–1000 μm in diameter at the lowest portion, becoming slightly thicker upward up to 950–1600 μm in the lower third portion and gradually more slender upward. However, in several fertile plants collected at Utoro main axes are not attenuate toward the base. The first order branches are produced in a spiral manner. They originate from the central cells of the apical portion of the main axis. One branch is formed per segment (Fig. 19). The first order branches develop in a manner similar to that of the main axis and bear progressively shorter and more slender branches. However, the several lower branches of the main axis do not develop well and often were not branched as in *R. confervoides*. They become determinate branchlets which take on a thorn-like shape and reach up to 1.5 mm long. The lower portion of the indeterminate branches of any order is provided with short thorn-like determinate branchlets as in the main axis (Pl. 7, B).

Axillary adventitious branches are produced from the outermost cortical cells and usually become fertile branches (Pl. 7, C, F; Fig. 20, A). Sometimes, axillary branches grow well, reaching up to 1.5 cm in length and also produce secondary, fertile axillary branches. In this alga the axillary branches are regularly formed in both gametangial and tetrasporangial plants.

Vegetative trichoblasts are common on the apical portion of branches. They are produced from the central cell in each segment and arranged in a spiral manner. They reach up to 1 mm in length or more and are divided 4 or 5 times in a pseudodichotomous manner. The first branching takes place in the suprabasal segment. The basal segment is always embedded in the cortex of branches bearing it. Young trichoblasts are rose in color, but they become lighter as they grow. Fully grown ones are almost colorless and eventually fall off.

The thallus structure of this species is essentially in agreement with that of *R. confervoides* and *R. lycopodioides* f. *tenuissima* described previously (Pl. 8, F–H; Fig. 18, B). The central cells of the main axis are 200 μm long near the base and reach up to 5 mm in the middle portion. Their length corresponds to the branch interval except in the lower portion where ordinary branches are absent and only adventitious stolons are present. Each pericentral cell is divided only one time transversely (Fig. 18, B). Cortices consist of 6–10-cell layers in the lowest portion of the main axis and

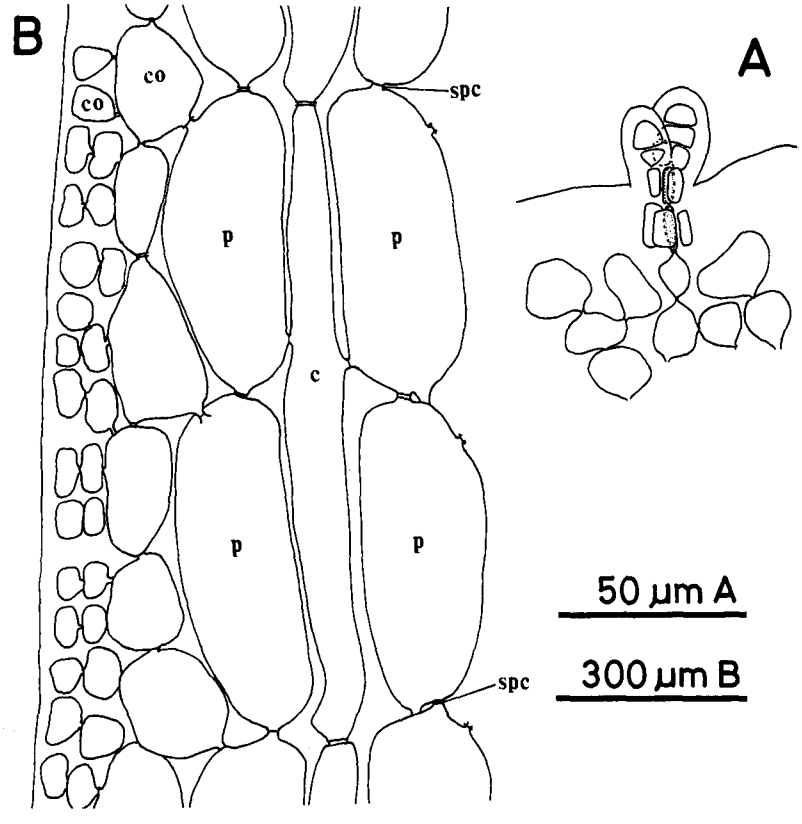

Fig. 18. *Rhodomela sachalinensis.* A. Longitudinal section of a stolon, showing an upright shoot developed from an outermost cortical cell. B. Longitudinal section of a determinate branchlet, showing the arrangement of central cells, pericentral cells (each divided trnsversely into two cells), and 2-3 layers of cortical cells.

6-8-cell layers in the middle portion. In well developed plants cortical cells of the lower portion of the main axis form a very tightly packed outer cortex which has 4-6 layers of cells (Pl. 8, F) as in *R. confervoides.*

Spermatangia, carpogonia and tetrasporangia are produced on separate plants. The spermatangia are formed superficially on unspecialized simple determinate branchlets of axillary branches (Pl. 7, C; Fig. 19). They are also produced on branchlets issuing from the apical portion of ordinary branches (Pl. 7, D). These spermatangial branchlets are slightly incurved and measure 200-600 μm long and 40-100 μm in diameter. The apical and proximal portions of the fertile branchlets remain sterile. The development of spermatangia is very similar to that of *R. confervoides.* However,

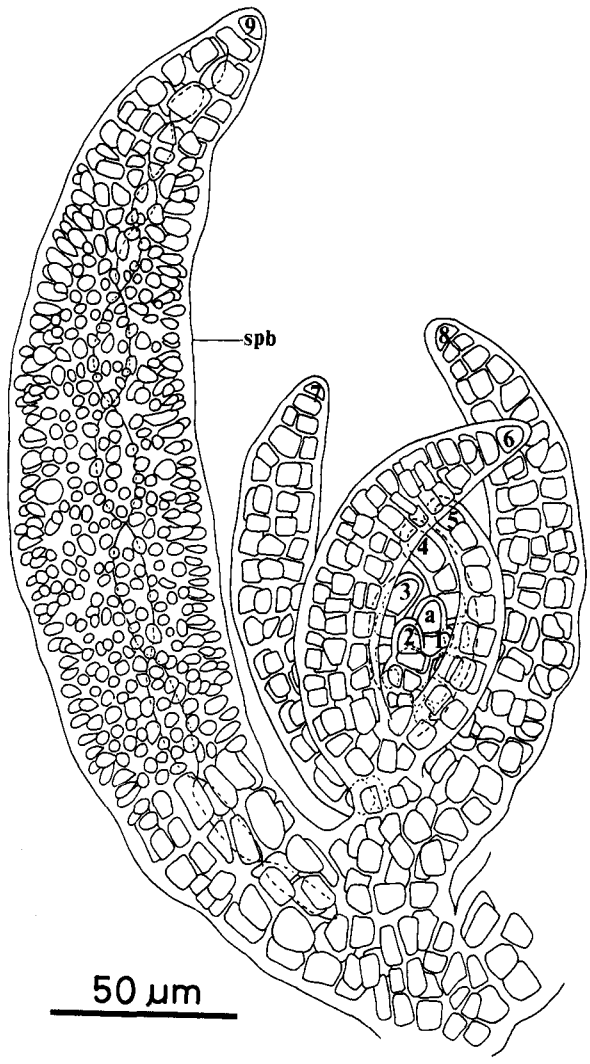

Fig. 19. *Rhodomela sachalinensis.* Tip of an axillary adventitious branch of a spermatangial plant forming spirally arranged spermatangial branchlets numbered in their sequence of formation.

the spermatangial formation is restricted to the simple determinate branchlets in this alga, whereas that of *R. confervoides* extends to the upper portion of the indeterminate branches.

The procarps are produced from the suprabasal segment of trichoblasts (Fig. 20, A, B). The fertile trichoblasts resemble vegetative trichoblasts described already in many respects and arise just behind the apex of the

axillary branches (Fig. 20, A). They are successively formed on the upper portion of the branches and arranged in a spiral manner (Fig. 20, A). One trichoblast is formed per segment. The development of the procarp is essentially in agreement with that of *R. confervoides*. The procarp before fertilization consists of a supporting cell, a 4-celled carpogonial branch and two groups (lateral and basal) of sterile cells (Fig. 20, B). Mature cystocarps are furnished with well developed pericarps, globose in shape, and measuring 380–500 μm in length and 380–550 μm in diameter (Fig, 20, C). Liberated carpospores are globular in shape, dark red in color, and measure 60–70 μm in diameter (Pl. 4, A).

The tetrasporangia are borne on simple determinate branchlets of ordinary branches (Pl. 7, E) as well as of axillary branches (Pl. 7, F). In the young fertile plants collected in June and July, tetrasporangial branchlets occur commonly on ordinary branches and sometimes on axillary branches. In accordance with the description of TOKIDA (1949), fully mature plants collected in August and September have only tetrasporangial branchlets borne on the axillary branches (Pl. 7, F). The tetrasporangial branchlets are densely aggregated and one of the characteristics of this species as pointed out by TOKIDA (1949). Two tetrasporangia are produced in each of 5–7 successive segments of the branchlets. Each sporangium is protected with two cover cells. Mature sporangia measure 88–100 μm $\times$ 95–105 μm in surface view and is divided tetrahedrally. Liberated tetraspores are identical with carpospores except in the size (Pl. 4, B). They are smaller than the latter and measure 50–65 μm in diameter.

Plants growing in the lower intertidal zone of a relatively wave exposed area at Hanasaki are smaller than those from Rausu and Utoro, which usually grow in the sublittoral zone. They reach up to 10 cm high and the first order branches are more closely set on the main axis (Pl. 3, D). However, the Hanasaki plant is identical with the Rausu plant in other respects. In addition, plants collected in tide pool at Hanasaki were as well developed as the Rausu plant. Cultured plants from the two localities demonstrate that they are morphologically in agreement with each other as will be shown later. Thus, the gross morphological dissimilarity shown by the Rausu and Hanasaki plants seems to be affected by different environments.

Culture study: Unialgal cultures were obtained from both isolated carpospores and tetraspores of the Rausu and Hanasaki plants as well as excised apical tips of indeterminate branches of the Akkeshi plant. Isolated spores were first cultured at 14°C, 14 : 10 LD. There was no difference in germination between the tetraspores and the carpospores in both the Rausu and the Hanasaki plants. The following description is based on the observa-

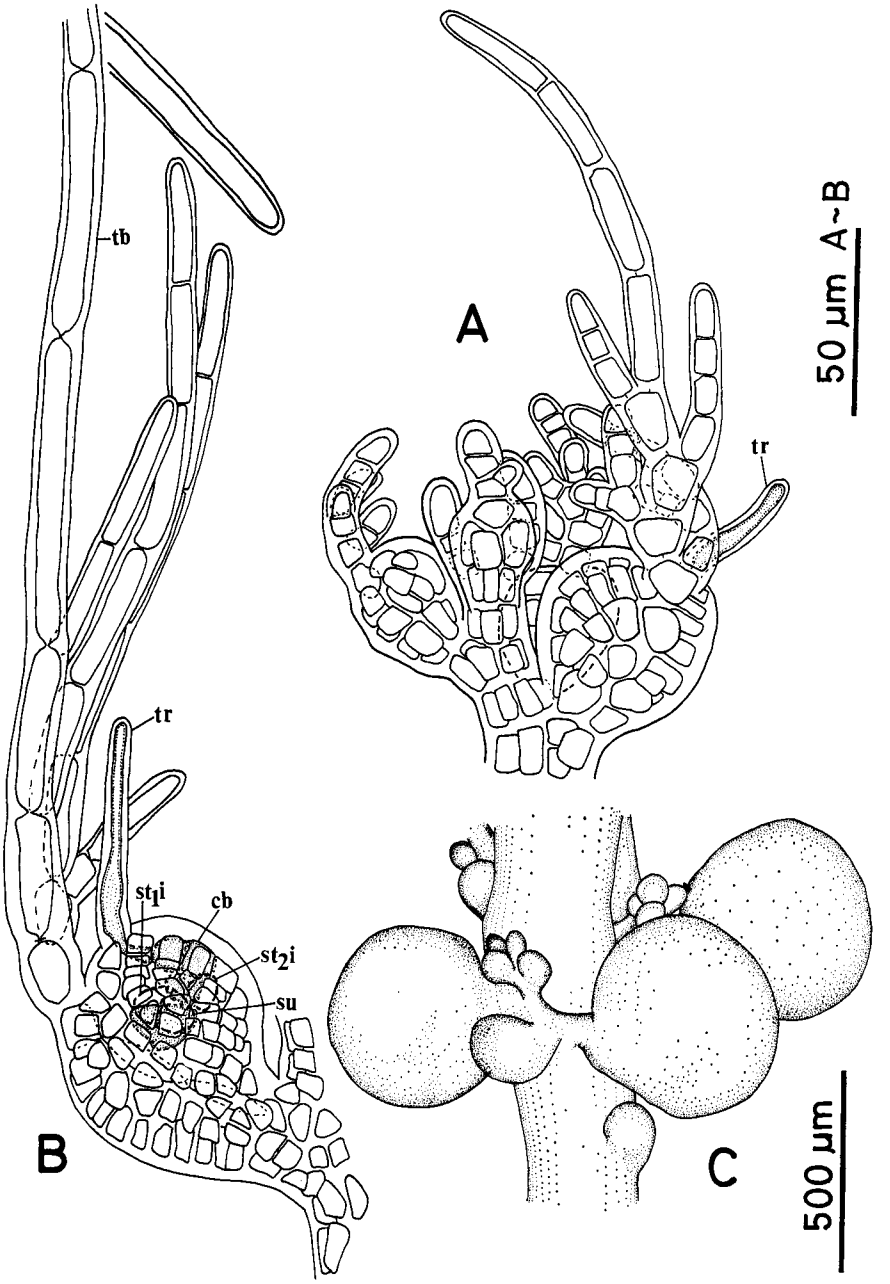

Fig. 20. *Rhodomela sachalinensis.* A. Tip of an axillary adventitious branch of a cystocarpic plant forming spirally arranged female fertile trichoblasts. B. Mature procarp. C. Mature cystocarps.

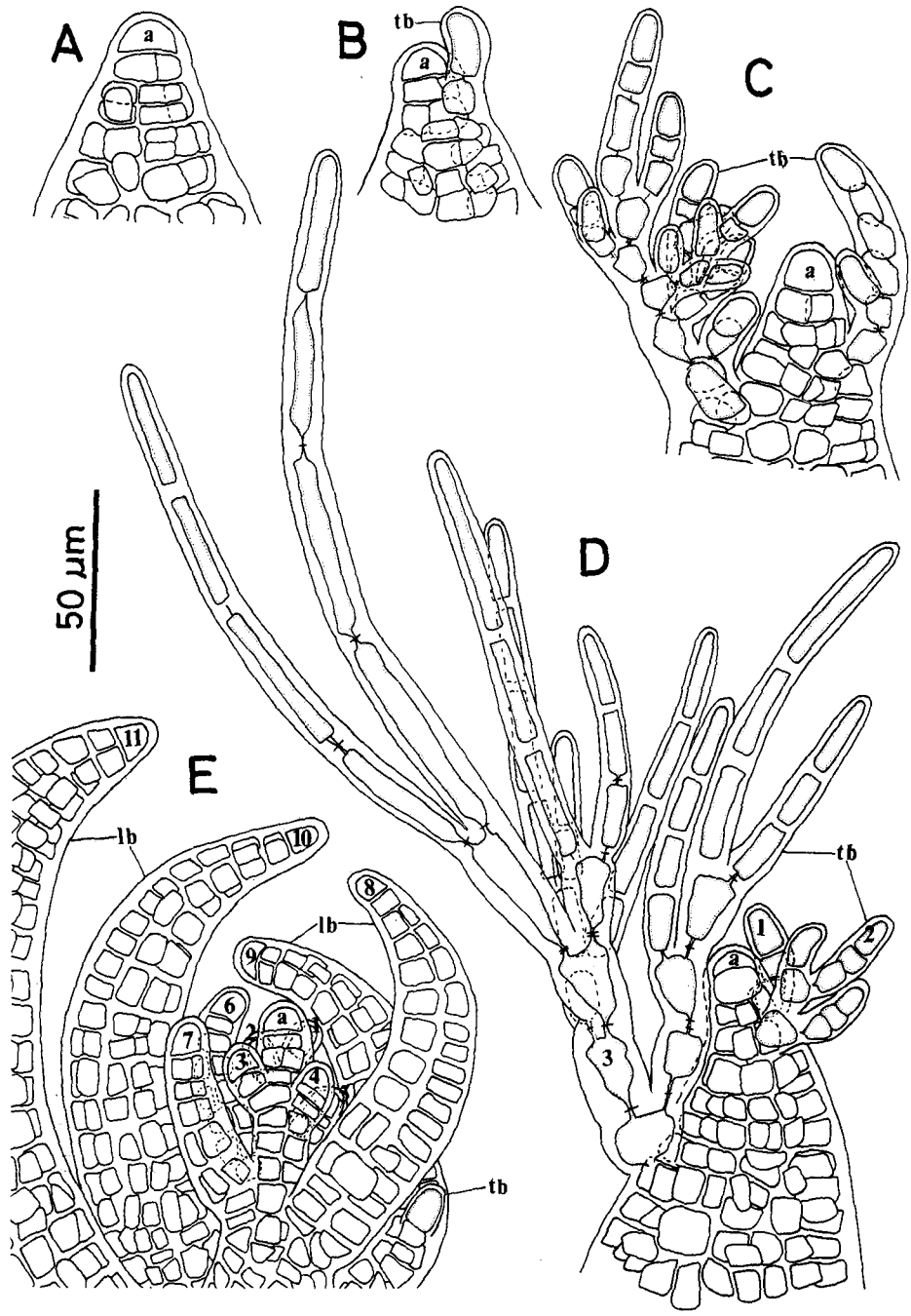

Fig. 21. *Rhodomela sachalinensis.* Stages in the development of the apical portion of sporelings. A. Five-day-old sporeling. B. Seven-day-old one issuing a trichoblast. C. Ten-day-old one issuing two trichoblasts. D. Thirteen-day-old one forming spirally arranged trichoblasts numbered in their sequence of formation. E. Two-month-old one forming spirally arranged ordinary branches numbered in their sequence of formation.

tion of tetraspores isolated from the Hanasaki plant growing in the lower intertidal zone.

The development of spores of this species closely resembles that of *R. confervoides* and *R. lycopodioides* f. *tenuissima* described above. Isolated tetraspores produced colorless rhizoids from one pole of the spore and pigmented upright shoots from the other within one day (Pl. 4, C). After 3 days, colorless rhizoids developed into either a multicellular filamentous holdfast (Pl. 4, E) or a multicellular discoid holdfast (Pl. 4, D). The latter type appeared to be dominant. Forty-eight were filamentous and 186 were discoid. The two types of holdfast grew into basal discs (Pl. 4, F–K). Sporelings grew by means of a large apical cell from which pericentral cells were subsequently cut off (Fig. 21, A). These pericentral cells simultaneously cut off cortical cells. The sporelings produced the first branch which developed into vegetative trichoblast within 7 days (Pl. 4, F; Fig. 20, B). Subsequent several vegetative trichoblasts were produced in a spiral manner (one per segment) as shown in Fig. 20, C, D. The sporelings grew straight as in *R. confervoides* and *R. lycopodioides* f. *tenuissima* (Pl. 4, I, J). The first ordinary branch was formed 16 days after inoculation.

After one month, plants reached up to 8 mm high and produced 10–12 ordinary branches of the first order in a spiral manner (Pl. 4, K; Fig. 21, E). The branches grew in a pattern similar to that of the primary main axis. Adventitious branches were formed from the axillary portion as well as from the lower portion of the main axis. Adventitious branches produced from the lower portion of the main axis developed into stolons (Pl. 4, M) later. Secondary erect axes were produced from the basal disc (Pl. 4, K). Vegetative trichoblasts were well developed in the cultured plants, reached up to 900 μm in length and were divided 4 times in a pseudodichotomous manner (Pl. 4, L). Vegetative trichoblasts of cultured plants were colorless and deciduous, although those of field-collected plants are light rose in color.

After 2 months several individuals bore spermatangia on determinate branchlets issuing from axillary branches as well as from the distal portion of indeterminate branches of the first and second orders. The spermatangial branches were quite similar to those of field plants (Pl. 4, N, O). No female gametangia were observed in 4-month-old cultured plants. Even 7 months after being transferred to the other different culture conditions, 5°C, 14 : 10 LD; 5°C, 10 : 14 LD; 10°C, 14 : 10 LD; 10°C, 10 : 14 LD; 14°C, 10 : 14 LD; 18°C, 14 : 10 LD and 18°C, 10 : 14 LD, female gametangia were not observed on any of the plants.

Plants derived from carpospores did not become fertile under any of the experimental conditions attempted even after more than one year. More-

over, plants developed from tetraspores and carpospores of the Rausu plant and those derived from excised apical tips of the Akkeshi plant did not become fertile under any of the experimental conditions attempted even after more than one year. However, cultured plants derived from the three localities did not show any difference in gross morphology and thallus structure. They are morphologically identical with each other.

Geographic distribution: According to the historic and contemporary specimens examined, this species is distributed along the east coast of south Sakhalin, the north and east coasts of Hokkaido, and the southern Kuriles (Fig. 22). These regions are washed by the East Sakhalin Current (cold current) in winter and by the Soya Current (warm current), which is a terminal branch of the Tsushima Current, in summer (TOKIDA, 1954; WATANABE, 1964). According to TOKIDA (1954), this species is also distributed along the coasts of Kamchatka, Aleutian Islands, Pribilof Islands

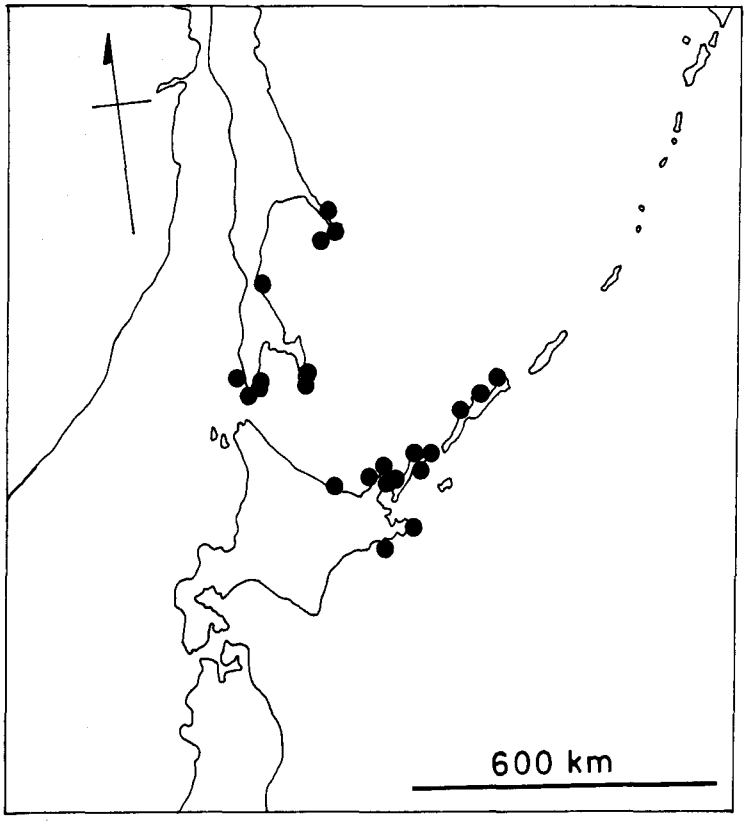

Fig. 22. Distribution of *Rhodomela sachalinensis* in Japan and adjacent waters.

and British Columbia. However, the just-mentioned regions cannot be accepted as the geographic records of this species as will be stated in the following chapter.

Taxonomic discussion

TOKIDA sent the Sakhalin specimens of *Rhodomela* to SETCHELL to ask his identification and he adopted the new combined name, *Rhodomela macracantha* (KÜTZING) SETCHELL for the Sakhalin plant on the basis of correspondence with SETCHELL (TOKIDA, 1934). According to TOKIDA (1934), SETCHELL wrote to him as follows. "On studying it, it seems truly to be a *Rhodomela*, but at the same time it is not very far from *Odonthalia*. It seems to be the plant represented by KÜTZING in the Tabulae Phycologicae under the name of *Lophura macracantha*. Long ago in our 'Algae of Northwestern America', Professor GARDNER and I referred this plant as a variety under *Odonthalia floccosa*, but it seems to me that it may be an independent species and may possibly be referred rather to *Rhodomela* than to *Odonthalia*. This is as far as we are able to advance in regard to that specimen." Since then, the alga has become known under that name (OKAMURA, 1936; TOKIDA, 1949, 1954; TAZAWA, 1957; DAWSON, 1961).

In describing *Rhodomela macracantha* from Sakhalin, TOKIDA (1949) stated that it is characterized by the tetrasprangial branches arising fasciculately from the axil of the branchlets. According to my examination of the Sakhalin specimens of *R. macracantha* identified by Emer. Prof. J. TOKIDA and preserved in his herbarium, the majority of the tetrasporangial specimens have only axillary tetrasporangial branches in accordance with TOKIDA's description, but a specimen collected at Airo on July 31, 1906 possesses tetrasporangial branchlets on both the axillary and ordinary branches as do younger fertile plants collected in Hokkaido and described above. Furthermore, the Sakhalin plant is similar to the Hokkaido plant described above in other features. Thus, I am convinced that they are the same species.

The alga under discussion, however, is distinguishable from KÜTZING's *Lophura macracantha*, which is the basionym of the Sakhalin *Rhodomela macracantha*, in two important taxonomic features. In the original description KÜTZING (1865) represented that *L. macracantha* has compressed thalli and alternate-distichous branching. On the contrary, the alga under discussion has terete thalli and spiral branching. Judging from the type description and illustration (KÜTZING, 1865), *Lophura macracantha* seems to be referable to *Odonthalia*.

SETCHELL and GARDNER (1903) recognized *Lophura macracantha* as

a form of *Odonthalia floccosa* and gave a new combined name, *O. floccosa* f. *macracantha* (KÜTZING) SETCHELL et GARDNER. They noted that *f. macracantha* is a coarser and laxer form than the f. *comosa* and is well represented by KÜTZING's figure. I have examined a herbarium specimen of *O. floccosa* f. *macracantha* determined by the late Prof. W. A. SETCHELL and deposited in the Herbarium of Tokyo University of Fisheries. That specimen (No. 5796) was collected from St. Paul Island, Pribilof Islands during 1896-97 and is cited by SETCHELL and GARDNER (1903). It fits their description very well and has a coarse and lax thallus branching in an alternate-distichous manner. It also has the compressed branches and appearance of *Odonthalia annae* in the external aspect, although that specimen is only a fragment which lacks the basal portion. Vegetative trichoblasts were not observed in the specimen. Thus, *O. floccosa* f. *macracantha* (KÜTZING) SETCHELL et GARDNER (1903) is entirely different from any species of *Rhodomela* and seems to be assignable to *Odonthalia.*

SETCHELL's *Rhodomela macracantha* from Sakhalin holds several morphological features common with *R. confervoides*, the type species of *Rhodomela*: terete thalli, spiral branching and trichoblasts. Hence, I propose to give a new name, *Rhodomela sachalinensis*, for SETCHELL's *R. macracantha* (in TOKIDA, 1934). The distinction of this species from other *Rhodomela* species will be stated in discussion of the species of *Rhodomela* (see p. 275).

TOKIDA (1949) emphasized that the Sakhalin plant agrees fairly well with a plant shown in OKAMURA's Icones of Japanese Algae, Pl. 186, fig. 2 (1922). Furthermore, he reduced OKAMURA's *R. subfusca* (in part) to be a synonym of *R. macracantha.* As will be mentioned in greater detail later, however, OKAMURA's *R. subfusca* includes at least three different species. The plant collected at Muroran and illustrated in his Pl. 186, fig. 2 is not identical with *R. sachalinensis*, but it is referable to *R. teres.* The plant collected at Abashiri and illustrated in his Pl. 186, fig. 3 seems to be identical with this species judging from the gross morphology. It has a short determinate branchlets which is a characteristic of this alga, although OKAMURA (1922) stated that "fig. 3 may be considered as weakly grown form as it is collected at Abashiri where the coast is washed by a terminal branch of the warm current pouring into the Ochotsk Sea".

According to TOKIDA (1949), the Kurile specimens described by NAGAI (1941) are identical with the Sakhalin plant. I have examined the Kurile specimens, which are preserved in NAGAI's Herbarium (SAPA) and are placed in a single cover, '*Rhodomela subfusca*'. Their localities are cited by NAGAI (1941). A check of his specimens reveals that the specimens include *R. sachalinenses* as well as other species, such as OKAMURA's southern

form of *R. subfusca* and *Neorhodomela aculeata*, both of which will be described later in this paper. His description of *R. subfusca* seems to be based on OKAMURA's southern form of *R. subfusca* and *R. sachalinensis*. Gross morphological characteristics such as plants arising from filiform hapters (stolons) and branchlets being short (0.5-2 mm long) fits *R. sachalinensis* very well, while the cystocarpic character described by NAGAI agrees with that of OKAMURA's southen form of *R. subfusca*. The Kurile specimens of *R. subfusca* reported by KAWABATA (1936) also include *R. sachalinensis* and *R. teres*.

Rhodomela teres (PERESTENKO) MASUDA, comb. nov.

Basionym : *Odonthalia teres* PERESTENKO, 1973, p. 64. pl. 2

Synonyms : *Rhodomela gracilis* YAMADA et NAKAMURA in YAMADA and TANAKA (non HARVEY, 1853), 1944 b, p. 171 ; TAZAWA, 1957, p. 33, fig. 2, pl. 1 (3), 1975, p. 158, pl. 10, B, fig. 42, G-I.
Rhodomela subfusca auct. non C. AGARDH ; OKAMURA, 1922 (*pro parte*), p. 151, pl. 186, fig. 2, 1936 (*pro parte*), p. 899 ; KAWABATA, 1936 (*pro parte*), p. 212, 1959, p. 295 ; INOH, 1944, p. 281, figs. 2, 5-6, 1947, p. 210, figs. 206-208.
Rhodomela confervoides auct. non SILVA ; CHIHARA, 1970, p. 113, pl. 57 (4).
Odonthalia floccosa auct. non FALKENBERG ; NAGAI, 1941 (*pro parte*), p. 242 ; TOKIDA, 1950, p. 150, 1954, p. 225.

Japanese name : *Hosoba-fujimatsumo* (YAMADA and NAKAMURA in YAMADA and TANAKA, 1944 b).

Materials

The plants used were gathered at Rausu, Muroran, Usujiri and Shirikishinai in Hokkaido from 1968 to 1973.

Rausu : *Masuda* 6620-6676, 6678-6687, 6689-6762 & 12976-12981 (i-1969, sterile ; iii-1969, spermatangial ; v-1968, spermatangial & procarpic ; vii-1968, cystocarpic & tetrasporangial ; viii-1968, ditto ; x-1968, ditto). Muroran : *Masuda* 7809-8030 & 8988-9016 (i-1971, sterile & spermatangial ; ii-1971, sterile, spermatangial & procarpic ; iii-1971, spermatangial & procarpic ; iv-1971, spermatangial & tetrasporangial ; v-1971, spermatangial, cystocarpic & tetrasporangial ; vi-1972, ditto ; vii-1970, cystocarpic & tetrasporangial ; vii-1971, sterile, cystocarpic & tetrasporangial ; viii-1970, cystocarpic & tetrasporangial ; ix-1970, tetrasporangial ; xi-1970, sterile ; xii-1970, sterile). Usujiri : *Masuda* 8962-8979 (iv-1973, sterile & spermatangial). Shirikishinai : *Masuda* 8939-8961 (sterile & spermatangial).

The herbarium specimens deposited in the herbaria listed below were also observed. KURILES Kunashiri Island: NAGAI Herb. (Sokobetsu, viii-1931, tetrasporangial; Kotankeshi, viii-1931, tetrasporangial). Shikotan Island: SAP 15492-15494 (vii-1933, cystocarpic & tetrasporangial; vii-1934, tetrasporangial), NAGAI Herb. (Shakotan, vii-1934, sterile & tetrasporangial, *Nagai* Nos. 5444, 5446, 5447, 5532 & 5534). SAKHALIN TOKIDA Herb. (Rakuma, vii-1930, tetrasporangial, viii-1927, cystocarpic; Hirochi, ix-1927, tetrasporangial; Nishinotoro, iv-1937, spermatangial; Ishihama, viii-1926, cystocarpic & tetrasporangial; Chishiya, iv-1937, procarpic). HOKKAIDO Rishiri Island: SAP 22855 (viii-1934). Rebun Island: YENDO Herb. (Kabuka, vii-1910). Rausu: SAP 24368-24369 (ix-1943, tetrasporangial). Hidaka: YENDO Herb. (vii-viii-1909). Muroran: SAP 11779, 11780, 12500, 12501, 19789, 19802, 19803, 23366, 23370, 24525, 25547, & 28557-28559 (iii-1943, spermatangial; v-1931; v-1935, cystocarpic & tetrasporangial; v-1949; vi-1935, tetrasporangial; vi-1953, spermatangial; vii-1935, cystocarpic). Todohokke: YENDO Herb. (ix-1917). Shirikishinai: SAP 28557 & 28558 (iv-1955, spermatangial), KAWABATA Herb. (i-1956, sterile; xii-1957, sterile), YENDO Herb. (ix-1917).

Parent plants for culture experiments were collected at Muroran as follows: cystocarpic plants on June 7, 1970, July 4, 1970, July 6, 1970, July 20, 1970 and June 27, 1972; and tetrasporangial plants on July 6, 1970, July 20, 1970 and June 30, 1972.

Description

Plants perennial, with several upright thalli arising from a basal disc and stolons; upright thalli terete, much branched up to 3-4 times in a spiral manner, attaining up to 30 cm in height, dark red in color when living, turning to black in drying, firm in texture, adhering imperfectly to paper in drying; main axis almost straight, 750-1200 μm in diameter in the lowest portion, reaching a maximum diameter of 1100-1550 μm in diameter in the lower third portion; determinate branchlets subulate; axillary adventitious branches numerous in tetrasporangial plants, closely aggregate; pericentral cells 6 in main axis and indeterminate branches, 5 in determinate branches; vegetative trichoblasts rare, simple; plants dioecious; spermatangia borne superficially on the upper portion of branches; cystocarps globose, 640-750 μm $\times$ 690-875 μm in size with rather wide ostioles; carpospores globular, 75-90 μm in diameter; tetrasporangia borne in pairs in 10-20 successive segments of simple branchlets, 100-110 μm $\times$ 100-120 μm; tetraspores 60-75 μm in diameter.

Observation

Habitat and Phenology: The following description is based on field observations at Muroran from 1970 to 1972. This alga grows abundantly on rocks in the upper sublittoral zone. It is found during all seasons of the year. Spermatangial plants appear at the end of January and are found until the end of June. Procarpic plants are seen from the middle of February to the beginning of April. Ripe cystocarpic and tetrasporangial plants are found from the begining of May to September. These plants continuously liberate carpospores and tetraspores during this time. From November to December branches fall off leaving the main axis and the lower first order branches, and proliferous branches are observed (Pl. 5, D). The proliferous branches from the lower portion of plants is also found on summer plants (Fig. 23, B). Thus, this species is perennial.

Morphology of field plants: The following description is based on materials from Muroran. Plants usually entangle with each other and assemble in clumps (Pl. 5, A, D). Several upright thalli arise from a small discoid holdfast and well developed stolons (Fig. 23, A). The stolons are anatomically identical with upright branches (Pl. 8, K) and attach to the substrate by small discs (Fig. 23, A). This alga closely resembles *R. sachalinensis* in having a stolon. Upright thalli are terete, branched 3-4 times in a spiral

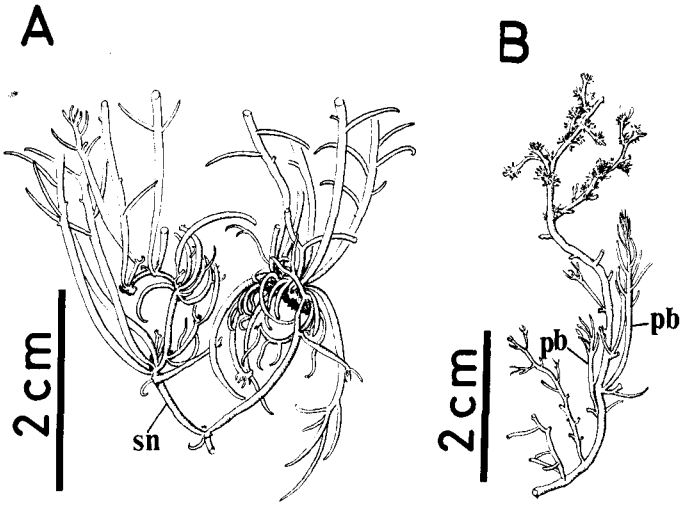

Fig. 23. *Rhodomela teres* (PERESTENKO) MASUDA. A. Basal portion of a field-collected plant with many upright thalli arising from a basal disc and stolons. B. Lower portion of a summer plant showing proliferous branches.

manner, and are up to 30 cm high. They are dark red in color when living and turn to black in drying. They are firm in texture and imperfectly adhere to paper in drying. Each upright thallus has a conspicuous main axis which is almost straight. The main axes are denudate below, 750–1200 μm in diameter in the lowest portion, 1100–1550 μm in diameter in the lower third portion, and attenuate toward the apex. The first order branches develop from central cells of the apical portion of the main axis. One branch arises from per segment. They are branched in a spiral manner as is the main axis except several lower branches and become up to 7 cm long in the middle portion of the main axis. The lower simple determinate branches of the first order are subulate, reach up to 1.2 cm long, and become recurved as they grow older. The subsequent order branches grow in the same manner as the first order branches.

Axillary adventitious branches are produced from the outermost cortical cells (Fig. 24, A). They are usually branched once spirally and bear reporductive structures. But, sometimes unbranched simple axillary branches may become fertile. Axillary branches are abundantly developed in tetrasporangial plants, whereas in gametangial plants they are scarce.

Vegetative trichoblasts are sometimes observed in young tetrasporangial plants. They are usually simple and arranged in a spiral manner (Fig. 26, A).

The thallus is of uniaxial construction composed of a central cell, six pericentral cells and several layers of cortical cells (Pl. 8, I). However, the simple determinate branchlets usually possess five pericentral cells (Pl. 8, L), whereas the main axis and other indeterminate branches have six pericentral cells. The central cell of the main axis is 150–200 μm long near the base, but it becomes gradually elongated reaching 3.5–4.0 mm long in the middle portion. Its length corresponds to branching interval of the main axis exclusive of the lower denudate portion. Each pericentral cell is divided transversely into two cells and the upper cell retains the pit-connection with the central cell, but the lower pericentral cell becomes linked with a pericentral cell of the underlying segment by the secondary pit-connection (Fig. 24, B). Furthermore, each pericentral cell cuts off two or three cortical cells outward which is also divided transversely. The lower cell of this division becomes linked with a cortical cell of the underlying segment by a secondary pit-connection as does the lower pericentral cell. Each cortical cell cuts off one or two cortical cells outward. This process is repeated so that there is a 4–5 layered cortex in the upper portion and a 10–11 layered cortex in the lower portion of the main axis of the first year plant. The cortex of the lower portion of the old main axis in the second year

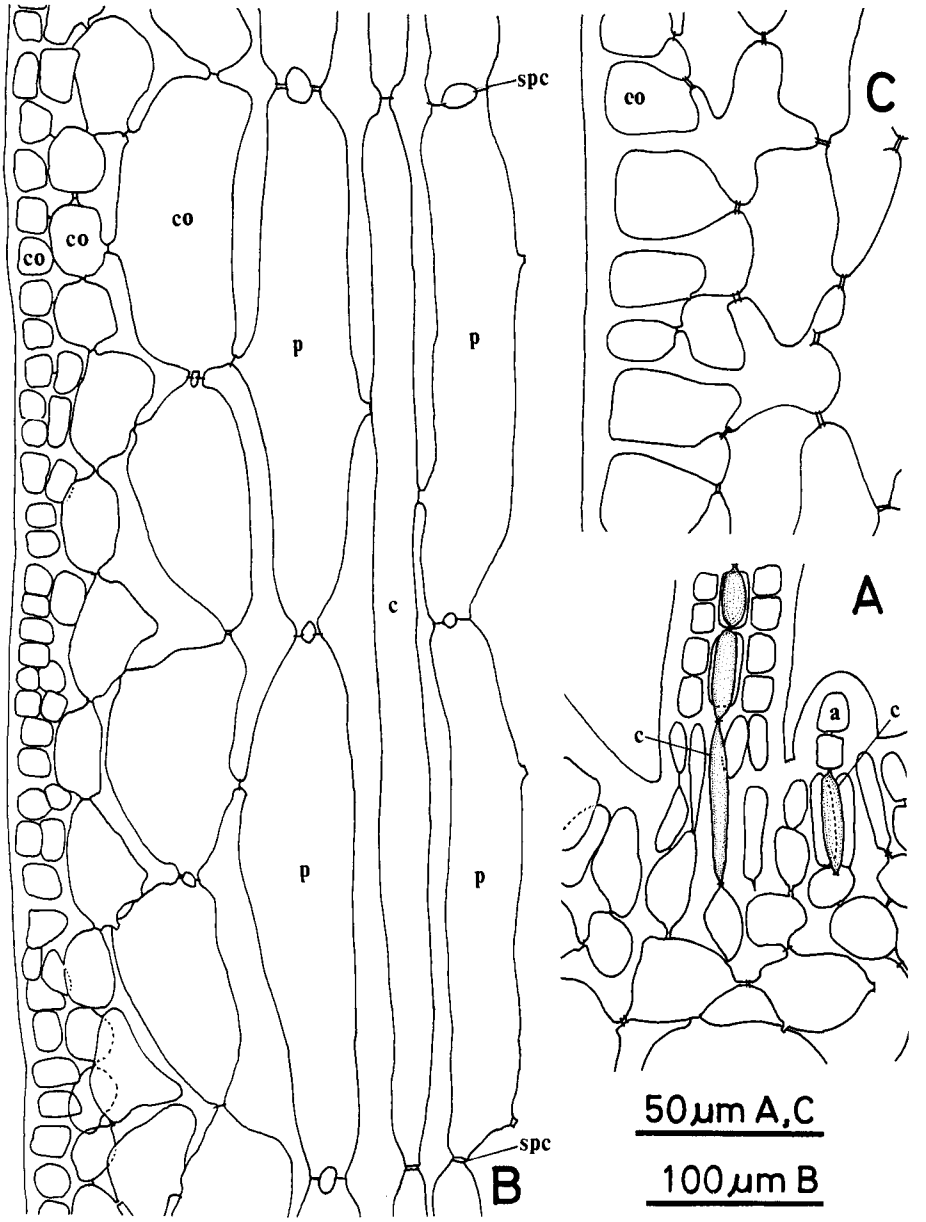

Fig. 24. *Rhodomela teres.* A. Longitudinal section of the upper portion of a main axis showing two axillary adventitious branches developed from outermost cortical cells. B. Longitudinal section of a determinate branchlet showing the arrangement of central cells, pericentral cells (each divided transversely into two cells), and 3–4 layers of cortical cells. C. Longitudinal section of the lower portion of a main axis, showing cortical cells.

plant consists of very tightly packed cortical cells (Pl. 8, J). The outermost cortical cells are not linked with the underlying cells by secondary pit-connections (Fig. 24, C).

Spermatangia, carpogonia and tetrasporangia occur on separate plants. The spermatangia are formed superficially on ordinary unspecialized branches (Fig. 25, A). They are borne on the upper portion of branches of the first to third orders (Pl. 7, G, H) as described by TAZAWA (1957, 1975). The spermatangial branches are usually divided 2-3 times in a spiral or pseudo-dichotomous manner (Pl. 7, G; Fig. 25, A), but sometimes remain simple (Pl. 7, H). According to TAZAWA (1957, 1975), the spermatangia are formed

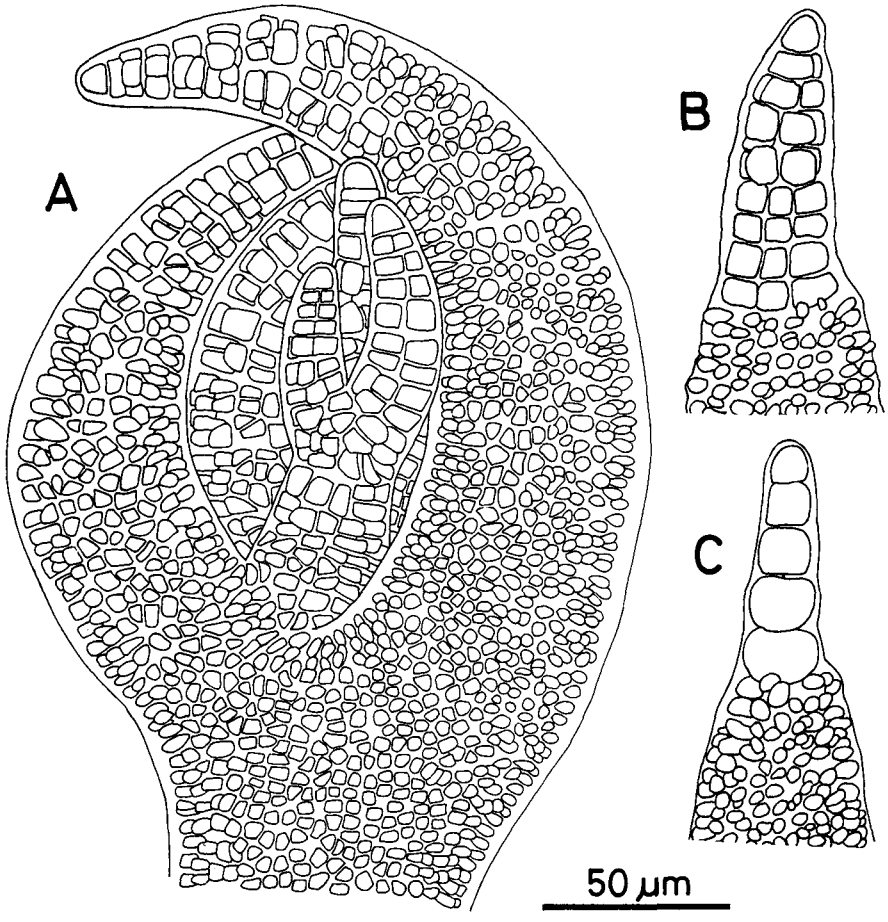

Fig. 25. *Rhodomela teres.* A. Tip of spermatangial branch. B–C. Tips of mature spermatangial branches, showing polysiphonous sterile portion (B) and monosiphonous sterile portion (C).

from the spermatangial mother cells developed from the outermost cortical cells. An outermost cortical cell produces two or three spermatangial mother cells by an oblique division. The spermatangial mother cell usually cuts off two spermatangia which are ellipsoidal in shape and measure 12–14 μm × 7–8 μm. The fertile branches are anatomically like the vegetative branches. The outermost cortical cells in spermatangial branches, except of the apical portion, become fertile. Apical sterile portions of spermatangial branches are usually polysiphonous (Fig. 25, B) as reported by TAZAWA (1957, 1975), but rarely monosiphonous (Fig. 25, C).

The procarps originate from the suprabasal segment of the trichoblast, which is light rose in color, and usually divided pseudodichotomously two times (Fig. 26, B, C, Fig. 27, A). The fertile trichoblasts arise at the apical portion of indeterminate branches. They are arranged in a spiral manner as are vegetative branches (Fig. 27, A). The two basal segments become polysiphonous and the suprabasal segment produces five pericentral cells. The carpognial branch is produced from the last formed pericentral cell on the adaxial side of the trichoblast as in *R. confervoides*. This pericentral cell functions as the supporting cell and produces a 4-celled carpogonial branch and two sterile cell groups. Mature cystocarps are globose in shape, having rather wide ostioles and measure 640–750 μm in length and 690–875 μm in diameter (Fig. 27, B). The carposporangia produced on terminal cells of the gonimoblast are long club-shaped and contain numerous chloroplasts. Carpospores are discharged through the ostioles. They are club-shaped while in the pericarps, and become globular after discharged. They are the same dark red in color as the thallus and measure 75–95 μm in diameter (Pl. 6, A).

The tetrasporangia are formed on simple branchlets which issue from the upper portion of ordinary branches as well as from axillary adventitious branches. In younger fertile plants collected in April and May the tetrasporangia were observed only on the branchlets issuing from ordinary branches (Pl. 8, I). The fertile axillary branches are commonly observed in fully mature plants found in summer. These axillary branches are borne numerously on the main axis as well as on indeterminate branches of any order and they are closely aggregated (Pl. 7, J). In all instances, the tetrasporangial branchlets are strongly curved. Thus, the sporophytic thallus differs strikingly in appearance from the sterile and gametophytic thalli. The tetrasporangial initials are cut off from pericentral cells and they are protected by two cover cells. Two tetrasporangia are produced in each of 10–20 successive segments of the branchlets. Mature sporangia are 100–110 μm × 100–120 μm in surface view and divided tetrahedrally. The tetraspores are

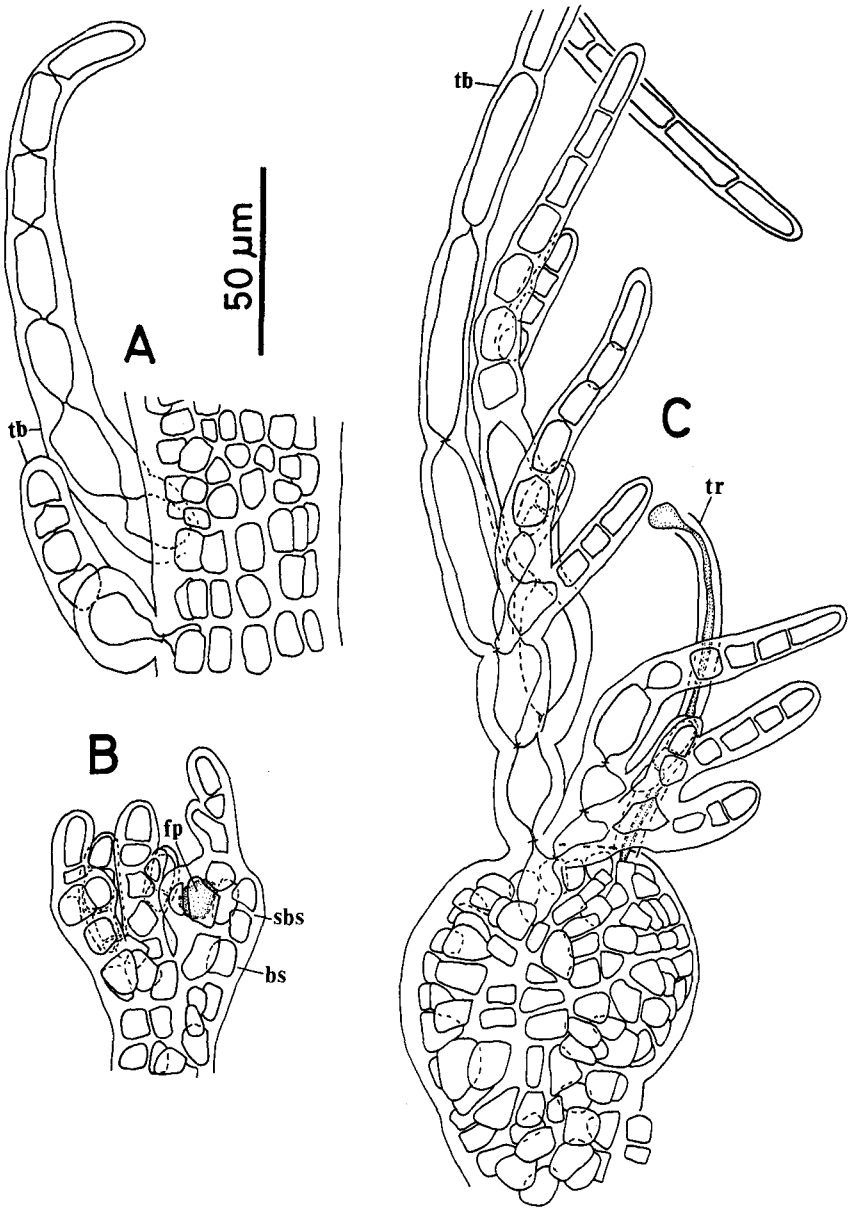

Fig. 26. *Rhodomela teres.* A. Trichoblasts borne on a tetrasporangial branchlet. B. Tip of an indeterminate branch forming spirally arranged female trichoblasts. C. Mature procarp.

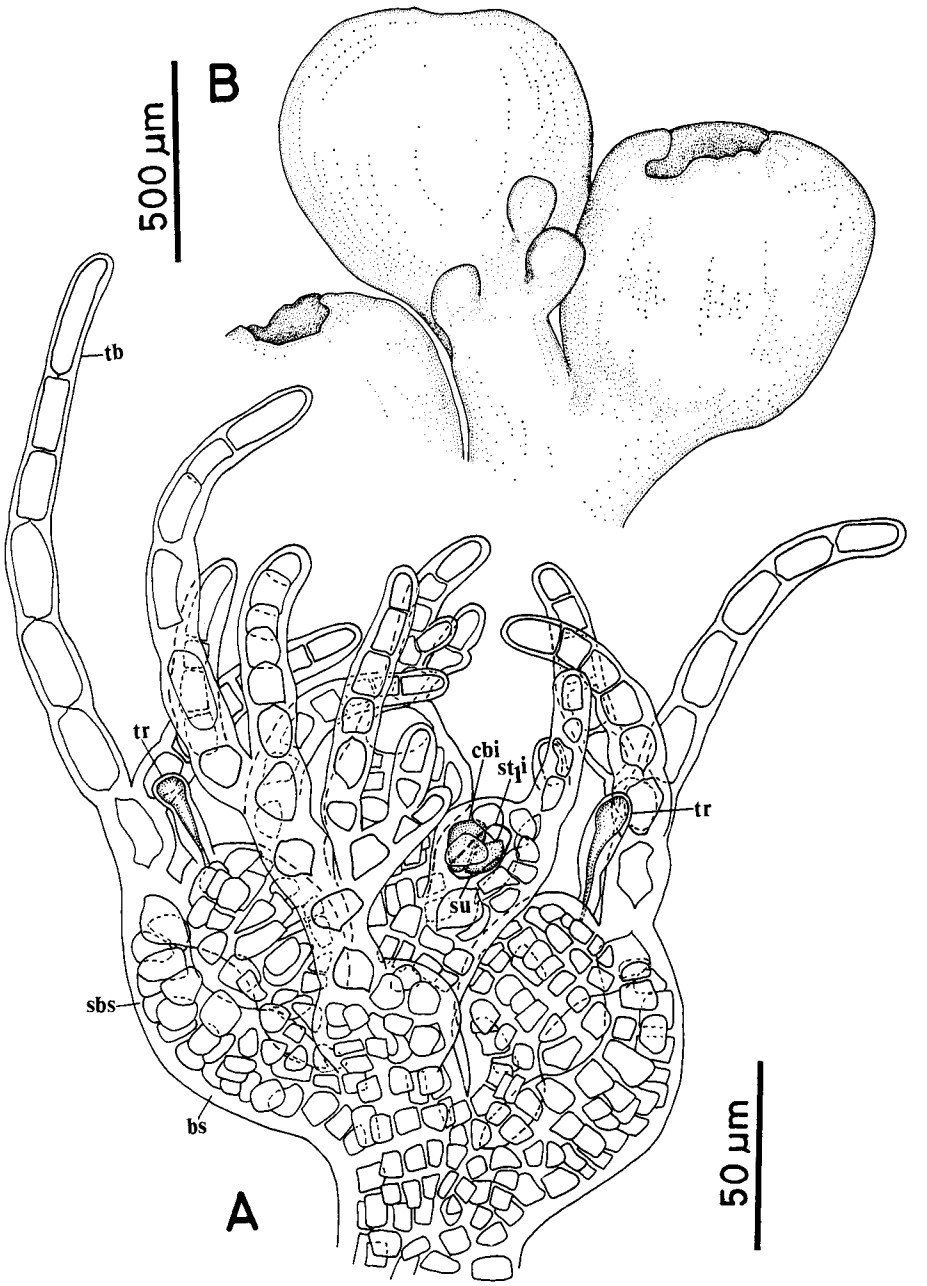

Fig. 27. *Rhodomela teres.* A. Spirally arranged female trichoblasts. B. Mature cystocarps.

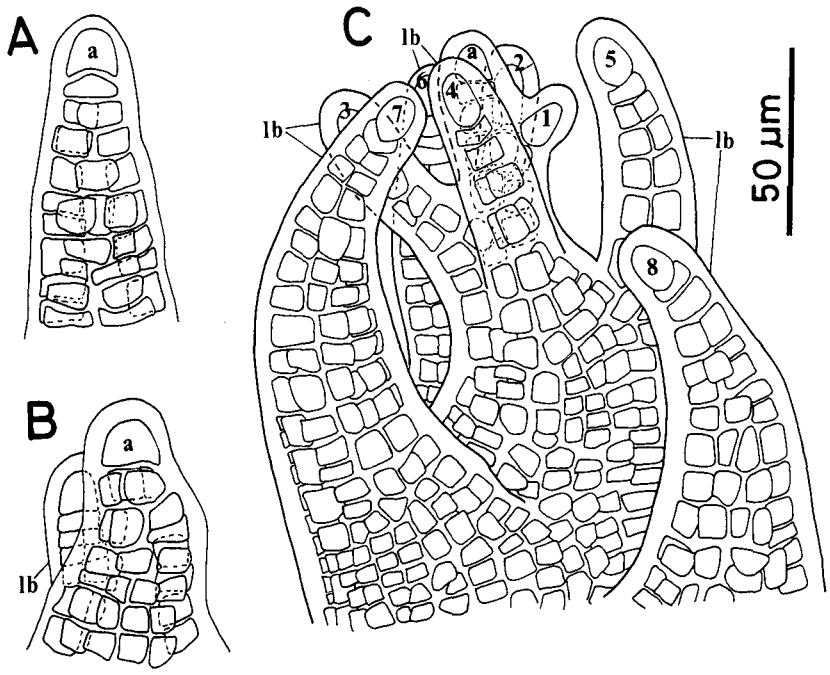

Fig. 28. *Rhodomela teres.* Stages in the development of the apical portion of sporelings. A. Ten-day-old sporeling. B. One-month-old sporeling issuing the first lateral branch. C. Two-month-old one forming spirally arranged ordinary lateral branches numbered in their sequence of formation.

discharged through an opening between the cover cells. Discharged tetraspores are similar to the carpospores in many respects. However, they are smaller than the latter, being 60–75 μm in diameter (Pl. 6, B).

Culture study: Unialgal cultures were obtained from isolated tetraspores and carpospores. Liberated tetraspores and carpospores were first cultured at 14°C, 14 : 10 LD. No apparent difference was found in germination between tetraspores and carpospores as already noted by INOH (1944, 1947). The tetraspore germination is described below. The tetraspores quickly attached to the substrate after liberation (Pl. 6, C), and within one day produced colorless rhizoids from one pole of the spore and pigmented upright shoot cells from the other (Pl. 6, D).

Colorless rhizoids formed either a multicellular filamentous holdfast (Fig. 29, D–F) or a multicellular discoid holdfast (Pl. 6, E; Fig. 29, A–C). Fifty-three were filamentous and 103 were discoid. Thereafter, filamentous holdfasts began to form discoid holdfasts also (Fig. 29, G; 30, A–C). They grew rapidly and developed into the pseudoparenchymatous discs in a short

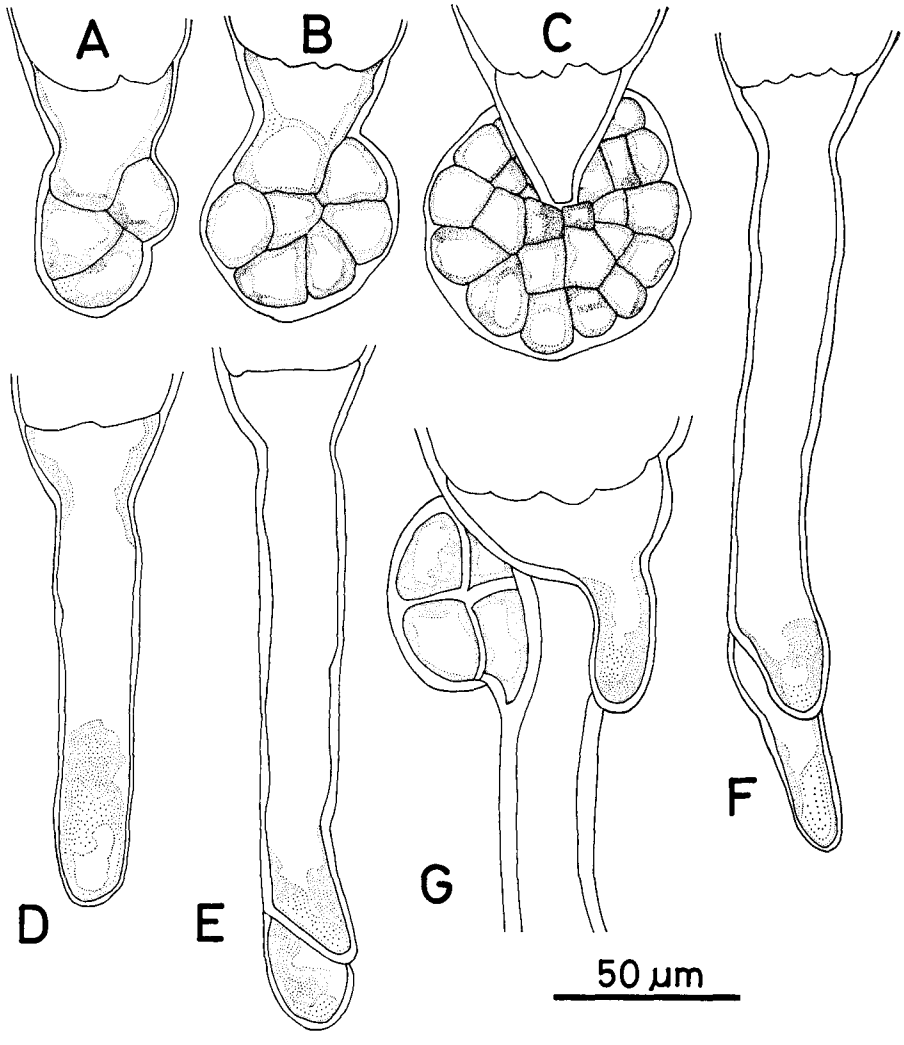

Fig. 29. *Rhodomela teree.* Stages in the development of holdfasts (A–C, & D–G, the same plant, respectively). A, D. Two days old. B, E. Three days old. C. Five days old. F. Four days old. G. Ten days old.

time. Plate 6, E–I illustrates various stages in the germination of tetraspores and early development of gametophytes. This development is like that for *Rhodomela subfusca* described by INOH (1944, 1947). Sporelings grew straight without branching (Pl. 6, G; Fig. 28, A). They produced several adventitions branches in the lower portion. Gradually, several secondary axes issued from the surface cells of the basal discs (Pl. 7, H, I).

After one month, the sporelings reached up to 1.2 cm high, and some of them issued a branch from the apical portion (Pl. 6, J ; Fig. 28, B). Five to six branches of the first order were subsequently issued from the central cells of the primary main axis within 2 months (Fig. 28, C). At that time, ten to twelve secondary shoots developed from a basal disc. Some of the secondary axes formed discoid holdfasts from the ventral side and became attached to the substrate. These, then, grew into stolons (Pl. 6, L ; Fig. 30, D). Several new shoots arose from the dorsal surface of the stolons (Fig. 30, D). Further, the adventitious discoid holdfasts were formed on the upper portion of upright branches (Pl. 6, K). This is a characteristic of cultured plants. In field plants, the adventitious discoid holdfasts issued from only the stolons.

Two months after inoculation, several cultures maintained at 14°C, 14 : 10 LD were transferred to 5°C, 14 : 10 LD, 10°C, 14 : 10 LD and 18°C, 14 : 10 LD. The plants transferred to 10°C, 14 : 10 LD grew well and attained a height of 4 cm 4 months after transfer (Pl. 5, H). At that time, they reached reproductive maturity and produced spermatangia or carpogonia on separate plants at the apical portion of the branches (Pl. 6, M, N). The development and structure of both spermatangia and carpogonia were quite similar to those of field-collected plants. Cultured male and female gametangial plants commonly bore the gametangia on the simple determinate branchlets. Thirty-five days after starting mixed cultures of male and female plants cystocarps liberated carpospores. The plants retained at 14°C, 14 : 10 LD and transferred to 18°C, 14 : 10 LD did not grow well and did not form reproductive organs after 12 months from initiation. Then, the cultures were terminated. Plants transferred to 5°C, 14 : 10 LD grew slowly and also did not form any reproductive organs even after 12 months from transfer.

The carpospores liberated from the aforementioned cultured plants were grown at 10°C, 14 : 10 LD. They developed in a pattern similar to that of the tetraspores. Several one-month-old germlings grown at 10°C, 14 : 10 LD were transferred to 5°C, 14 : 10 LD, 14°C, 14 : 10 LD and 18°C, 14 : 10 LD. They grew in a pattern similar to that of the tetrasporelings under each condition. Tetrasporangia were formed at the apical portion of the simple determinate branchlets at 10°C, 14 : 10 LD 10 months after germination (Pl. 6, O).

The plants derived from carpospores of field material did not form any reproductive structures 12 months after transfer from 14°C, 14 : 10 LD to 5°C, 10 : 14 LD ; 5°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 10°C, 14 : 10 LD ; and 18°C, 14 : 10 LD.

Anatomically, the cultured plants are essentially the same as field plants.

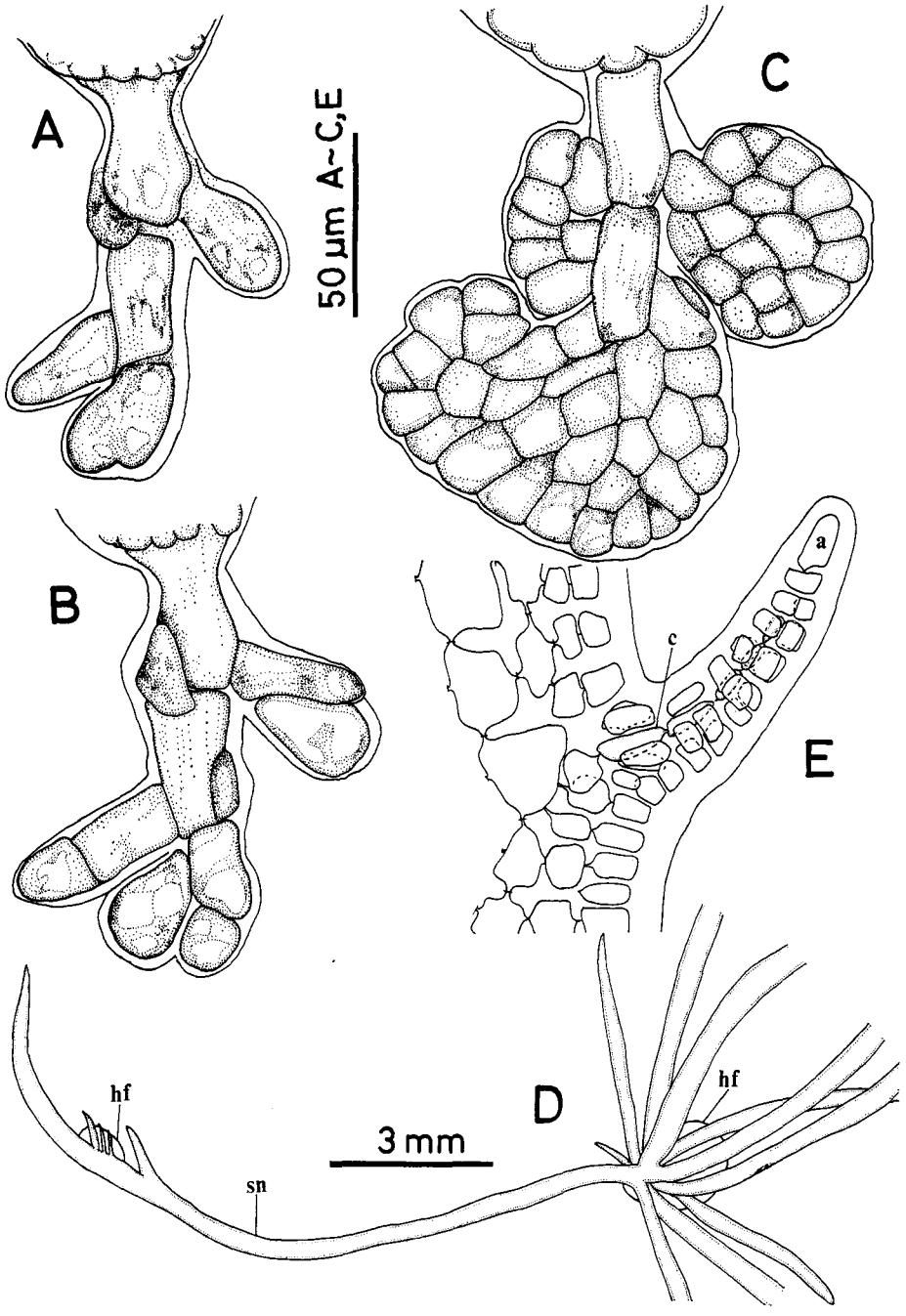

Fig. 30. *Rhodomela teres.* A–C. Stages in the development of a holdfast: A, four days old; B, five days old; C, eight days old. D. Basal portion of a 2-month-old plant with several upright thalli arising from a basal disc and a stolon. E. Longitudinal section of a main axis of a 2-month-old plant, showing an adventitious branch developed from an outermost cortical cell.

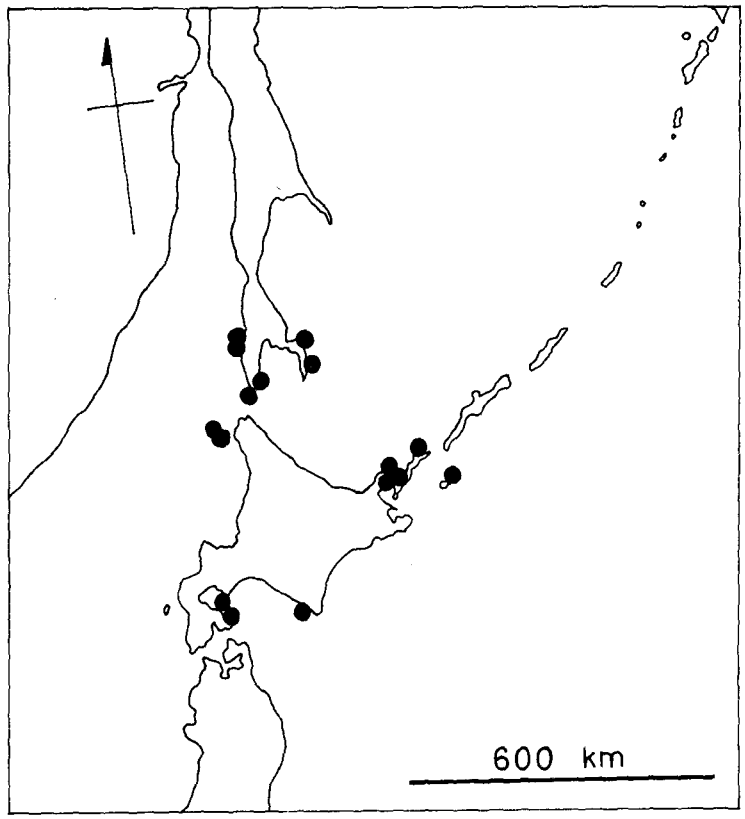

Fig. 31. Distribution of *Rhodomela teres* in Japan and adjacent waters.

However, vegetative trichoblasts were not observed on cultured plants. Further, adventitious branches were not formed in the axil, but they were formed randomly from cortical cells (Fig. 30, E).

Geographic distribution: On the basis of my collection data and a check of herbarium specimens cited previously (see materials), this alga is distributed from the southern Kurile Islands and Sakhalin to Hokkaido. Fig. 31 shows the present known range of this species.

Taxonomic discussion

In Japan this alga has been called *Rhodomela gracilis* YAMADA et NAKAMURA (in YAMADA and TANAKA, 1944 b). It was first described on the basis of material collected from Muroran. In describing the alga YAMADA and NAKAMURA gave only a brief diagnosis in Japanese. "This species is allied to *Rhodomela macracantha* (KÜTZING) SETCHELL reported from Robben Island, Sakhalin, but it differs from the latter by having slightly slender

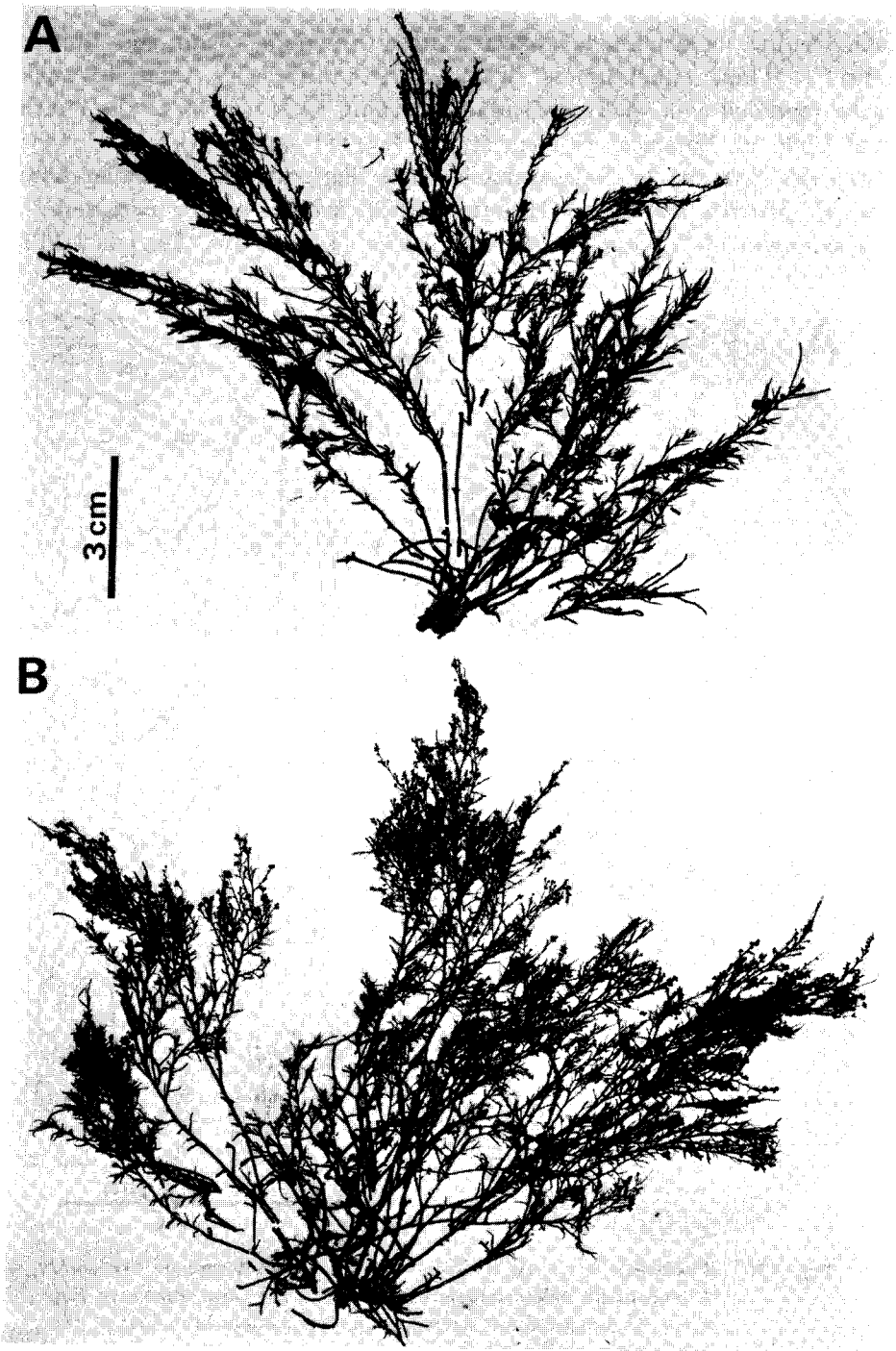

Fig. 32. *Rhodomela teres.* A. Paratype specimen of *Odonthalia teres* PERESTENKO collected in Opricznik Bay on August 20, 1965 (LE, leg. L. P. PERESTENKO). B. Cystocarpic specimen of *Odonthalia teres* determined by PERESTENKO, which was collected in Opricznik Bay on August 23, 1965 (SAP, leg. L. P. PERESTENKO). Scale in A applies also to B.

thalli. It has been already collected from Shikotan Island and Muroran (transl.)". Their establishment of *R. gracilis* without a Latin description can be regarded as a valid puplication according to Article 36 of the international Code of Botanical Nomenclature (STAFLEU *et al.*, 1978). However, *R. gracilis* YAMADA et NAKAMURA is made illegimate by the earlier homonym, *R. gracilis* (KÜTZING) HARVEY (1853), which is now considered to be a synonym of *R. confervoides* f. *gracilior* (J. AGARDH) TAYLOR (1957).

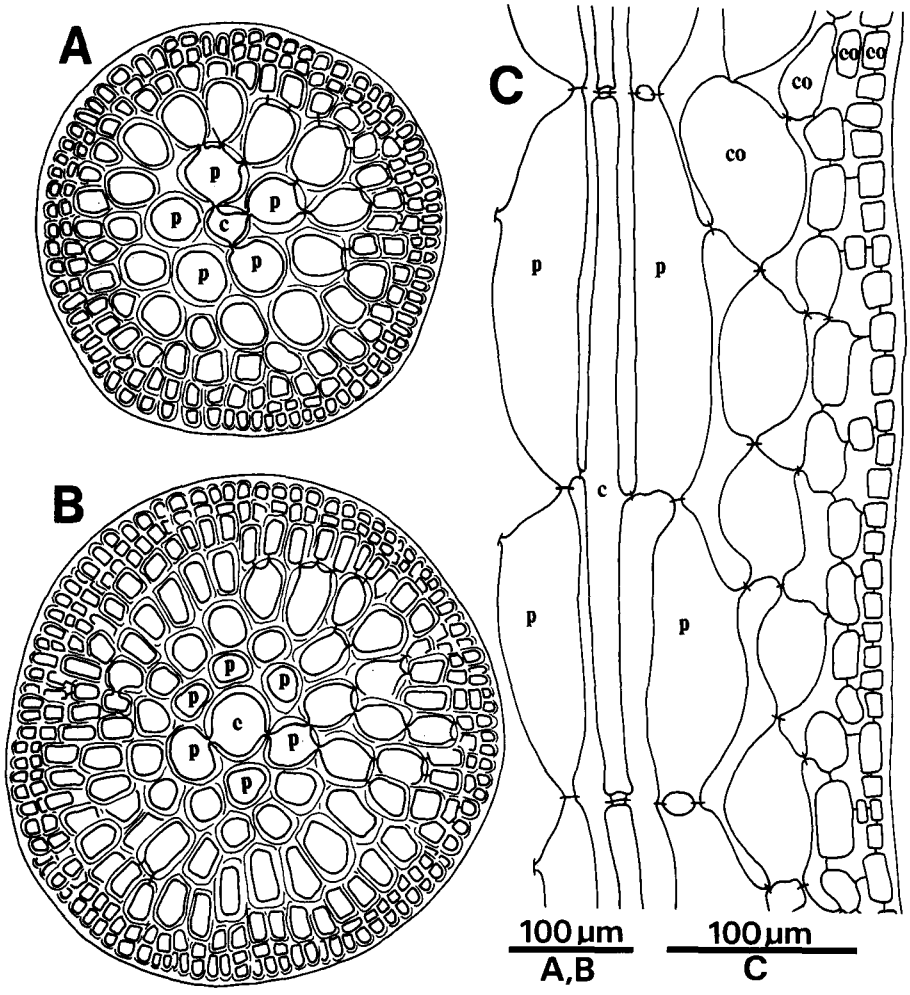

Fig. 33. *Rhodomela teres.* A, B. Cross sections of a determinate branchlet (A) and of an indeterminate branch (B) of the plant shown in Fig. 32, B. C. Longitudinal section of a determinate branchlet of the plant shown in Fig. 32, B.

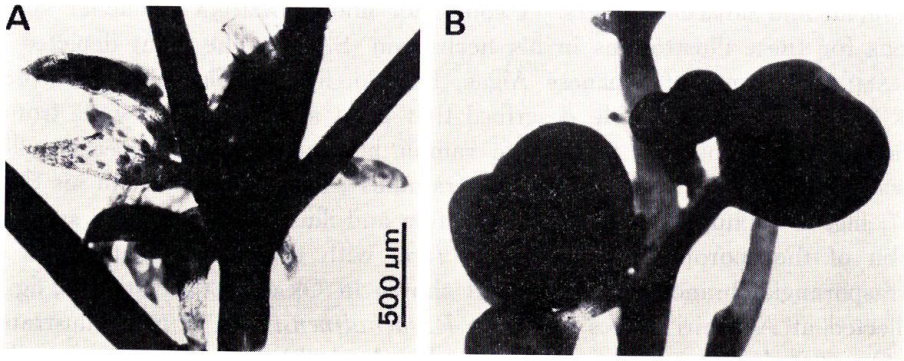

Fig. 34. *Rhodomela teres.* A. Tufted tetrasporangial branchlets formed in the axil of the plant shown in Fig. 32, A. B. Cystocarps borne on the plant shown in Fig. 32, B.
Scale in A applies also to B.

PERESTENKO (1973) described *Odonthalia teres* based on material collected in Opricznik Bay facing the Sea of Japan. According to PERESTENKO (1973), it resembles *Odonthalia floccosa*, but differs from the latter species in having terete thalli, stolon and spiral branching. I examined two tetrasporangial specimens of *O. teres* designated as the paratype on the label on loan from the Herbarium of the Komarov Botanical Institute of the Academy of Sciences, Leningrad (LE). These were collected from the type locality on August 20, 1965 by L. P. PERESTENKO. One of these is shown in Fig. 32, A. Furthermore, a cystocarpic specimen presented to SAP from LE was examined (Fig. 32, B). This was collected also from the type locality on August 23, 1965 by L. P. PERESTENKO. An examination of the specimens reveals that *Odonthalia teres* is identical with the aforementioned *Rhodomela gracilis* YAMADA et NAKAMURA in gross mophology (Fig. 32, A, B), anatomical structures (Fig. 33, A–C) and reproductive structures (Fig. 34, A, B). It is concluded that the two algae are conspecific. The entirely terete thalli, spiral branching and vegetative trichoblasts ally the alga in question with *Rhodomela confervoides*, the type species of *Rhodomela* and justify the transfer of this alga to *Rhodomela*. The distinction of this alga from other *Rhodomela* will be given in the next part 'Discussion of the species of *Rhodomela*'.

In describing *Rhodomela subfusca* from Japan, OKAMURA (1922) stated as follows: "many forms are met with in our specimens differing in several minute characters cheifly according to their localities and they may be separated in other days into some numbers of varieties." OKAMURA also illustrated the four forms considered as the representatives of *R. subfusca*

in Japan and adjacent waters. I could not find OKAMURA's voucher specimens for these illustrations in his herbarium (SAP). The plant depicted in OKAMURA's Icones of Japanese Algae, Pl. 186, fig. 2 collected at Muroran fits *R. teres* very well. He described that plant as follows :" in some fronds a small branch bearing tetrasporic ramuli becomes stunted appearing like fasciculately arising from the axil of a ramulus", and illustrated it in his Plate 187, fiig. 8. Thus, OKAMURA's description and illustration show the summer habit of the sporophytic plant of *R. teres* with the characteristic tufts of tetrasporangial branchlets. The plant shown in OKAMURA's Plate 186, fig. 3 collected at Abashiri agrees well with *R. sachalinensis*. The plant illustrated in OKAMURA's Plate 186, fig. 4 collected at Iwaizaki, which has been called the southern form, differs from *Rhodomela* in several respects as pointed out earlier (MASUDA, 1972). This plant will be reported later as *Neorhodomela munita* in this paper. The plant from Shumsh Island, which is shown in OKAMURA's Plate 186, fig. 1 and called the northern form, and *R. teres* are conspecific according to TAZAWA (1975). OKAMURA's figure of the Shumsh plant certainly suggests an affinity with *R. teres* and these plants seem to be identical. However, its reproductive structure needs to be clarified before identification. OKAMURA's northern form of *R. subfusca* should be retained in doubtful position until the Shumsh plant become available. Three plants of OKAMURA's *R. subfusca* are not linked with each other by intermediate forms and should be treated as the distinct species stated above. Nevertheless, they have been confused with each other and sometimes even with other species by Japanese phycologists.

KAWABATA (1936, 1959) reported *R. subfusca* from Shikotan Island, southern Kuriles and from Shirikishinai, Hokkaido. KAWABATA's Kurile plants include two species, *R. teres* (SAP 15492, 15493, 15494) and *R. sachalinensis*. His Shirikishinai plants are identical with *R. teres*. CHIHARA's (1970) *R. confervoides* based on material from Muroran and deposited in TNS is actually *R. teres*. As TOKIDA (1949) and TAZAWA (1957) pointed out, the occurrence of genuine *R. confervoides* (=*R. subfusca*) has not been established in Japan.

TOKIDA (1950, 1954) reported *Odonthalia floccosa* from Sakhalin. Voucher specimens of his *O. floccosa* (Pl. 5, C) compare very favorably with *R. teres* in every respect, but they differ from the descriptions of genuine *O. floccosa* given by ESPER (1802), TURNER (1808) and FALKENBERG (1901). Voucher specimens of NAGAI's *O. floccosa* collected from Kurile Islands (1941) include *R. teres* in part (Pl. 5, B).

INOH (1944, 1947) reported the early development of spores of *Rhodomela subfusca* using materials collected at Muroran. Judging from the

spore color and the early developmental stages of the tetraspores, his *R. subfusca* is nothing but *R. teres*.

Discussion of the species of *Rhodomela*

Up to now nine species have been ascribed to the genus *Rhodomela*: 1) *R. confervoides* (HUDSON) SILVA (1952), the type species, 2) *R. lycopodioides* (LINNAEUS) C. AGARDH (1822), 3) *R. larix* (TURNER) C. AGARDH (1822), 4) *R. virgata* KJELLMAN (1883), 5) *Rhodomela macracantha* (KÜTZING) SETCHELL (in TOKIDA, 1934), 6) *R. patagoniensis* TAYLOR (1939), 7) *R. gracilis* YAMADA et NAKAMURA (non HARVEY) (in YAMADA and TANAKA, 1944 b), 8) *R. sibirica* A. ZINOVA et VINOGRADOVA (in VINOGRADOVA, 1973 a) and 9) *R. munita* PERESTENKO (1980). Of these, in this paper *R. macracantha* is replaced by *R. sachalinensis* MASUDA as mentioned previously. *R. gracilis* is reduced to the synonymy with *R. teres* (PERESTENKO) MASUDA which is transferred from *Odonthalia*. Furthermore, *R. larix* and *R. munita* will be transferred to the newly established genus *Neorhodomela*. The status of *R. patagoniensis* needs verification. It has four pericentral cells and tetrasporangia arranged in one row (TAYLOR, 1939), whereas the species of *Rhodomela* usually have six or seven pericentral cells and tetrasporangia arranged in two rows. Thus, six species are now assignable to the genus *Rhodomela* with certainty. *R. confervoides* includes three forms, f. *confervoides*, f. *gracilior* (J. AGARDH) TAYLOR (1957) and f. *rochei* (HARVEY) TAYLOR (1957). *R. lycopodioides* includes five forms, f. *lycopodioides*, f. *cladostephus* (J. AGARDH) KJELLMAN (1875), f. *setacea* KJELLMAN (1883), f. *flagellaris* KJELLMAN (1883) and f. *tenuissima* (RUPRECHT) KJELLMAN (1883).

In the present study four taxa of the genus, the typical form of *R. confervoides*, *R. lycopodioides* f. *tenuissima*, *R. sachalinensis* and *R. teres* are described. I have never encountered the other two forms of *R. confervoides*, the other four forms of *R. lycopodioides*, *R. virgata* and *R. sibirica* in th field and could not obtain materials for detailed investigation. At presente I am unable to assess the taxonomic relationships among all the taxa of the genus. The following taxonomic discussion of the genus is limited to that of the four taxa investigated.

R. confervoides, *R. lycopodioides* f. *tenuissima* and *R. sachalinensis* are similar to each other in the juvenile stage of the sporelings (Pl. 2, D-G; Fig. 10, E, F; Pl. 4, F-J). The sporelings of the three taxa bear first vegetative trichoblasts. *R. teres* differs strikingly from the three taxa in this stage (Pl. 6, F, G). The sporelings do not bear vegetative trichoblasts.

In further developmental stages, the frequent occurrence of vegetative trichoblasts in the main axis is characteristic of *R. lycopodioides* f. *tenuissima*. After the formation of ordinary branches of the first order, the main axes of this alga bear vegetative trichoblasts again replacing the ordinary branches, and so the vegetative trichoblasts are sporadically present on well developed plants. However, the main axes of *R. confervoides* and *R. sachalinensis* bear ordinary branches successively. Moreover, the main axes of *R. lycopodioides* f. *tenuissima* become thick in the lower portion and contrast with the upper filiform portion (Figs. 13, 14). This taxon is characterized by this feature (MASUDA and SHIMIZU, 1980).

R. confervoides, *R. lycopodioides* f. *tenuissima* and *R. sachalinensis* bear numerous vegetative trichoblasts in the growing apex of branches of any order. However, *R. teres* does not bear vegetative trichoblasts regularly.

The development of branches borne on the lower portions of the main axes and of the branches of any order characterizes each taxon examined. In *R. lycopodioides* f. *tenuissima* the branches grow indeterminately, but those of the other taxa remain simple. The simple determinate branchlets of *R. confervoides* and *R. teres* are subulate and up to 1 cm or more in length, whereas those of *R. sachalinensis* are thorn-like and up to 2 mm in length.

Short adventitious branches formed on the middle to upper portions in advanced stage and bearing reproductive structures characterize *R. sachalinensis* and *R. teres*, although adventitious branches formed on the lower portion of the main axes in juvenile stages and growing indeterminately are common to the taxa examined. The adventitious branches of *R. sachalinensis* are formed numerously in the axil both on the gemetophytic (Pl. 4, O; 7, C) and sporophytic thalli (Pl. 7, B. F). Those of *R. teres* are numerous only on the sporophytic thalli (Pl. 7, J) and scarce on the gametophytic thalli. *R. confervoides* bears sometimes the adventitious branches in the axil. *R. lycopodioides* f. *tenuissima* is devoid of this type of adventitious branches.

As to reporductive structures, the following features characterize each taxon examined. *R. sachalinensis* possesses only simple spermatangial branchlets (Pl. 4, N, O; 7, C, D; Fig. 19), whereas *R. confervoides*, *R. lycopodioides* f. *tenuissima* and *R. teres* possess divided spermatangial branches (Pl. 2, I; 6, M; 7, G; Fig. 3; 25, A). *R. confervoides* bears also the spermatangial branches on trichoblasts (Fig. 3). The form and size of cystocarps are characteristic of each taxon: *R. confervoides* having urceolate or ovoid cystocarps (Pl. 2, L-N, P) measuring 550-670 μm $\times$ 440-600 μm; *R. lycopodioides* f. *tenuissima* having oblate or broadly ovoid cystocarps (Fig. 9, F, G)

measuring 230–300 μm × 320–450 μm ; *R. sachalinensis* having globose cystocarps (Fig. 20, C) measuring 380–500 μm × 380–550 μm ; and *R. teres* having globose cystocarps (Fig. 27, B ; 34, B) measuring 640–750 μm × 690–875 μm. The tetrasporangia of *R. confervoides* and *R. lycopodioides* f. *tenuissima* are formed both on ultimate and penultimate orders branches, whereas those of *R. sachalinensis* and *R. teres* are borne only on short determinate branchlets of the ultimate order (Pl. 6, O ; 7, E, F, I, J ; Fig. 34, A).

Thus, the taxa examined here are quite distinct from each other. From the ontogenetic point of view, the developmental pattern of the sporelings shows taxonomic relationships among the taxa. *R. confervoides*, *R. lycopodioides* f. *tenuissima* and *R. sachalinensis* are similar in the pattern, whereas *R. teres* is separate from the three taxa. Although *R. confervoides*, *R. lycopodioides* f. *tenuissima* and *R. sachalinensis* show characteristic features as growth advances, the similar development of the sporelings seems to be an evidence of their close relationships.

Finally, the distinction of *R. sachalinensis* and *R. teres* from other taxa of the genus is summarized below. The two species are distinguished from all known taxa by having stolons and tufted tetrasporangial branchlets borne in the axil. *R. sachalinensis* is distinguished from the taxa including *R. teres* by short thorn-like branchlets, simple spermatangial branchlets and small globose cystocarps. *R. teres* differs from the taxa including *R. sachalinensis* in having a few vegetative trichoblasts and large globose cystocarps.

Neorhodomela MASUDA, gen. nov.

Plantae thallis rectis pluribus e disco basali communi effecti ; thalli recti multo ramosi, teres, crescentes e singula cellula apicali exposita, quae spiratim instituta et ramos determinatos indeterminatosque efficit ; cellulae pericentrales sex (interdum quinque), hae cellulae pericentrales singulae transverse se dividentes, cellula superiore cellula centrali semper connexa ; celluae pericentrales cellulas corticeas extrinsecus abscissae ; hae cellulae corticeae dein et anticlinaliter et periclinaliter se dividentes ; rami adventitii e cellulis corticeis extimis axis et ramorum effecti ; trichoblasti vegetativi et fertiles in latere abaxiali ramorum determinatorum et indeterminatorum portati, biseriatim in modo fractiflexo, interdum spiratim in ramis indeterminatis, decidui ; spermatangia in trichoblastis fertilibus portata ; procarpium in segmento suprabasali trichoblasti fertilis portatum, pericarpio tectum quum trichogyne receptoria est, ex cellula sustinenti et ramo carpogoniali quatuorcellulari et turmis cellularum sterilium duarum constans ; cystocarpium maturum pericarpio bene evoluto ; tetrasporangia in ramis immutatis binatim in unoquoque

segmento effecta, tetraedrice divisa.

Species typica: *Neorhodomela munita* (PERESTENKO) MASUDA

Plants with several upright thalli arising from a common basal disc; upright thalli much branched, terete, with growth from a single exposed apical cell, which is spirally organized and produces determinate and indeterminate branches; pericentral cells six (sometimes five), these pericentral cells each undergoing a transverse division, the upper cell retaining connection with the central cell; the pericentral cells cut off cortical cells outward; these cortical cells then undergoing both anticlinal and periclinal divisions; adventitious branches developed from the outermost cortical cells of the axis and branches; vegetative and fertile trichoblasts borne on the abaxial side of determinate and indeterminate branches, in two rows in a zigzag manner, sometimes spirally on indeterminate branches, deciduous; spermatangia borne on fertile trichoblasts; procarp borne on the suprabasal segment of fertile trichoblast, covered by pericarp when trichogyne is receptive, consisting of a supporting cell, a four-celled carpogonial branch and two sterile cell groups; mature cystocarp with well developed pericarp; tetrasporangia produced in pairs per segment in unmodified branches, tetrahedrally divided.

Type species: *Neorhodomela munita* (PERESTENKO) MASUDA

Neorhodomela munita (PERESTENKO) MASUDA, comb. nov.

Basionym: *Rhodomela munita* PERESTENKO, 1980, p. 192, fig. 253.

Synonyms: *Rhodomela subfusca* auct non C. AGARDH; COTTON, 1915, p. 112; OKAMURA, 1922 (*pro parte*), p. 151, pl. 186, fig. 4, pl. 187, figs. 1, 3, 6, 7, 13, 1936 (*pro parte*), p. 899, fig. 421, 1, 2; HOWE, 1924, p. 141; INAGAKI, 1933, p. 66; NAGAI, 1941 (*pro parte*), p. 235; SEGAWA, 1956, p. 121, pl. 72 (589); TAZAWA, 1957, p. 33, fig. 1 (7-9), 1975, p. 160, pl. 10, A, fig. 42, F.

Rhodomela larix auct non C. AGARDH; HIROSE, 1957, p. 103; NODA, 1967, p. 54.

Japanese name: Ito-fujimatsu (OKAMURA, 1922)

Materials

The materials examined were collected from Hokkaido and Honshu from 1968 to 1973. HOKKAIDO Utoro: *Masuda* 6552, 6556-6558, 6560, 6562 & 12332-12356 (v-1968, spermatangial; vi-1969, spermatangial, cystocarpic & tetrasporangial; vii-1968, cystocarpic & tetrasporangial; viii-1968, ditto; x-1968, ditto). Rausu: *Masuda* 6551, 6553-6555, 6559, 6561 & 12357-12361 (v-1968, spermatangial; vi-1969, cystocarpic & tetrasporangial). Ak-

keshi : *Masuda* 12362-12466 (vi-1970, spermatangial, cystocarpic & tetrasporangial ; vi-1971, ditto ; vii-1970, ditto, leg. I. YAMADA). Muroran : *Masuda* 12467-12864 & 13013-13019 (i-1971, sterile ; ii-1971, ditto ; iii-1971, ditto ; iii-1972, sterile & spermatangial ; iv-1971, spermatangial, cystocarpic & tetrasporangial ; v-1970, ditto ; v-1971, ditto ; vi-1970, ditto ; vi-1972, ditto ; vii-1970, sterile, spermatangial, cystocarpic & tetrasporangial ; vii-1971, ditto ; vii-1970, sterile & cystocarpic ; ix-1970, sterile, spermatangial, cystocarpic & tetrasporangial ; x-1970, sterile, cystocarpic & tetrasporangial ; xii-1970, sterile). Shirikishinai : *Masuda* 12878-12892 (iv-1973, spermatangial, cystocarpic & tetrasporangial). HONSHU Aomori Pref. : *Masuda* 12893 & 12894 (Omazaki, v-1973, cystocarpic). Okayama Pref. : *Masuda* 12895-12956 (Tamano, vi-1970, cystocarpic & tetrasporangial, leg. T. OHMORI ; vi-1971, ditto, leg. T. OHMORI).

The herbarium sperimens deposited in the herbaria listed below or sent to me by Drs. H. HIROSE and M. NODA were also observed. KURILES Etorof Island : NAGAI Herb. (Arimoe, viii-1930, tetrasporangial). Kunashiri Island : NAGAI Herb. (Atoiya, viii-1929, spermatangial, cystocarpic & tetrasporangial ; Tofutsu, viii-1936, cystocarpic & tetrasporangial ; Tomari, vii-1936, cystocarpic & tetrasporangial ; Kotankeshi, viii-1936, spermatangial, cystocarpic & tetrasporangial ; Nikishiro, viii-1929, cystocarpic). SAKHALIN TOKIDA Herb. (Kaiba-to, vii-1930, spermatangial, cystocarpic & tetrasporangial). HOKKAIDO Rebun Island : KAWABATA Herb. (vii-1960, cystocarpic). Nemuro : SAP (Bentenjima, vi-1969, leg. M. MASUDA). Hidaka : SAP 28556 (Higashi-shizunai, v-1955, spermatangial). Toi : SAP 23510 (iv-1940). Okushiri Island : SAP 25187 & 25188 (Aonae, iii-1944). Otaru : SAP 28555 (iv-1955, spermatangial). HONSHU Aomori Pref. : SAP 7896 & 24217 (Asamushi, non date). Iwate Pref. : SAP 26995 (Taneichi, iv-1952). Niigata Pref. : *Noda* 1057, 2332 (Sado Island, iii-1956, tetrasporangial ; Shiiya misaki, xi-1971, tetrasporangial) ; YENDO Herb. (Sado Island, xii-1909, leg. T. OBARA). Toyama Pref. : *Noda* 1543 (Toyama Bay, non date, cystocarpic & tetrasporangial, leg. K. OSHIMA). Okayama Pref. : HIROSE (Shiaku Island, vi-1953, tetrasporangial). KYUSHU Fukuoka Pref. : YOSHIDA in SAP (Hakata-wan, ii-1961, tetrasporangial, leg. M. ICHIKI ; Waita, iii-1954, tetrasporangial, leg. M. ICHIKI).

The following plants were used for culture experiments : cystocarpic plants collected at Muroran on June 3, 1970, and on July 31, 1970, and at Tamano on April 26, 1971 ; tetrasporangial plants collected at Rausu on June 14, 1971, at Akkeshi on June 26, 1971, at Muroran on July 3, 1970, and on July 23, 1970.

Description

Plants perennial, with several upright thalli arising from a common, expanded basal disc; upright thalli terete, branched four times in a spiral manner, attaining up to 35 cm high, dark brown in color, soft in texture, fairly well adhering to paper in drying; main axis almost straight, 500–850 μm in diameter in the lowest portion, becoming gradually thicker upward, 1050–1500 μm in diameter in the lower third portion, tapering toward the apex; the first order branches growing well, bearing progressively many shorter and more slender branches; adventitious branches numerous, growing indeterminately; determinate branchlets very slender, 130–170 μm in diameter; vegetative trichoblasts formed on the apical portion of determinate and indeterminate branches, numerous, rose-colored, divided four times in a pseudodichotomous manner; plants dioecious; spermatangial branchlets ellipsoid, 230–400 μm $\times$ 100–160 μm in size; cystocarps pyriform, 400–590 μm $\times$ 350–500 μm in size with rather wide ostioles; carpospores dark brownish-yellow in color, 67.5–87.5 μm in diameter; tetrasporangia formed in two rows on 7–15 successive segments of branches of ultimate and penultimate orders, each provided with two cover cells, 110–120 μm $\times$ 100–110 μm in size; tetraspores 55.0–77.5 μm in diameter.

Observations

Habitat and phenology: This species inhabits places sheltered from the dashing of waves in the middle to lower intertidal zone and grows on rocks or pebbles. The following information is based on observations at Muroran during 1970–1972. This alga can be found throughout the year. Young sterile plants are present from December to February. Plants with proliferous branches are seen from late September to December. Macroscopically the proliferous branches are distinguished from the old axis by their slightly lighter color. Plants achieve their most luxuriant growth in May attaining a height of 35 cm. Mature spermatangial plants appear in late March and can be found until late June. Mature cystocarpic and tetrasporangial plants are found from late Apirl and discharge carpospores and tetraspores at least until late July. Then, the upper portions of the fertile upright thalli are torn off leaving only short main axis and branches of the first order. However, small fertile plants, which are apparently the first year plants, appear during August, September and October. These plants seem to be new shoots produced from the basal disc or new plants developed from the spores liberated in spring.

Morphology of field plants: The following account is given on the basis of specimens collected at Muroran unless otherwise indicated. Plants

consist of several upright terete thalli arising from a common expanded basal disc. The upright thalli are dark brown in color and have a soft texture. They adhere fairly well to paper in drying except old specimens.

This alga has numerous indeterminate branches which are produced ordinarily from the central cells of the growing apices and adventitiously from the outermost cortical cells (Pl. 9, A, B). In addition to these branches, the second year plants have several proliferous branches growing vigorously. Well developed plants, particularly second year ones, show a very complicated gross morphology.

Each upright thallus has a visible main axis which is almost straight. The main axes are 500–850 μm in diameter in the lowest portion and become thicker upward reaching up to 1050–1500 μm in diameter in the lower third portion. Ordinary branches of the first order are formed from the central cell of the apical portion of the main axis. One branch is formed on each segment. The branches are arranged in a spiral manner and grow in a manner similar to that of the main axis. They are divided into progressively shorter and more slender branches up to the fifth order. Several of the lower branches do not develop well and remain short. The branches are sometimes undivided and incurved reaching up to 2.5 mm in length. These determinate branchlets bear only vegetative trichoblasts.

Adventitious branches are abundantly produced from the outermost cortical cells. They are numerous especially in the axil, but are common in the other portion. The branches are slighlty attenuate toward the proximal portion and reach their maximum size in the lower third portion. Ordinary branches, in contrast, are not attenuate toward the proximal portion.

Vegetative trichoblasts are seen throughout the year, but are best developed in spring plants. They reach up to more than 1 mm and are divided in a pseudodichotomous manner 3–4 times (Pl. 15, A). The basal segment is always embedded in the cortex of branches bearing it, but the suprabasal segment, from which the first branching takes place, is free of the cortex as in the upper portion (Pl. 15, A). The longest segments are 150–200 μm long and 15.0–17.5 μm broad. Young trichoblasts are rose in color and become lighter as they grow old. Adult trichoblasts are almost colorless and eventually fall off. The trichoblasts are borne on the apical portion of determinate branchlets as well as on young indeterminate branches. They are produced on each segment and are arranged in a zigzag manner in two rows along the abaxial convex side of the branches (Fig. 35, A, B). This arrangement is one of characteristic features of this alga and related species.

The thallus structure of this alga is essentially in agreement with that of *Rhodomela*. The thallus is of uniaxial construction composed of a central

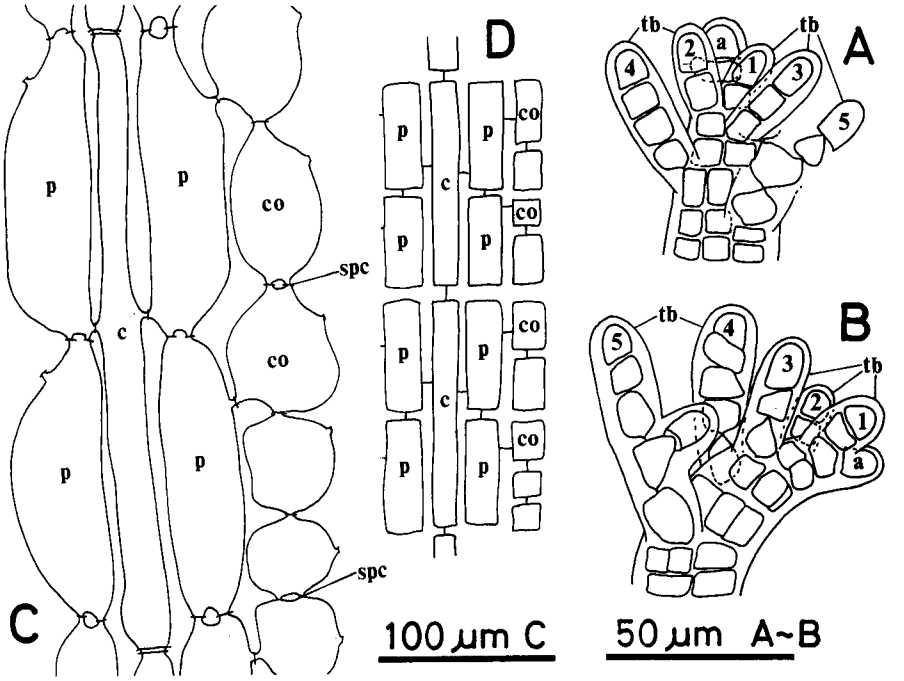

Fig. 35. *Neorhodomela munita* (PERESTENKO) MASUDA. A, B. Young trichoblasts formed on the abaxial side of branchlets and arranged in a zigzag manner, numbered in their sequence of formation (A, in abaxial view). C. Longitudinal section of a branch showing the arrangement of a central cell, pericentral cells, and cortical cells. D. Diagram of longitudinal section.

axial cell, six (rarely five) pericentral cells, and several layers of cortical cells (Pl. 17, A, C, D). The central axial cell of the main axis is short and 200–250 μm in length near the base and lengthens gradually upward reaching 4–5 mm in length in the middle portion. Its length corresponds with the branching intervals of the main axis, except in the lower portion where ordinary branches are absent and only adventitious branches are present. Each pericentral cell is divided one time transversely and the upper cell retains the pit-connection with the central axial cell, while the lower one becomes linked with a pericentral of the underlying segment by the secondary pit-connection (Fig. 35, C). Furthermore, each pericentral cell cuts off two or three cortical cells outward (Pl. 17, A, C, D). Each cortical cell is divided also transversely, and the lower cell becomes linked with the upper cortical cell of the underlying segment by the secondary pit-connection as does the pericentral cell. The cortical cells cut off again one or two cortical cells outward (Pl. 17, A, C, D). This process is repeated several times, so that

the polysiphonous structure is entirely obscured (Fig. 35, D). As a result, there is a 10-12 layered cortex in the middle portion of the main axis (Pl. 17, D) and a 6-7 layered cortex in the lower portion in first year fertile plants (Pl. 17, C). In second year plants outer cortical cells of the lower main axis constitute a packed 3-7 layered cortex (Pl. 17, A, B).

Spermatangia, carpogonia, and tetrasporangia are formed on separate plants. The spermatangia are produced only on the fertile trichoblast, which is usually simple. In this respect this alga differs essentially from any species of *Rhodomela*. The fertile trichoblasts arise successively from

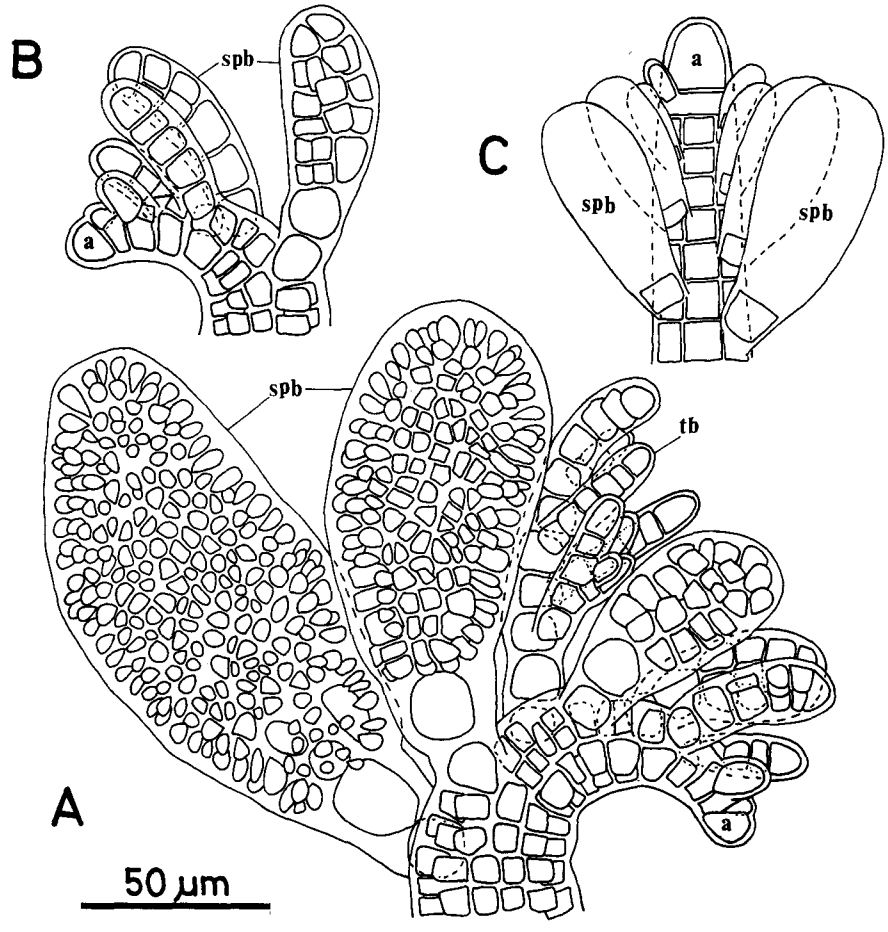

Fig. 36. *Neorhodomela munita*. A-C. Spermatangial branclets formed on the abaxial convex side of determinate branchlets and arranged in a zigzag manner (A, field-collected plant; B, cultured plant; C, diagram in abaxial view).

the apical portion of the determinate branchlets of ordinary and adventitious indeterminate branches. Sometimes vegetative trichoblasts are interspersed with them (Fig. 36, A). Young spermatangial branchlets are not distinguishable from vegetative trichoblasts (Fig. 36, A, B). The spermatangial branchlets become polysiphonous except in the proximal two segments which remain monosiphonous. They are sometimes formed on the branched trichoblast which is morphologically identical with vegetative one (Fig. 37, B). Mature spermatangial branchlets are ellipsoid in shape, measure 230–400 μm × 100–160 μm, and usually curve in the same direction as the apical portion of the branchlets bearing them (Pl. 15, B). TAZAWA (1957) showed the external feature of the spermatangial branchlets of this alga, but he did not mention their arrangement. The spermatangial branchlets are arranged in two rows in a zigzag manner on the abaxial side of the determinate branchlets (Fig. 36, C).

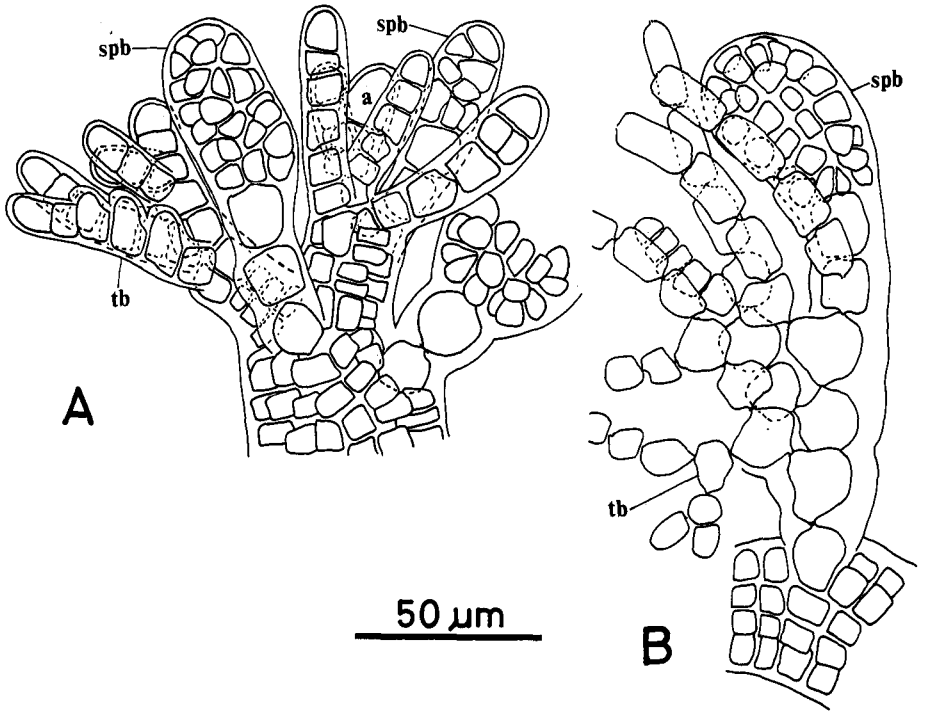

Fig. 37. *Neorhodomela munita.* A. Apical portion of an indeterminate branch forming spirally arranged spermatangial branchlets and vegetative trichoblast (cultured plants). B. Spermatangial branchlet borne on a branched trichoblast (field-collected plant).

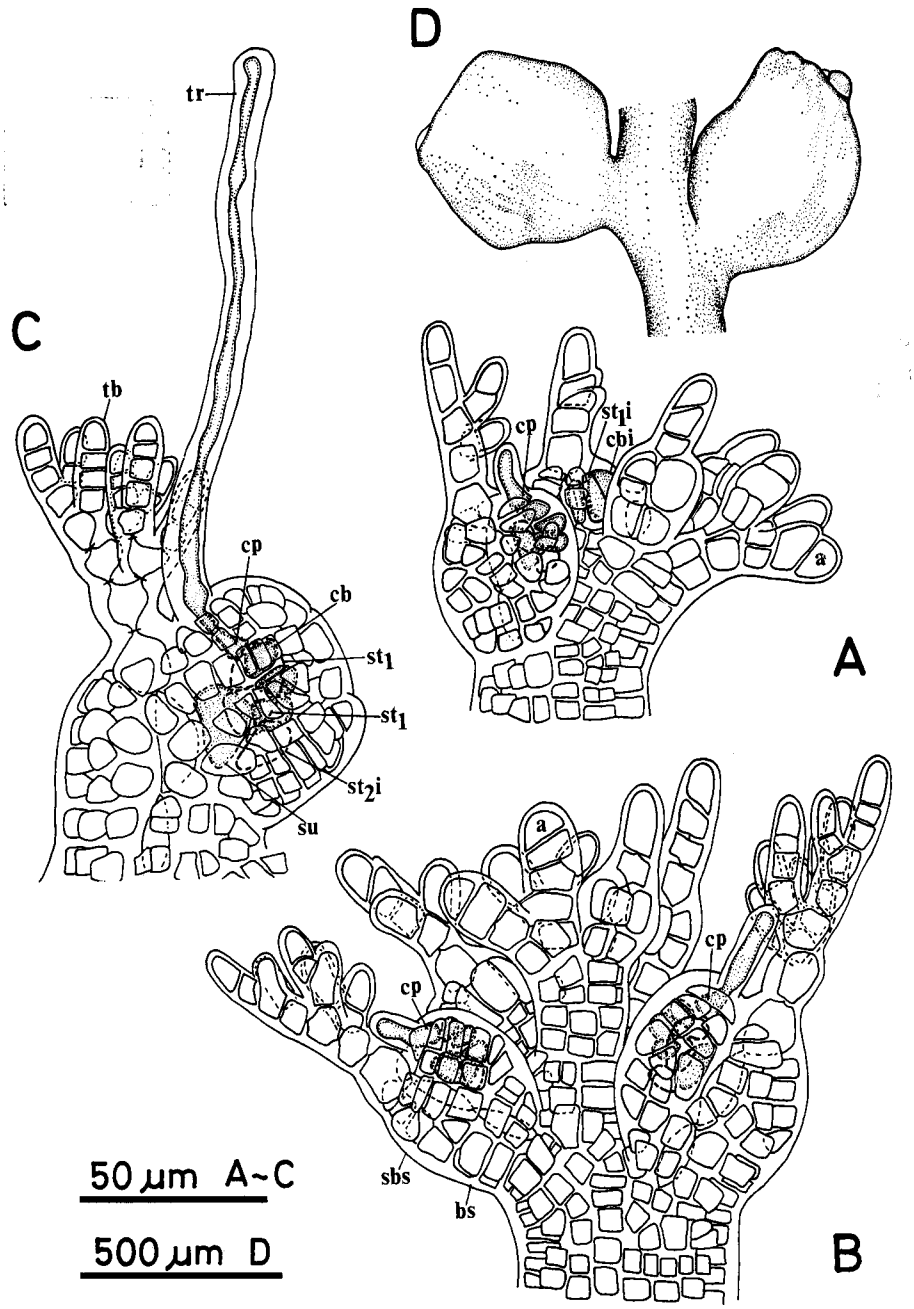

Fig. 38. *Neorhodomela munita.* A. Apical portion of a determinate branchlet, showing the zigzag arrangement of female trichoblasts on the abaxial convex side. B. Apical portion of an indeterminate branch, showing the spiral arrangement of female trichoblasts. C. Mature procarp. D. Mature cystocarps.

The procarps are formed on fertile trichoblasts. The trichoblasts arise on the apical portion of the determinate branchlets of ordinary and adventitious branches. They are arranged in two rows along the abaxial side of the branchlets as in vegetative trichoblasts (Pl. 15, C; Fig. 38, A). The fertile trichoblasts are also produced on the apical portion of indeterminate branches and are usually arranged in a spiral manner replacing vegetative branches (Fig. 38, B).

The development of the procarp begins with the suprabasal segment of the fertile trichoblast bearing five pericentral cells as in *Rhodomela*. The carpogonial branch is produced from the last formed pericentral cell (the fifth), which is formed on the adaxial side of the trichoblast and functions as the supporting cell. The fifth pericentral cell of the suprabasal segment produces a four-celled carpogonial branch and two sterile cell groups. They are surrounded by a pericarp before fertilization (Fig. 38, C). I was not able to observe the development of the auxiliary cell and the gonimoblast filaments. As the cystocarp develops, the monosiphonous portion of the fertile trichoblasts falls off. The carposporangia are terminally produced on gonimoblast filaments and are distinguished from vegetative cells of the pericarp by containing numerous chloroplasts. Mature cystocarps are furnished with well developed pericarps. They are pyriform in shape, measuring 400–590 μm × 390–500 μm and have rather wide ostioles (Pl. 15, D, E; Fig. 38, D) through which the carpospores are discharged. Liberated carpospores are globular and dark brownish-yellow. They measure 67.5–87.5 μm in diameter. (Pl. 10, A).

The tetrasporangia are formed on the upper portions of unspecialized ordinary and adventitious branches of ultimate and penultimate orders. The branches are usually incurved and provided with dorsal trichoblasts as are vegetative branches. Two tetrasporangia are usually produced in each of 7–15 successive segments of the fertile branches (Pl. 15, F). The tetrasporangia are formed from the pericentral cells and are protected by two cover cells. Mature tetrasporangia protrude slightly from the tetrasporangial branches and measure 110–120 μm × 100–110 μm in size in surface view and are divided tetrahedrally. Tetraspores are liberated between the cover cells. Discharged tetraspores resemble carpospores except in their size (Pl. 10, B). They are smaller than the latter and 55.0–77.5 μm in diameter.

The following is additional information on plants collected from other places. Plants from Utoro, Rausu and Tamano have rather long vegetative trichoblasts reaching up to more than 2 mm. These trichoblasts are deeper rose in color than those of plants from other localities. Their color is conspicuous to the naked eye in living materials as well as in pressed speci-

mens. The carpospores and tetraspores from Akkeshi plants have nearly the same size as in Muroran plants and are 70–85 μm and 52.5–77.5 μm in diameter, respectively.

Culture study: Unialgal cultures were obtained from carpospores and tetraspores (Muroran isolates) and from excised apical tips of indeterminate branches (Rausu, Akkeshi and Tamano isolates). The spores and excised apical tips were first cultured at 14°C, 14 : 10 LD.

The description given below is based on observations of the development of tetraspores in Muroran isolate. The tetraspores soon attached to the substrate (Pl. 10, C) and grew into bipolar sporelings of several cells within one day. As shown in Plate 10, D, they differentiated into colorless rhizoidal portion produced from one pole of the spore and a pigmented upright shoot portion from the other pole. After 3 days, the sporelings became slightly recurved (Pl. 10, E, F). The rhizoids were divided repeatedly so as to form either a monosiphonous filamentous holdfast (Pl. 10, F) or a discoid holdfast (Pl. 10, E), both of which were multicellular as in *Rhodomela* (Fig. 40, A, E). Twenty-one were filamentous and 47 were discoid. Both types eventually developed into the same kind of discoid holdfasts (Fig. 40, A–G). The sporelings increased by means of a large apical cell from which pericentral cells were cut off. The pericentral cells simultaneously cut off cortical cells. Within 3 days, the sporeling produced a first branch, which grew into a vegetative trichoblast. Subsequently, several trichoblasts developed from the dorsal side of each segment, the sporelings became bent more strongly (Pl. 10, G–I; Fig. 39, B–D), and each segment increased gradually in length. Thus, the intervals between trichoblasts became longer. The vegetative trichoblasts were arranged in a zigzag manner in two rows along the dorsal side of the sporelings (Fig. 39, B–D). Young vegetative trichoblasts curved in the same direction as the apical portion of the sporeling. Later, they became straight and were visible to the naked eye. Young trichoblasts were light rose in color and later became almost colorless as in field-collected plants (Pl. 10, G–I). The trichoblasts were divided pseudodichotomously 3–4 times reaching up to 1 mm or more. They were deciduous and began to shed successively in the lower portion of sporelings. The basal disc of cultured plants of this alga grew well as did those of field-collected plants and later produced many secondary upright shoots from the superficial cells (Fig. 40, I).

Within 14 days adventitious branches were produced from the outermost cortical cells on the lower portion of the main axis (Fig. 40, H). They grew in a manner similar to the main axis. Ordinary branches of the first order were first observed in 16-day-old plants. Subsequently, the ordinary

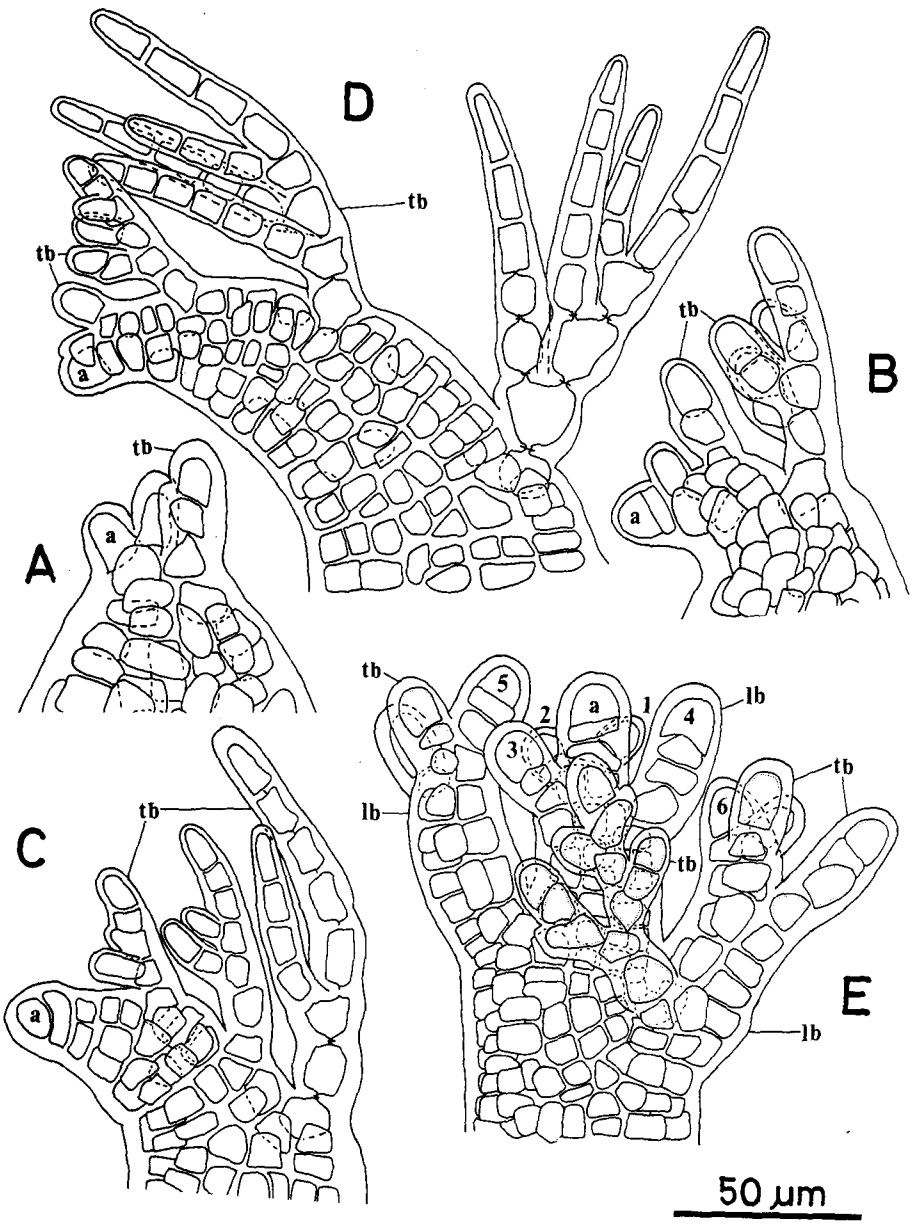

Fig. 39. *Neorhodomela munita.* Stage in the development of the apical portion of sporelings. A–D. Early stages of sporelings issuing trichoblasts on the dorsal side: A, three days old; B, five days old; C, six days old; D, seven days old. E. Twenty-one-day-old sporeling forming spirally arranged ordinary branches numbered in their sequence of formation.

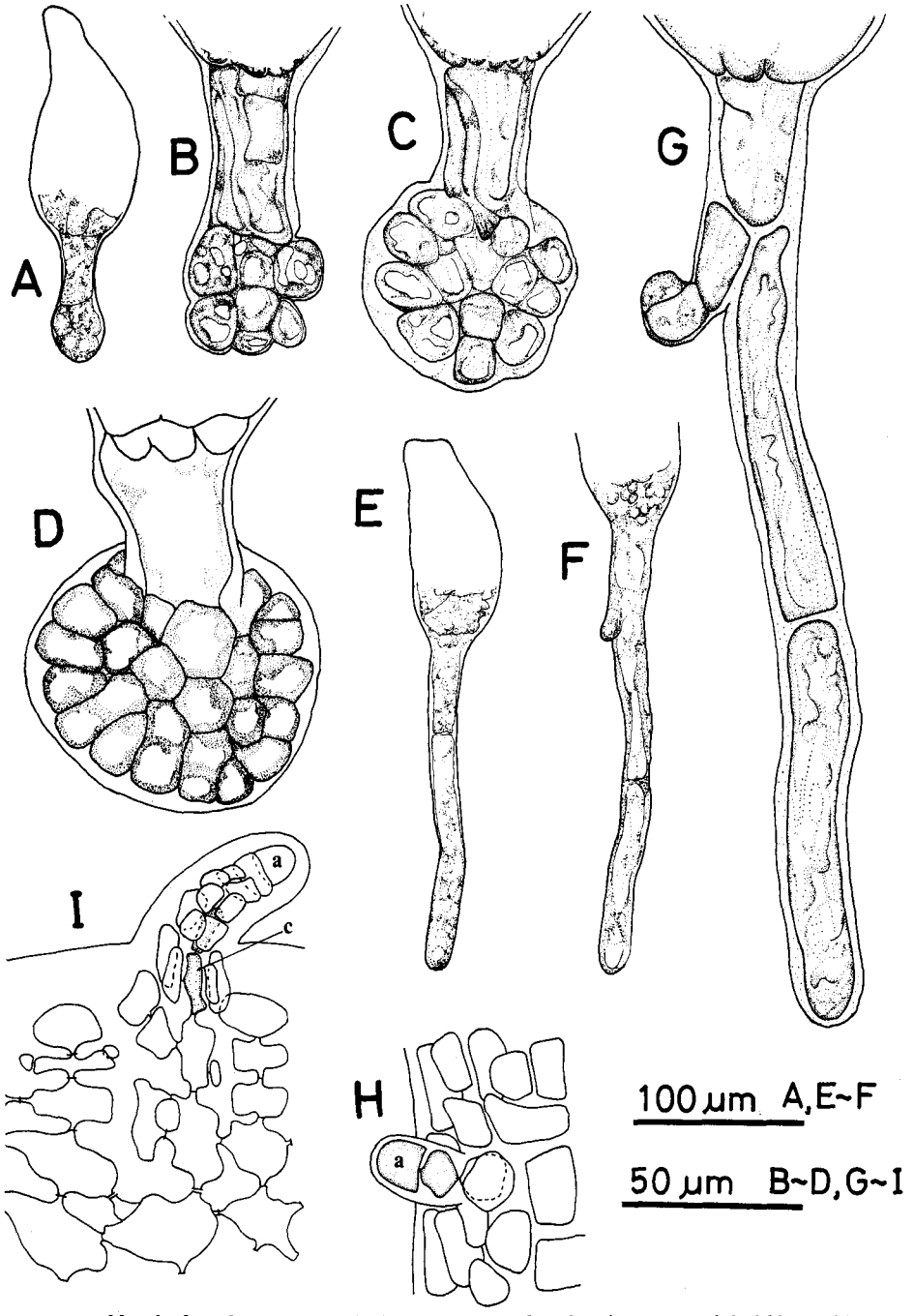

Fig. 40. *Neorhodomela munita.* A–G. Stages in the development of holdfasts (A–D & E–G, the same plant, respectively): A, E, three days old; B, four days old; C, five days old; D, nine days old; F, six days old; G, thirteen days old. I. Longitudinal section of a basal disc, showing a secondary upright shoot developed from a superficial cell. H. Surface view of the lower portion of the primary axis of a 13-day-old plant showing an adventitious branch developed from an outermost cortical cell.

branches were formed in a spiral manner (Fig. 39, E) They were sometimes produced along the dorsal side in succession as were the vegetative trichoblasts (Pl. 10, J). However, they later became arranged in a spiral manner. These branches were successively formed on each segment as development of the main axis proceeded. With successive formation of the first order branches the main axis gradually strainghtened. As a result, plants became upright (Pl. 10, K). After one month, plants reached up to 1 cm high and produced 10–12 branches of the first order. The branches were strongly incurved, producing several vegetative trichoblasts along their abaxial side. Several secondary axes issued from the basal disc became well developed as was the primary axis. The adventitious branches mentioned above grew indeterminately and produced several branches. Adventitious branches also were issued from the middle to upper portion of the primary and secondary axes. They were usually borne in the axil, sometimes randomly. They developed in a manner quite similar to the primary axis. The first order branches of the primary and secondary axes grew indeterminately and formed many branches of the subsequent order. As growth advanced, the gross morphology of cultured plants became complicated.

After 2 months, plants reached up to a height of 3.5 cm and produced spermatangia or procarps on separate plants. Both gametangia were borne on the apical portion of determinate branchlets issued from the indeterminate branches of the first to third orders as well as from adventitious branches (Pl. 10, M-O; Fig. 36, B). They were on the abaxial convex side of branchlets as were those of field-collected plants. However, in a few instances, they were also formed on the apical portion of indeterminate branches. In the latter case, they occurred where vegetative laterals would normally occur and thus were arranged in a spiral manner (Fig. 37, A). Their development and structure were quite similar to the field-collected plants described above. In cultures containing spermatangial plants (Pl. 9, C), procarpic plants bore ripe cystocarps from which viable carpospores were discharged within 21–30 days (Pl. 9, D; 10, P). However, procarpic plants established in single culture did not produce cystocarps.

Liberated carpospores were quite similar to those from field-collected plants. Their diameters were 72.5–85.0 μm. Germination of these carpospores and subsequent development of sporelings were the same as those of tetraspores described above. The sporelings grew into plants similar in morphology to parent gametophytes. Within 2 months the plants reached reproductive maturity (Pl. 9, E) and formed tetrasporangia in a manner quite similar to that described for field-collected plants and subsequently discharged

numerous viable tetraspores (Pl. 10, Q). The tetraspores were idenctial with those of field-collected plants in all respects.

To test the effect of temperatures and photoperiods on the growth and maturation of sporelings, 7-day-old plants derived from carpospores mentioned in the preceding paragraph and grown at 14°C, 14 : 10 LD were transferred to the following eight conditions : 5°C, 14 : 10 LD ; 5°C, 10 : 14 LD ; 10°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD ; 18°C, 10 : 14 LD and 22°C, 14 : 10 LD. Three plants were shifted to each condition. The plants grew more rapidly at 14–22°C than at 5–10°C and they grew best in long day conditions. The tetrasporangia were formed and the tetraspores were discharged from the plants 3 months after transfer at 10°C, 14 : 10 LD ; 14°C; 10 : 14 LD ; 18°C, 14 : 10 LD ; 18°C, 10 : 14 LD and 22°C, 14 : 10 LD, 5 months after transfer at 10°C, 10 : 14 LD, and 8 months after transfer at 5°C, 14 : 10 LD and 5°C, 10 : 14 LD.

Excised apical tips of the indeterminate branches of the cystocarpic plants from Tamano and those of the tetrasporangial plants from Rausu and Akkeshi developed well as did the sporelings of the Muroran isolates described above. In the Tamano isolate apomictic development (without fertilization) of the carposporophyte was not observed. The Rausu and Akkeshi isolates reached reproductive maturity and discharged tetraspores within 2–3 months at 14°C, 14 : 10 LD. Liberated tetraspores germinated and grew into fertile dioecious gametophytes within 2 months at 14°C, 14 : 10 LD in a pattern quite similar to that of the Muroran isolates mentioned above. Mature cystocarps were observed on female gametophytes one month after starting mixed cultures of male and female plants, although female plants established in single culture did not produce cystocarps.

Crossing experiment between the Muroran, Rausu, Akkeshi and Tamano isolates was attempted, although there was no difference in morphology between the four isolates. In order to obtain vigorously growing fertile plants preparations were made prior to this experiment. Clonal stock cultures of the isolates were cut into fragments about 2 cm in length and transferred to the experimental condition for one month. This crossing experiment was tested in duplicate between every isolate at 14°C, 14 : 10 LD. Self crosses were included as controls. Fertilization was determined by the occurrence of carposporophyte development and carpospore liberation. As stated previously, in the isolates apomictic development of the carposporophyte was not observed. In all crossing combinations attempted, the carposporophytes developed and discharged viable carpospores one month after. Further, the carposporelings of all crosses gave rise to morphologically identical mature tetrasporophytes 2 months after. Thus, sexual reproduction has been ob-

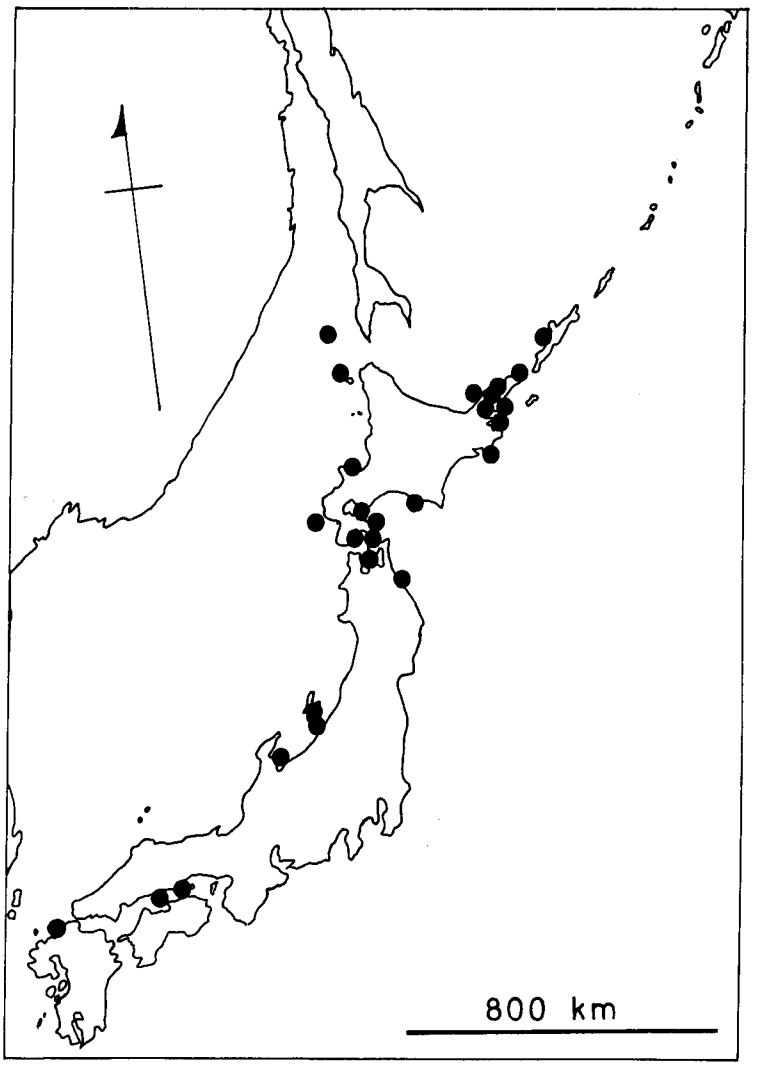

Fig. 41. Distribution of *Neorhodomela munita* in Japan and adjacent waters.

served in laboratory crossing experiment between the four isolates and it appears that all the populations of this species are freely interfertile.

Geographic distribution: This species is distributed, as far as our collections extend (see materials), to the regions where the coast is washed by the Tsushima Current and its terminal branches, the Soya Current and the Tsugaru Current. Fig. 41 illustrates the present known range in Japan and adjacent waters.

Taxonomic discussion

The alga under study is identical with the southern form of OKAMURA's (1922) '*Rhodomela subfusca*' which differs from genuine *R. subfusca* (=*R. confervoides*) and includes three species as stated previously in this paper. Of the three species, *Rhodomela sachalinensis* and *R. teres* were already described. The alga in question is nothing but *Rhodomela munita* which was recently established based on material collected in Posjeti Bay facing the Sea of Japan by PERESTENKO (1980). The original description and illustration of *R. munita* are in agreement with the aforementioned characterization of the alga in question. This alga differs from *Rhodomela* in several taxonomic features as will be discussed in detail in the 'Systematic remarks of the tribe Rhodomeleae'.

This species has been confused with other species by previous workers. The records of '*Rhodomela subfusca*' from Japan and adjacent waters need verification. According to a check of herbarium specimens, description and illustration, those reports were reviewed. NAGAI's '*R. subfusca*' from the KURILES (1941) includes three species, *Rhodomela sachalinensis*, *Neorhodomela munita* and *N. aculeata*. SEGAWA's illustration of '*R. subfusca*' clearly shows the habit of *N. munita*. The '*R. subfusca*' described by INAGAKI (1933) on the basis of specimens collected from Oshoro Bay, west coast of Hokkaido also fits *N. munita* well in gross morphology. The Chinese '*R. subfusca*' reported by COTTON (1915) and HOWE (1924) appears, as they thought also, to be a different species from the European and American *R. confervoides* (=*R. subfusca*). It seems rather more similar to *N. munita* than to *R. confervoides* judging from HOWE's description (1924).

This species has been confused with *Neorhodomela larix* by HIROSE (1957) in the Shiaku Islands of the Seto Inland Sea, and by NODA (1967) in Sado Island of the Sea of Japan. An examination of their voucher specimens reveals that the plants are not referable to *N. larix* because of the absence of thick setaceous branchlets. They are identical with *N. munita* in all respects.

Neorhodomela aculeata (PERESTENKO) MASUDA, stat. et comb. nov.

Basionym: *Rhodomela larix* (TURNER) C. AGARDH subsp. *aculeata* PERESTENKO, 1967, p. 148, figs. 1, 2; 1980, p. 120, fig. 252.

Synonyms: *Rhodomela larix* auct. non C. AGARDH; OKAMURA, 1902, p. 66, 1912, p. 81, 1922, p. 154, pl. 188, figs. 1-4, 1933, p. 94, 1936, p. 898; INAGAKI, 1933, p. 65; KAWABATA, 1936, p. 77, 1959, p. 295; TAKAMATSU,

1938 a, p. 68, pl. 4, fig. 2, 1938 b, p. 137, 1939, p. 78; NAGAI, 1941, p. 235; YAMADA and TANAKA, 1944 a, p. 77; YAMADA and KINOSHITA, 1948, p. 18, pls. 21, 22; HASEGAWA, 1949, p. 71; TOKIDA, 1954, p. 221; KAWASHIMA, 1955, p. 159; SEGAWA, 1956, p. 121, pl. 72 (588); TAZAWA, 1957, p. 31, fig. 1 (1-6), 1975, p. 158, pl. 10, C, fig. 42, A-E; IWAMOTO, 1960, p. 42, pl. 10, D-F, 15, A; FUNAHASHI, 1966, p. 144; CHIHARA, 1970, p. 113, pl. 57 (3).

Rhodomela subfusca auct. non C. AGARDH; NAGAI, 1941 (*pro parte*), p. 235.

Japanese name: Fujimatsumo (OKAMURA, 1912).

Materials

The materials used were collected from Hokkaido and northern Honshu from 1968 to 1973. HOKKAIDO Utoro: *Masuda* 6438-6464 & 12957-12973 (v-1968, spermatangial & tetrasporangial; vi-1969, ditto; vii-1968, ditto; viii-1968, cystocarpic & tetrasporangial; x-1968, ditto). Rausu: *Masuda* 6465-6538, 12974 & 12975 (i-1969, sterile; iii-1969, sterile; v-1968, spermatangial & tetrasporangial; vii-1968, ditto; viii-1968, spermatangial, cystocarpic & tetrasporangial; x-1968, cystocarpic & tetrasporangial). Nemuro: *Masuda* 8528, 8533-8539, 8541, 8636-8639, 8767 & 8878-8881 (Habomai, v-1968; Hanasaki, ix-1970, spermatangial, cystocarpic & tetrasporangial; x-1970, cystocarpic & tetrasporangial). Akkeshi: *Masuda* 8526, 8530, 8768-8771 & 13030-13082 (vi-1970, spermatangial, cystocarpic & tetrasporangial; vi-1971, ditto; vii-1970, spermatangial, leg. I. YAMADA). Muroran: *Masuda* 8497-8525, 8531, 8532, 8542-8599, 8601-8633, 8642-8759, 8761-8763, 8774-8818, 8825-8862, 8867, 8868, 8870-8872 & 13145-13176 (i-1971, sterile; ii-1971, ditto; iii-1971, ditto; iv-1971, spermatangial, cystocarpic & tetrasporangial; v-1971, ditto; vii-1971, ditto; viii-1970, cystocarpic & tetrasporangial; ix-1970, ditto; x-1970, ditto; xi-1970, ditto; xii-1970, ditto). Usujiri: *Masuda* 13083-13085 (iv-1973). Esan-misaki: *Masuda* 13086-13088 (iv-1973). Shirikishinai: *Masuda* 13089-13099 (iv-1973). HONSHU Aomori Pref.: *Masuda* 8819-8824 & 13098-13144 (Tappi-zaki, vii-1971, leg. Y. NANAO; Omazaki, v-1973, spermatangial, cystocarpic & tetrasporangial: Shiriyazaki, v-1973, ditto).

The herbarium specimens deposited in the herbaria listed below were also observed. KURILES Shumsh Island: NAGAI Herb. (Kataoka-wan, vii-1930, tetrasporangial). Paramshir Island: NAGAI Herb. (Suribachi-wan, viii-1932; Chitose-wan, vii-1930; Kakumabetsu, viii-1932, tetrasporangial; Kamogawa, vii-1932, tetrasporangial). Etorof Island: NAGAI Herb. (Shibetoro, viii-1931; Bettobu, viii-1930). Kunashiri Island: SAP 22025 (Tofutsu, viii-1936), NAGAI Herb. (Atoiya, viii-1929, Nos. 402, 405; Rebun-iso, vii-

1929, No. 438; Furukamappu, viii-1930, No. 2367; Tofutsu, viii-1936; Kotankeshi, viii-1936; Toshoro, viii-1931; Shibetoro, viii-1931; Sokobetsu, viii-1931). Shikotan Island: SAP 15507, 15508 & 22870 (vii-1933, vii-1934), NAGAI Herb. (Shakotan, vii-1934, Nos. 5521, 5522; Notoro, non date, No. 3900). SAKHALIN TOKIDA Herb. (Sakaehama, viii-1929, tetrasporangial, No. 900; Hota, viii-1932, tetrasporangial, No. 662; Merei, vii-1906, tetrasporangial; Nishinotoro, viii-1935, cystocarpic). HOKKAIDO Rebun Island: KAWABATA Herb. (vii-1960, tetrasporangial). Rishiri Island: YENDO Herb. (viii-1899). Abashiri: SAP 20032 (vi-1934). Hidaka SAP 22868, 25404 & 25497 (vii-1930, viii-1943; Samani, vii-1943). Muroran: SAP 12496, 12497, 23363, 23364, 24298, 25296 & 28554 (v-1931; vi-1953, spermatangial; vii-1935; vii-1943, cystocarpic; x-1944). Abuta: SAP 7928 (viii-1928). Toi: SAP 23511 (iv-1940). Fukushima: YENDO Herb. (ix-1917, leg. L. ROSENBAUM). Matsumae: YENDO Herb. (ix-1917, leg. L. ROSENBAUM). Esashi: SAP 23550 (iv-1940). Okushiri Island: SAP 25239, 25240 (Aonae, x-1943; Kamoishi, x-1943). Oshoro: SAP 14078, 24745 (iii-1944; vi-1931). Yagishiri Island: YENDO Herb. (viii-1910). HONSHU Aomori Pref.: YENDO Herb. (Tappi-zaki, x-1917, leg. L. ROSENBAUM; Shimofuro, iv-1903; Shiriya, viii-1917, leg. L. ROSENBAUM; Shiranuka, iv-1903), SAP 7921, 21835 (Asamushi, vii-1940; Oshima, non date). Iwate Pref.: SAP 26996, 26997 & 27882 (Nakano, vii-1951, vii-1954; Fudai, vii-1952).

Parent plants for culture experiments were as follows: cystocarpic plants collected at Muroran on August 29, 1970 and September 15, 1970, and at Hanasaki, Nemuro on September 27, 1970 and October 17, 1970; tetrasporangial plants collected at Muroran on September 14, 1970 and November 17, 1970 and Hanasaki on September 27, 1970 and October 17, 1970.

Description

Plants perennial, with several upright thalli arising from a common expanded basal disc; upright thalli terete, attaining up to 36 cm high, dark brown in color, rather robust and tough in texture, not adhering to paper in drying except for young plants; main axis almost straight, stout, 800-1400 μm in diameter in the lower portion, becoming gradually thicker upward, 1400-1800 μm in diameter in the lower third portion, tapering gradually toward the apex; the majority of the first order branches simple, setaceous, up to 7-10 mm in length and 450-500 μm in diameter, several of these growing indeterminately, provided with the fourth order branches; adventitious branches numerous in the axil, growing well; pericentral cells usually 6, sometimes 5 in determinate branchlets; vegetative trichoblasts numerous on the apical portion of young determinate and indeterminate branches,

rose-colored, divided four times pseudodichotomously ; plants dioecious ; spermatangial branchlets narrowly ellipsoid, 300–500 μm × 85–120 μm ; cystocarps almost globose to broadly ovoid, 400–500 μm × 360–480 μm ; carpospores dark brownish-yellow, 70.0–97.5 μm in diameter ; tetrasporangia borne in two rows on 6–11 successive segments of ultimate order branchlets, each provided with two cover cells, 110–125 μm × 105–115 μm ; tetraspores 60–80 μm in diameter.

Observations

Habitat and Phenology: This species is the commonest representative of this genus in Hokkaido and is the most prominent occupant of the middle to lower intertidal zone. It occurs attached to rock in places exposed to wave action forming dense carpets. It also inhabits sheltered places where it very often grows together with *Neorhodomela munita*. In these instances, they grow in close proximity to each other and their holdfasts sometimes appear to combine to one another. At Akkeshi this alga is often found growing in the upper sublittoral zone, where it associates with *Odonthalia annae*.

Phenological observations were executed at Muroran from 1970 to 1971. Plants of this alga can be found in all seasons. They achieve their most luxuriant growth in late spring to early summer. The size of upright thalli decreases with increasing exposure. It reaches up to 36 cm high in populations growing in the lower intertidal zone. Young sterile plants, which arise secondarily from a basal disc, can be seen throughout the year. Thus, the basal disc apparently persists throughout the year. Spermatangial plants appear in early April and last until July. Mature cystocarpic plants can be seen from mid-May to late December. Mature tetrasporangial plants are found from late Apirl to late December. Both cystocarpic and tetrasporangial plants continue to discharge carpospores and tetraspores in these months. Cystocarpic plants collected on April 30, 1971 were immature judged on the basis of cystocarp size. However, tetrasporangial plants collected at that time discharged viable tetraspores. Afterward, the upper portions of the fertile upright thalli fall off leaving short main axes and branches of the first order. However, several adventitious branches which issue from cortical cells remain sterile and may become fertile in the following season. Thus, this alga is apparently perennial.

Morphology of field plants: The following description is given on the basis of materials collected at Muroran. This information is supplemented by observations on specimens from other localities in Japan. Plants have several upright, terete thalli arising from a common discoid holdfast

as illustrated by OKAMURA (1922), and YAMADA and KINOSHITA (1948). The basal disc is well expanded as in *N. munita*. Plants are dark brown in color. They have a rather robust and tough texture by which this species is easily distinguishable from *N. munita*, which has a delicate and soft texture. Young specimens imperfectly adhere to paper in drying and old ones do not adhere to paper at all. Each erect thallus has a conspicuous main axis which is almost straight and stout. Main axes are 800–1400 μm in diameter just above the basal disc, becoming gradually thicker upward, and reach 1400–1800 μm in diameter in the lower third portion. The main axes successively produce lateral branches from the central cells in the growing apex (Fig. 42, A). They are arranged in a spiral manner as in *N. munita*. However, the development of the first order branches differs from that of *N. munita*. In this alga many ordinary branches of the first order stop growth during early development and become determinate, whereas in *N. munita* only a few lower branches become determinate.

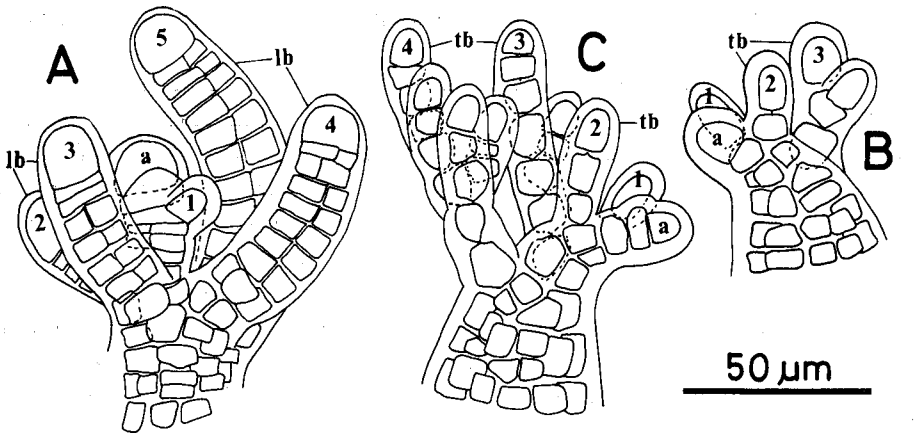

Fig. 42. *Neorhodomela aculeata* (PERESTENKO) MASUDA. A. Apical portion of an indeterminate branch forming spirally arranged branches numbered in their sequence of formation. B, C. Young trichoblasts borne on the abaxial convex side of determinate branchlets and arranged in a zigzag manner, numbered in their sequence of formation.

Determinate branchlets formed on the main axis are setaceous and usually incurved producing vegetative trichoblasts along the abaxial convex side. The determinate branchlets are 1.5–2.8 mm in length in the lower portion of the main axis and reach up to 7–10 mm in length and 450–500 μm in diameter in the upper third portion. Midway up the main axis these determinate branchlets are replaced by indeterminate branches, and then,

further up they again replace the latter. Thus, the indeterminate branches, which develop in a manner quite similar to the main axis and are provided with the fourth order branches in well developed ones, are randomly produced from the main axis at first. However, the indeterminate branches are produced much more in the upper portion where the determinate branchlets are sporadically present.

Adventitious branches are usually limited to the axils and are distinguished from ordinary branches by the attenuate proximal portion. The axillary adventitious branches develop indeterminately and contribute to the ramification of the plant together with indeterminate ordinary branches. Well ramified plants of this alga are somewhat similar to *N. munita* in gross morphology (Pl. 11, A). However, the ramifications of this alga are not so complicated as *N. munita*, which has numerous indeterminate branches. In general aspect some plants of this alga bear a resemblance to *Cryptomeria japonica*, a Gymnospermae as shown in Plate 11, F (YAMADA and KINOSHITA, 1948; SEGAWA, 1956). In old plants the determinate branchlets are lost successively from the lower portions leaving well developed axillary adventitious branches.

Vegetative trichoblasts of this alga have an appearance quite similar to that of *N. munita*. The most well developed trichoblasts are found in May. They are abundantly produced on the apical portion of determinate branchlets as well as on the apical portion of young axillary adventitious branches. The vegetative trichoblasts are located in a zigzag manner in two longitudinal rows along the abaxial convex side of branches (Pl. 16, A; Fig. 42, B, C). They are rose-colored when young, but they become lighter colored as they grow old. Eventually, they become almost colorless and fall off. They are up to 1.5 mm in length and divided four times pseudodichotomously. This arrangement of the trichoblasts allies this species with *Neorhodomela*.

The thallus structure of this alga is basically in aggreement with that of *N. munita* (Pl. 17, F; Fig. 46, A). The central axial cell is 200 μm in length just above the basal disc and reaches a length of 1.5–2.0 mm in the middle portion of the main axis. The six pericentral cells are usually formed (Pl. 17, F), but five pericentral cells are sometimes formed especially in determinate branchlets. The main axes of this alga have 13–14 layers of cortical cells in the lower portion and 15–16 layers in the middle portion of the main axis in first year plants.

Spermatangia, carpogonia, and tetrasporangia are produced on separate plants. The spermatangia are only borne on fertile trichoblasts, which are in a position quite similar to vegetative trichoblasts, as in *N. munita*. When

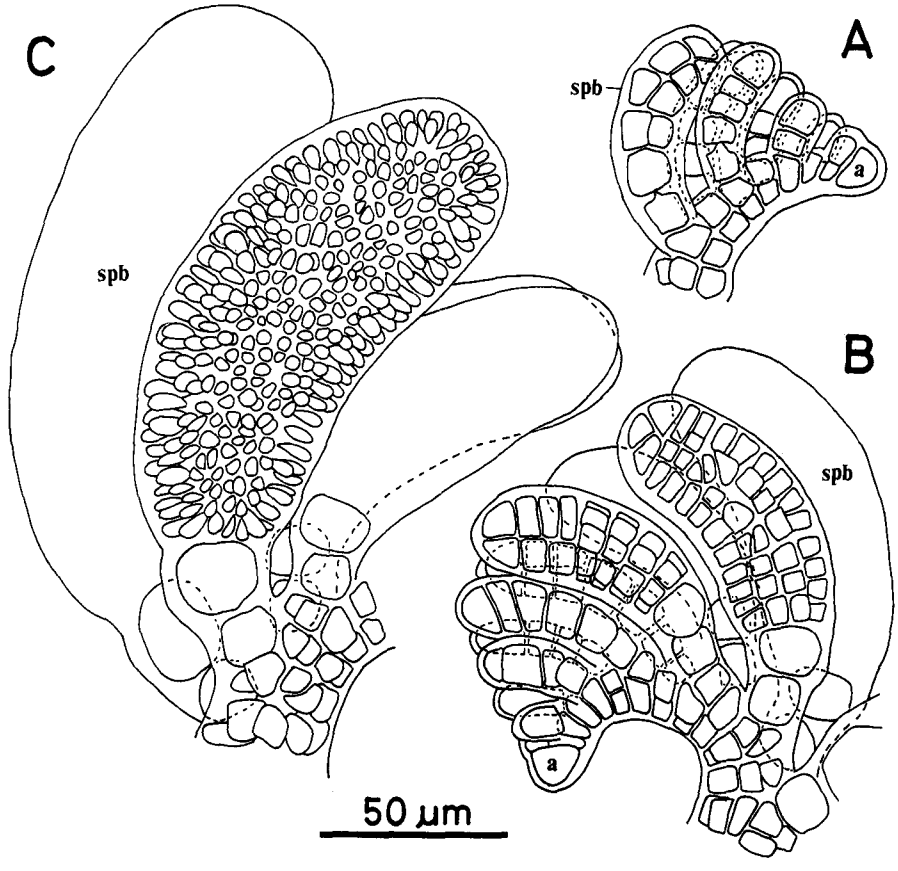

Fig. 43. *Neorhodomela aculeata.* A–C. Spermatangial branchlets borne on the abaxial convex side of determinate branchlets and arranged in a zigzag manner.

plants reach maturity, they successively bear fertile trichoblasts replacing vegetative ones on the ultimate order branchlets of ordinary and axillary adventitious branches (Pl. 16, B). However, the fertile trichoblasts are sometimes replaced by vegetative ones further up the branchlets. They become polysiphonous and fertile except in the proximal two or sometimes three segments (Fig. 43, A–C). TAZAWA's illustrations (1957, 1975) show the external aspect of the spermatangial branchlet, but he did not describe its arrangement. The branchlets are arranged in a regularly zigzag manner in two longitudinal rows along the abaxial convex side of vegetative determinate branchlets. Mature spermatangial branchlets usually curve in the same direction as the apical portion of the vegetative branchlets bearing them and are narrowly ellipsoid in shape. They are larger than those described

by TAZAWA (1957) and measure 300–500 μm in length and 85–120 μm in diameter. The spermatangial feature is the second point allying this alga with the genus *Neorhodomela*.

The procarps are borne on the suprabasal segment of fertile trichoblasts in a manner quite similar to that of *N. munita* described previously. The fertile trichoblasts are produced on the apical portion of the ultimate order branchlets of ordinary and axillary adventitious branches. They are characteristically located in a zigzag manner along the abaxial convex side of the branchlets (Pl. 16, C; Fig. 44, A). Thus, the arrangement of the fertile trichoblasts also strongly ally this alga with the genus *Neorhodomela*. The fertile trichoblasts are also borne on the apical portion of indeterminate branches in a spiral manner replacing vegetative laterals (Fig. 44, B). Observations indicate that only the suprabasal segment of the trichoblast contributes to reproductive activity. The monosiphonous portion of the trichoblast develops well (Fig. 44, C) and eventually sheds as the cystocarp growth advances. Mature cystocarps are almost globose to broadly ovoid in shape and measure 400–500 μm in height and 360–480 μm in diameter (Pl. 16, D; Fig. 44, D). Carpospores discharged through the distal ostiole of mature cystocarps are globular and dark brownish-yellow. They measure 70.0–92.5 μm in diameter (Pl. 12, A). The carpospores from the Nemuro plants are quite similar to those from the Muroran plants in their morphological features.

The tetrasporangia are produced on the ultimate order branchlets of ordinary and axillary adventitious branches. The fertile branchlets are morphologically identical with sterile branchlets. They usually have dorsal trichoblasts and are incurved as are the vegetative branchlets. Two tetrasporangia are produced on each segment of the fertile branchlets so that the tetrasporangia form two longitudial rows on 6–11 successive segments. The tetrasporangia originate from pericentral cells and are protected by two cover cells. Mature tetrasporangia do not protrude from the branchlets, measuring 110–125 μm × 105–115 μm in surface view and are divided tetrahedrally (Pl. 16, E). Liberated tetraspores look like the carpospores in their morphological features, but they are smaller than the latter (Pl. 11, B). They vary from 60 μm to 80 μm in diameter. The tetraspores from the Nemuro plants are quite similar to those from the Muroran plants.

Culture study: Unialgal cultures were obtained by isolating carpospores and tetraspores of the Muroran and the Nemuro plants. The spores were first cultured at 14°C, 14 : 10 LD. The following account is of carpospore germination in materials collected at Muroran.

As shown in Plate 12, C–H, the early developmental stages of spores are quite similar to *N. munita* and closely ally this alga with the latter.

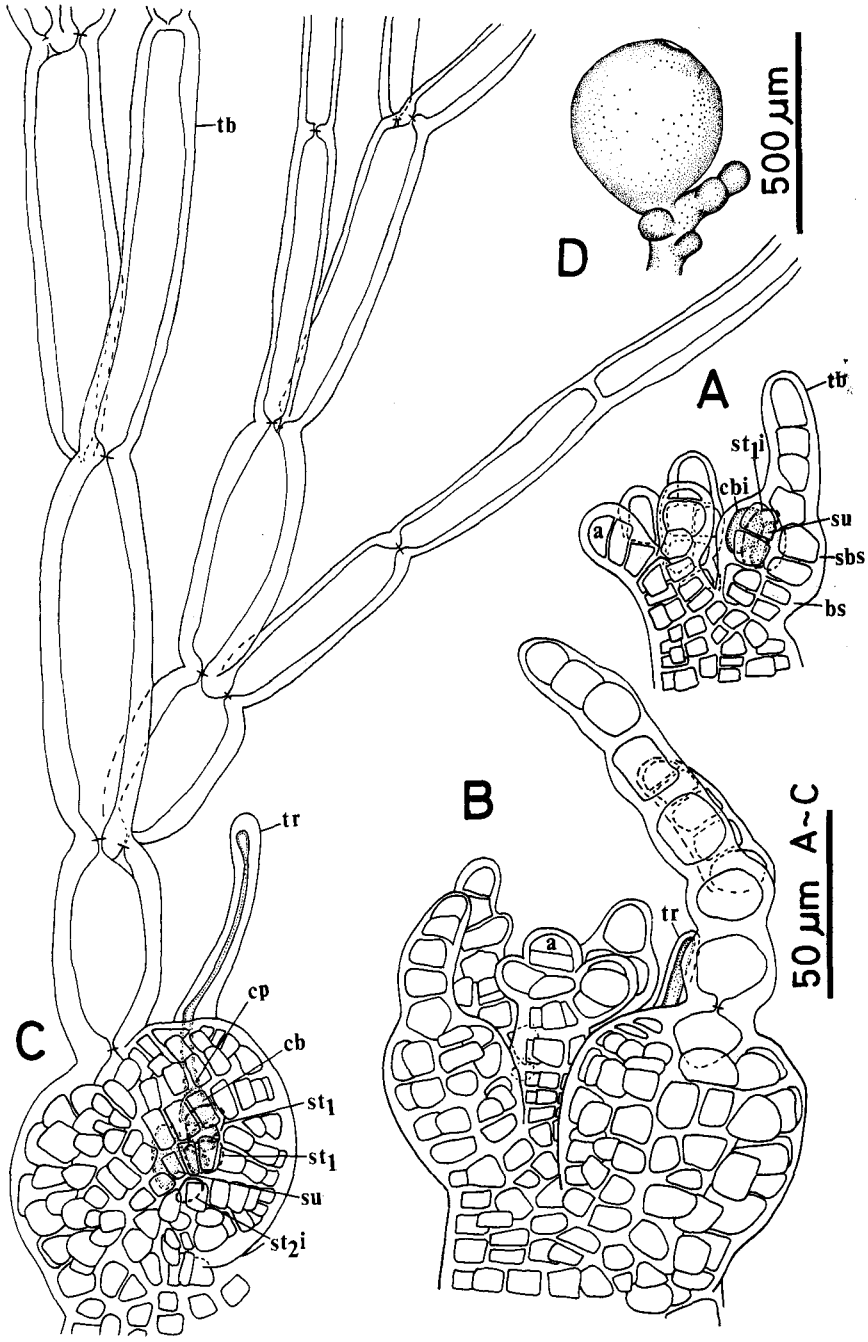

Fig. 44. *Neorhodomela aculeata.* A. Apical portion of a determinate branchlet, showing the zigzag arrangement of female trichoblasts on the abaxial convex side. B. Apical portion of an indeterminate branch, showing the spiral arrangement of female trichoblasts. C. Mature procarp. D. Mature cystocarp.

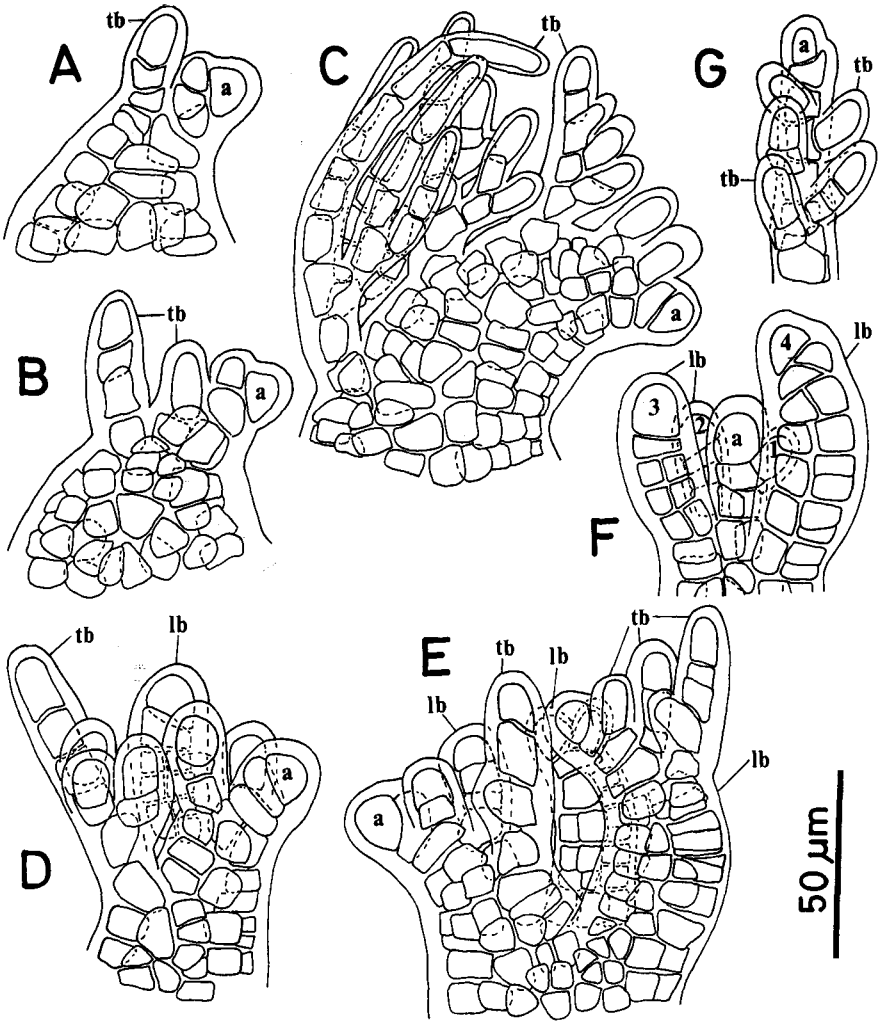

Fig. 45. *Neorhodomela aculeata.* A–F. Stages in the development of the apical portion of sporelings. A–E, early stages of sporelings issuing trichoblasts and ordinary branches on the dorsal side: A, three days old; B, five days old; C, seven days old; D, fourteen days old; E, fifteen days old; F, seventeen-day-old sporeling forming spirally arranged lateral branches numbered in their sequence of formation. G. Tip of a young adventitious branch, showing the zigzag arrangement of trichoblasts from 2-month-old culture.

After 7 days, sporelings reached a height of 300–420 μm and were clearly bent downward. They produced 4–5 vegetative trichoblasts, which were identical with those of field-collected plants, on the dorsal side of each seg-

ment (Pl. 12, F ; Fig. 45, A–C). These trichoblasts developed vigorously and were divided 3–4 times pseudodichotomously reaching up to 1 mm. They began to shed from the lower portion of the sporelings. The multicellular discoid holdfast and filamentous holdfast developed into a pseudoparenchymatous basal disc and produced the secondary upright shoots from the surface cells (Pl. 12, H). The sporelings grew rapidly and showed characteristic features of this genus within 14 days (Pl. 12, G–H). At this stage it was impossible to distinguish this alga from *N. munita*. The sporelings produced the first polysiphonous ordinary branch on the dorsal side (Fig. 45, D) replacing vegetative trichoblasts in 14 days. As growth advanced, the sporelings successively bore 4–5 ordinary branches along the dorsal side (Pl. 12, I; Fig. 45, E). Subsequently, new branches were produced on the flanks and then on the ventral side of the sporelings. Afterward, the first order branches became arranged in a spiral manner on the primary axis (Fig. 45, F). The apex of the primary axis turned upward by this successive formation of branches of the first order as in *N. munita*. Consequently, the sporelings stood upright (Pl. 12, K).

Plants became up to 0.6–1.1 cm high and produced 10–14 branches of the first order after one month. Six pericentral cells (Pl. 17, G) divided transversely into 2 tiers which lay next to the central cell cut off 3–4 tiers of cortical cells (Fig. 46, A). Adventitious branches were continuously formed from cortical cells in the lower portion of the primary axis. Simultaneously, the secondary upright shoots issued from the basal disc. They developed in a manner quite similar to that of the primary axis.

After one and a half month adventitious branches arose from the cortical cells in the axils of the primary axis (Pl. 12, L ; Fig. 46, B). The axillary adventitious branches developed indeterminately in a manner similar to that of the main axis. After 2 months the plants became up to 2.2–3.0 cm high and reached reproductive maturity (Pl. 11, E). In this stage cultured plants of this alga are clearly distinguished from those of *N. munita* by branching density. The first order branches of this alga did not branch but bore many vegetative trichoblasts on the abaxial convex side (Pl. 12, J), and a few of them did develop into indeterminate branches. However, cultured plants as well as field-collected plants of *N. munita* always possess abundant indeterminate first order branches.

The tetrasporangia were abundantly formed on the ultimate order branchlets of axillary adventitious branches. They were also borne on the first order branchlets issuing from the upper portion of the plants (Pl. 12, M). They were located in two longitudinal rows of 7–14 successive segments (Pl. 12, M). Mature tetrasporangia were 115–125 μm $\times$ 105–115 μm and di-

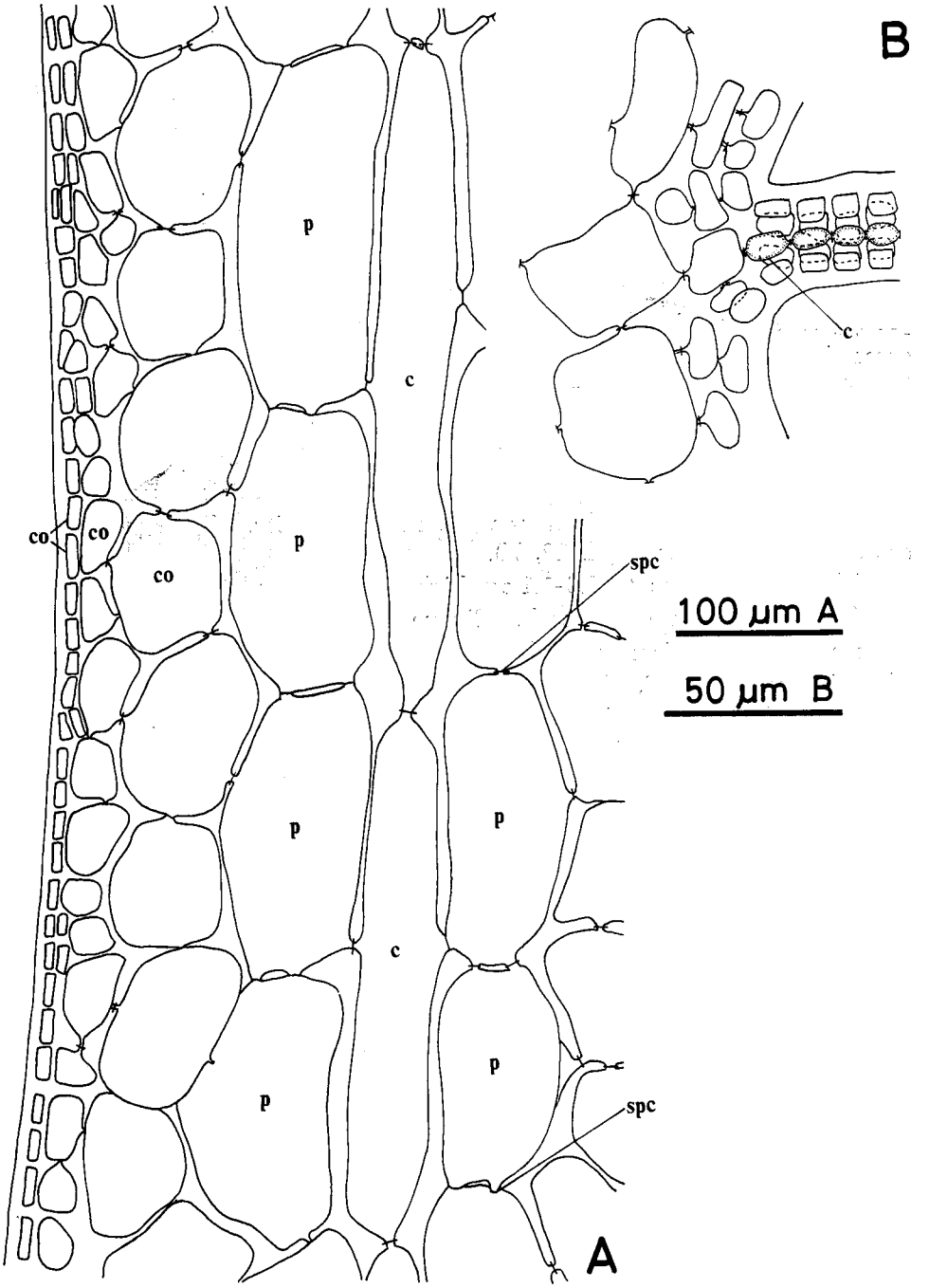

Fig. 46. *Neorhodomela aculeata.* Longitudinal sections of the main axes of cultured plants. A. Middle portion of a one-month-old plant, showing the arrangement of central cells, pericentral cells, and cortical cells. B. Upper portion of a two-month-old plant, showing an axillary branch developed from an outermost cortical cell.

vided tetrahedrally as in field-collected plants. Then, the tetrasporangia began to discharge viable tetraspores. Liberated tetraspores were quite similar to those from field-collected plants. They were 62.5-78.8 μm in diameter.

The tetraspores germinated just as in the case of the carpospores described above and subsequently developed into dioecious gametangial plants bearing spermatangia or carpogonia after 2 months (Pl. 11, B, C). Both gametangia were borne on fertile trichoblasts which issued from first order determinate branchlets as well as from the ultimate order branchlets of the axillary adventitious branches in a manner quite similar to those of field-collected plants (Pl. 12, N-P). Some plants produced spermatangia and procarps on the same thallus. The male and female trichoblasts were borne on separate branchlets or branches in many cases, but sometimes they were borne in close proximity on the same branch.

Mature cystocarps (Pl. 12, Q) were observed on female plants in a mixed culture with male plants 21 days after mixture. However, the formation of cystocarps was not observed while female plants established in single culture. The cystocarps were quite similar to those of field-collected plants and measured 400-580 μm in height and 430-480 μm in diameter. Viable carpospores were discharged through the ostioles. They were quite similar to those from field-collected plants and 77.5-87.5 μm in diameter.

Carpospores derived from the Nemuro plants germinated and gave rise to mature tetrasporangial plants after 2 months in a manner quite similar to that of the aforementioned Muroran isolate. However, two cultured tetrasporangial plants bore both tetrasporangia and spermatangial branchlets on the same thallus. The spermatangial branchlets developed at the apical portion of the tetrasporangial branchlets replacing vegetative trichoblasts. The tetrasporangial branches of such plants were abundant and spermatangial branchlets were less numerous. The tetrasporangial branches and the spermatangial branchlets were quite identical with those formed on the normal tetrasporangial and spermatangial plants. Liberated tetraspores from the normal and aberrant plants were quite identical to those from the Muroran isolates and were 62.5-81.0 μm in diameter. Subsequently, they grew into mature gametangial plants bearing either spermatangia or procarps in a manner quite similar to the Muroran isolates after 2 months.

The effect of temperatures and photoperiods on the growth and maturation of carpospore and tetraspore germlings was tested. Three-day-old carposporelings and ten-day-old tetrasporelings both of which were derived from the Muroran isolates and grown at 14°C, 14 : 10 LD. They were transferred to the following eight conditions: 5°C, 14 : 10 LD; 5°C, 10 : 14 LD; 10°C,

14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD ; 18°C, 10 : 14 LD and 22°C, 14 : 10 LD. Three or five plants were introduced into each condition. They grew more rapidly at 10–22°C than at 5°C and grew best in long day conditions. In these plants, the first order branches were formed at shorter intervals at 14–22°C than at 5–10°C. This indicates that the elongation of the central cell is small at higher temperature. In the carposporelings, the tetrasporangium formation and tetraspore liberation were

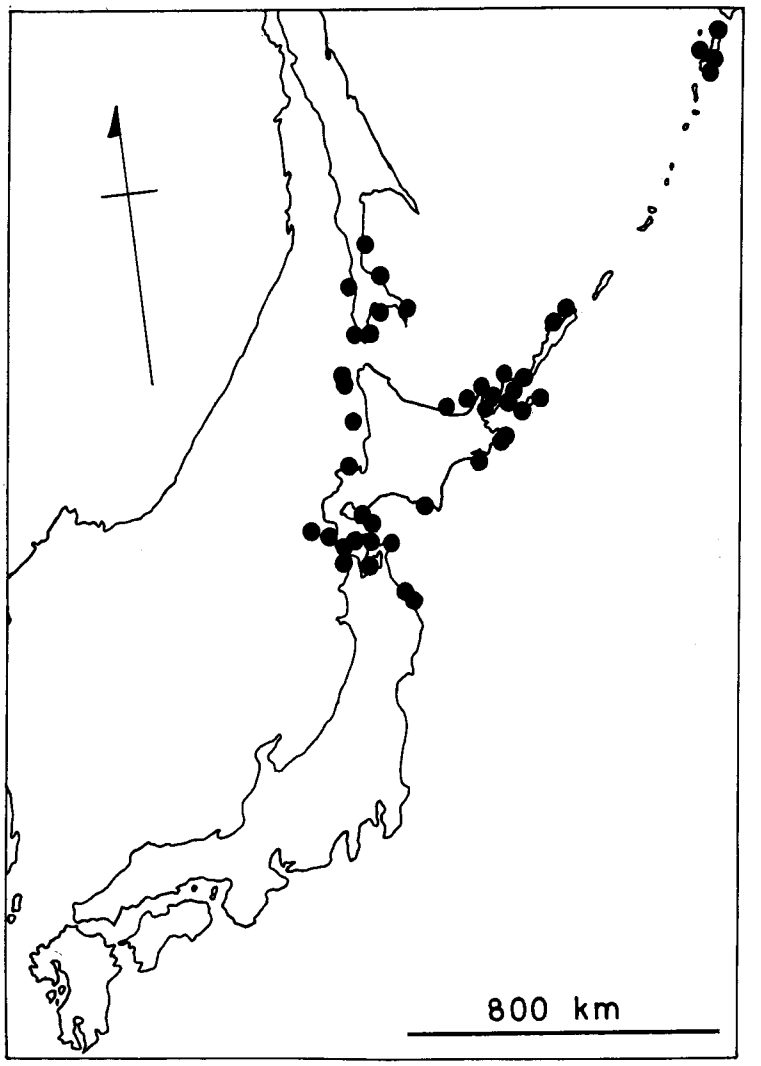

Fig. 47. Distribution of *Neorhodomela aculeata* in Japan and adjacent waters.

observed 3 months after transfer at 10°C, 14 : 10 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD ; 18°C, 10 : 14 LD and 22°C, 14 : 10 LD, 5 months after at 10°C, 10 : 14 LD, and 9 months after at 5°C, 14 : 10 LD and 5°C, 10 : 14 LD. The tetrasporelings produced spermatangia or carpogonia within 5 months after transfer under all conditions tested.

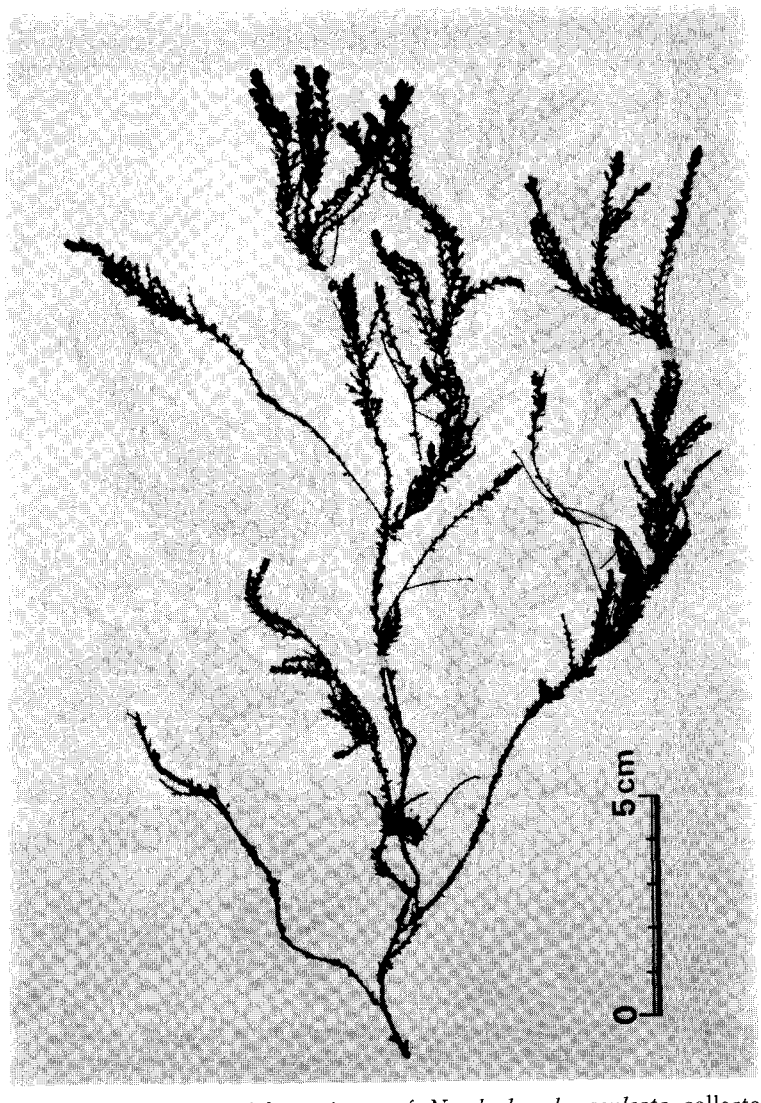

Fig. 48. Tetrasporangial specimen of *Neorhodomela aculeata* collected at Bamfield, Vancouver Island in August 1973 (SAP, leg. T. B. WIDDOWSON).

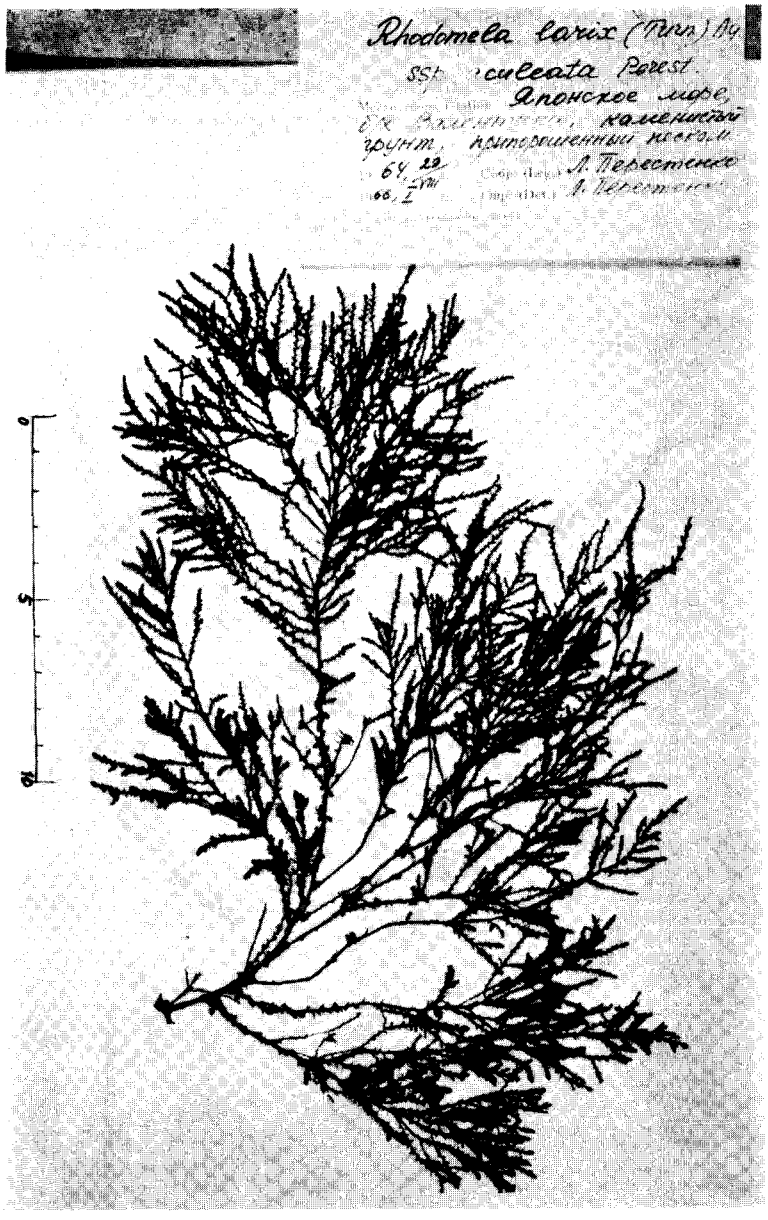

Fig. 49. Holotype specimen of *Rhodomela larix* subsp. *aculeata* PERESTENKO collected in Balentin Bay on August 29, 1964 (LE, leg. L. P. PERESTENKO).

Cross fertilization between the Muroran and Nemuro isolates was attempted. The experiment was executed by the same procedure as that of *N. munita* stated previously. All the crosses were positive and cystocarp development and subsequent carpospore liberation occurred one month after starting each mixed culture of both male and female plants.

Geographic distribution: In Japan and adjacent waters, this alga are found in localities inhabtied by *N. munita* as Fig. 47 illustrates. However, this alga has not been found from the central and southern coasts of the Sea of Japan. In addition, the geographic distribution extends to the northern Kurile Islands and Sakhalin. It is of interest that tetrasporangial specimens collected at Bamfield, Vancouver Island, British Columbia, by T. B. WIDDOWSON and determined as *Rhodomela lycopodioides* are identical with this alga in every respect. The specimens were sent to me from L. D. DRUEHL (Fig. 48). Thus, the geographic distribution of this alga extends eastward to the North America, where the distribution overlaps with that of *N. larix* which is described in the next part.

Taxonomic discussion

Since OKAMURA (1902) reported the occurrence of this alga on the shores of Japan, it has been reported from various localities in northern Japan and has been called *Rhodomela larix*. PERESTENKO (1967) distinguished the two subspecies, subsp. *larix* and subsp. *aculeata* PERESTENKO in *R. larix*. According to PERESTENKO (1967), subsp. *aculeata* is characterized by the simple aculeate branchlets covering the main axis and indeterminate branches. The habit photograph of the holotype specimen taken by I. YAMADA shows clearly the characteristic feature (Fig. 49). I examined a cystocarpic specimen of the subspecies determined by PERESTENKO, which was collected in Possiet Bay facing the Sea of Japan on July 3, 1965 by herself and presented to SAP. This specimen is very similar in gross morphology to the holotype and also to the specimen shown in my Plate 11, F. It is also in agreement with the alga under discussion in other taxonomic features, size and shape of cystocarps, presence of axillary adventitious branches with indeterminate growth and absence of thick subulate branchlets. Thus, the alga under discussion corresponds to subsp. *aculeata*. The present study reveals that the PERESTENKO's two subspecies should be distinguished at the species level on the basis of clear differences in the ontogeney of sporelings and presence of a sterility barrier as will be shown in detail later.

Neorhodomela larix (TURNER) MASUDA, comb. nov.

Basionym: *Fucus larix* TURNER, 1819, p. 23, pl. 207.

Synonyms: *Rhodomela larix* (TURNER) C. AGARDH, 1822, p. 376; POSTELS and RUPRECHT, 1840, p. 14; HARVEY, 1853, p. 24, 1862, p. 168; J. AGARDH, 1863, p. 886; FALKENBERG, 1901, p. 600; SETCHELL and GARDNER 1903, p. 330; COLLINS, 1913, p. 122; KYLIN, 1925, p. 75; SMITH, 1944, p. 374; DOTY, 1947, p. 196; SCAGEL, 1957, p. 241; ABBOTT and HOLLENBERG, 1976, p. 741.

Lophura larix (TURNER) KÜTZING, 1849, p. 850, 1865, p. 14.

Fuscaria larix (TURNER) RUPRECHT, 1850, p. 219.

Materials

The specimens examined were collected from the west coast of North America from 1973 to 1980. Glacier Point, Vancouver Island (vii-1973, cystocarpic & tetrasporangial, leg. L. D. DRUEHL) (Pl. 11, G). Port Renfrew, Vancouver Island (ix-1973, spermatangial & tetrasporangial, leg. L. D. DRUEHL). Bodega Head, Sonoma Co., California (v-1973, tetrasporangial, leg. J. A. WEST) (Pl. 11, H). Duxbury Reef, Marin Co., California (xi-1980, sterile & cystocarpic, leg. J. A. WEST and M. MASUDA). Monterey State Beach, San Mateo Co., California (x-1978, tetrasporangial, leg. I. K. LEE and A. M. NONOMURA).

The following herbarium specimens were also observed: (1) sterile specimens collected at Lands End, California in January 1929 by Y. YAMADA (Herb. YAMADA in SAP) (Pl. 11, I) and (2) sterile specimens collected at Golden Gate, San Francisco, California in February 1896 (P. B. A. 241).

Parent plants for culture experiments were collected intertidally at Port Renfrew, Vancouver Island on September 15, 1973 and shipped to Muroran by L. D. DRUEHL. Culture experiments were set up 8 days after collection.

Description

Plants with several upright thalli arising from a common, perennial basal disc; upright thalli terete, attaining up to 30 cm high, brownish black, tough and flexible in texture, not adhering to paper in drying except for young plants; main axis almost straight, stout, 850-1000 μm in diameter just above the base, becoming gradually thicker upward, 1800-2000 μm in diameter in the middle portion, tapering gradually upward, producing successively branches in a spiral manner with very short interval; the majority of the first order branches simple or bifurcate, subulate, up to 10-12 mm in length and 800-1000 μm in diameter, several of these growing indeterminately,

provided with the fourth order branches; adventitious branches numerous in the axil, sometimes on the adaxial side of simple determinate branchlets, short, less than 2 cm in length; pericentral cells six, frequently five in determinate branchlets; vegetative trichoblasts appearing just prior to the formation of reproductive structures, along the apical portion of the abaxial side of determinate branchlets in two rows in a zigzag manner, or on the apical portion of indeterminate branches in a spiral manner, almost colorless, a few in number divided two or three times pseudodichotomously; plants dioecious; spermatangial branchlets narrowly ellipsoid, 330-500 μm $\times$ 70-140 μm; cystocarps broadly ovoid, 520-730 μm $\times$ 410-640 μm; tetrasporangia borne in two rows on 7-20 successive segments of ultimate order branchlets, each provided with two cover cells, 115-130 μm $\times$ 125-135 μm; tetraspores dark brownish red in color, 65-82 μm in diameter.

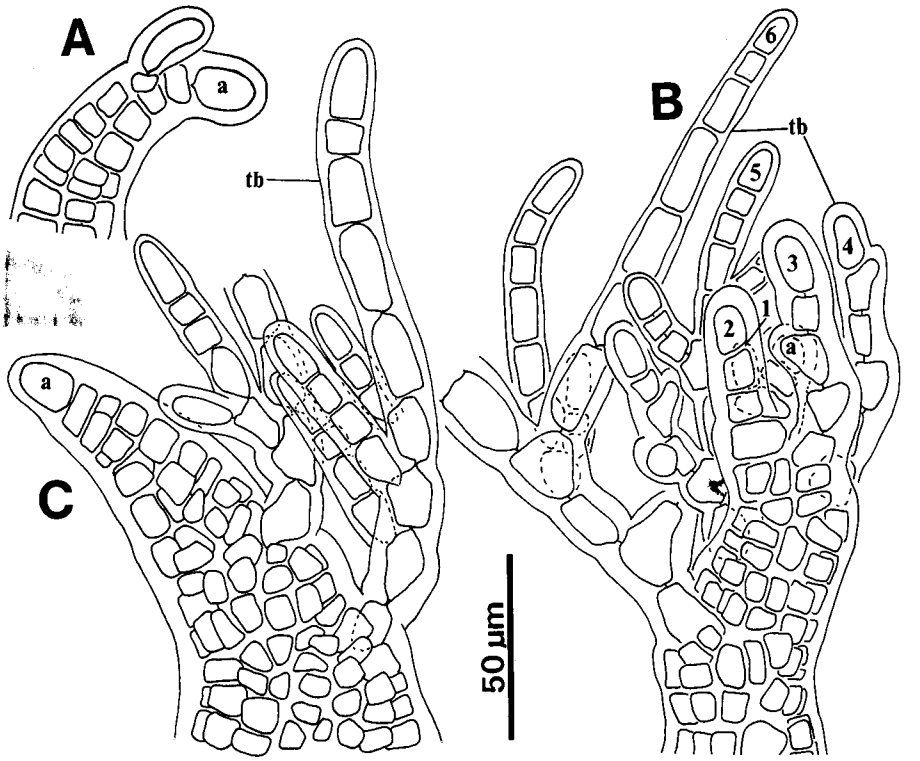

Fig. 50. *Neorhodomela larix* (TURNER) MASUDA. A-C. Vegetative trichoblasts: A, C, on determinate branchlets (A, Vancouver Island, C, California); B, on an indeterminate branch and arranged in a spiral manner, numbered in their sequence of formation (California).

Observations

Habitat: This species grows on rocks in the middle intertidal zone in Vancouver Island (DRUEHL, pers. comm.). It also occurs intertidally on the coasts of Oregon to California (SMITH, 1944; DOTY, 1947). I collected this species from Duxbury Reef, Marin County, California, with J. A. WEST. It grows in tide pools in the lower intertidal zone. According to ABBOTT and HOLLENBERG (1976), upright thalli of this species are annual. The specimens collected at Duxbury Reef on November 22, 1980 had young secondary axes arising from the basal discs. This suggests that at least the basal disc is perennial.

Morphology of field plants: The following description was based on plants collected from Vancouver Island, British Columbia. It is supplemented by observations on specimens from California. The plants consist of several upright terete thalli arising from a common expanded basal disc. They are brownish black in color, becoming almost black in drying, and have a tough and flexible texture. Young specimens adhere to paper in drying and old ones do not adhere to paper at all. Fertile plants are 10–15 cm high (those from California being larger than Vancouver plants and reaching up to 30 cm high). Each upright thallus possesses a conspicuous main axis which is almost straight and stout. Main axes are 850–1000 μm in diameter just above the basal disc, becoming gradually thicker upward, and reach a maximum diameter of 1800–2000 μm in the middle portion. The main axes successively produce branches of the first order in a spiral manner with a very short interval between each branch (TURNER, 1819). The majority of the first order branches stop growth during early development and remain simple or bifurcate. They are subulate and beset closely around the main axis. They are 5–6 mm in length in the lower portion of the main axis and reach up to 10–12 mm in length and 800–1000 μm in diameter in the middle to upper portions. In young plants these determinate branchlets of the first order make an acute angle with the main axis and are incurved. However, in old plants they become obviously recurved. Several of the first order branches are indeterminate and grow in a manner similar to the main axis (TURNER, 1819). These indeterminate branches are sporadically present and reach up to 8 cm in length. Some of these develop well and are provided with the fourth order branches. A tetrasporangial plant at hand is devoid of indeterminate branches growing well (Pl. 11, H).

Adventitious branches are usually formed in the axils and originate from the outermost cortical cells. They are also borne on the adaxial side of simple determinate branchlets. Some adventitious branches develop well

as do indeterminate branches of the first order, but the vast majority of these are short, less than 2 cm in length and bear reproductive structures.

Plants collected in July and September from Vancouver Island possess only short trichoblasts on determinate branchlets (Fig. 50, A). California plants collected in May have well developed trichoblasts on the apical portion of branches (Fig. 50, B, C). However, their number is less fewer than *N. munita* and *N. aculeata*. The trichoblasts are usually arranged in a zigzag manner along the abaxial convex side of branches (Fig. 50, B). They are sometimes located in a spiral manner on indeterminate branches (Fig. 50, C). They are almost colorless, reaching up to 1 mm in length and are divided two or three times pseudodichotomously.

The pericentral cells are six in the main axis and indeterminate branches (Pl. 17, H), but they are frequently five in the determinate branchlets. The pericentral cells undergo a transverse division and are divided into two cells (Pl. 17, I). The upper pericentral cell retains the pit-connection with the central axial cell, but the lower one become linked by the secondary pit-connection with a pericentral cell of the underlying segment. The pericentral cells cut off two or three cortical cells outward (Pl. 17, H). Each cortical cell is divided also transversely once (Pl. 17, I). The cortical cells cut off

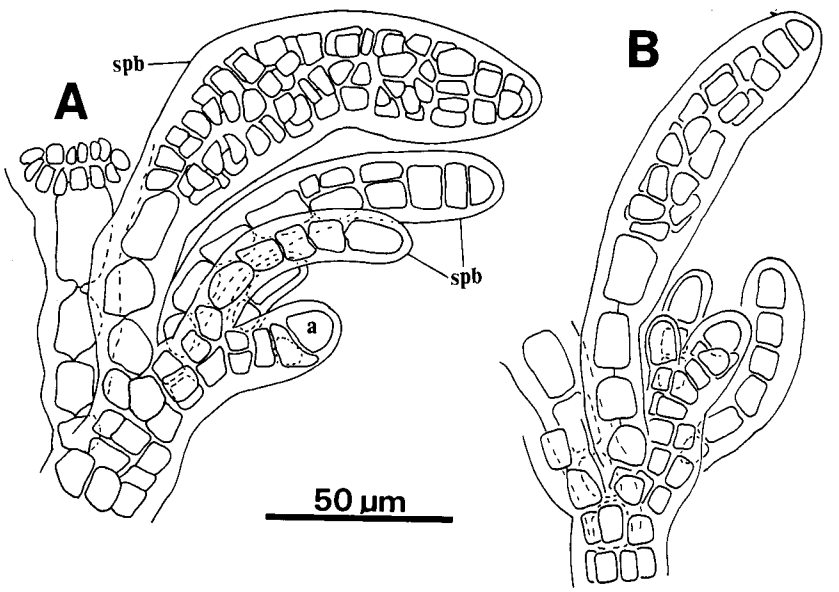

Fig. 51. *Neorhodomela larix*. A, B. Spermatangial branchlets (Vancouver Island): A, on a determinate branchlet, arranged in a zigzag manner; B, on an indeterminate branch, arranged in a spiral manner.

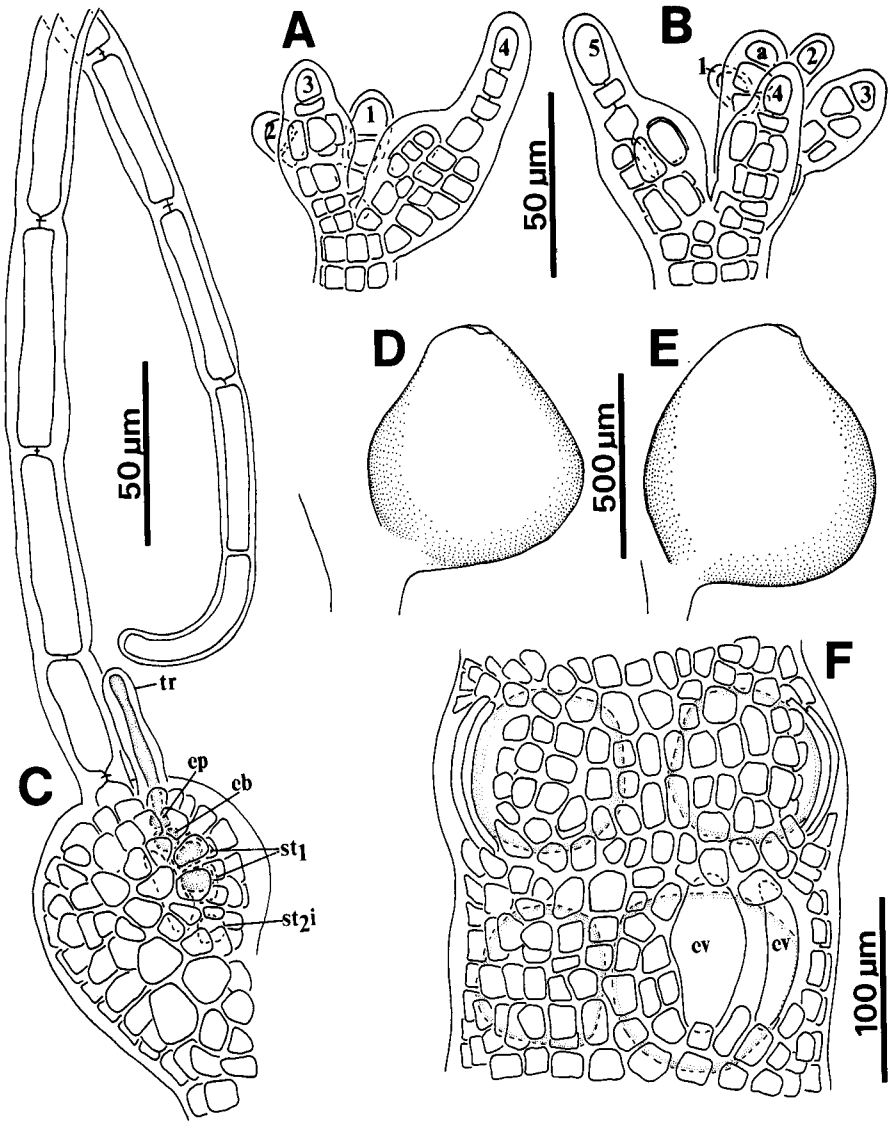

Fig. 52. *Neorhodomela larix.* A, B, C & D, Vancouver Island; E & F, California. A, B. Female trichoblasts: A, those arranged in a zigzag manner and numbered in their sequence of formation (abaxial view, apical cell behind the first trichoblast); B, those arranged in a spiral manner and numbered in their sequence of formation. C. Mature procarp. D, E. Mature cystocarps. F. Tetrasporangia.

one or two cortical cells outward. This process is repreated so that there is a 10-16 layered cortex in the lower portion of the main axes and a 6-8 layered cortex in their upper portion.

Spermatangia, carpogonia and tetrasporangia are borne on separate plants. These reproductive structures were produced on ordinary branches of the first to fourth orders and axillary adventitious branches. The spermatangia are only borne on fertile trichoblasts (Pl. 16, F; Fig. 51, A, B). The spermatangial branchlets are arranged in a zigzag manner in two longitudinal rows along the abaxial convex side of determinate branchlets (Fig. 51, A), but they are arranged in a spiral manner at the apical portion of indeterminate branches (Fig. 51, B). Mature spermatangial branchlets usually curve in the same direction as the apical portion of the vegetative branchlets bearing them and are narrowly ellipsoid in shape (Pl. 16, F). They produce numerous spermatangia except in the two to four proximal segments which remain monosiphonous structure. Fertile portions of the spermatangial branchlets are 330-500 μm in length and 70-140 μm in diameter.

The procarps are borne on the suprabasal segment of fertile trichoblasts (Fig. 52, A, B). The fertile trichoblasts are arranged in a spiral manner at the apical portion of indeterminare branches (Fig. 52, B) and in a zigzag manner on determinate branchlets (Fig. 52, A). However, they are sometimes arranged in a spiral manner on determinate branchlets. Mature procarps consist of a four-celled carpogonial branch and two sterile cell groups (Fig. 52, C). The monosiphonous portion of fertile trichoblasts grows well and eventually falls off as pericarp growth advances. Mature cystocarps are broadly ovoid in shape and measure 520-730 μm in height and 410-640 μm in diameter (Pl. 16, G, H; Fig. 52, D, E). These features are in agreement with those of the California plants examined.

The tetrasporangia are formed on ultimate order branchlets which are aggregate and storongly incurved (Pl. 16, I) (TURNER, 1819). The size of the tetrasporangial branchlets are variable, 800-5000 μm in length and 200-300 μm in diameter. The tetrasporangia are borne in pairs in 7-20 successive segments of the branchlets. Each sporangium ia provided with two cover cells (Fig. 52, F). Mature tetrasporangia protrude slightly from the branchlets and measure 115-130 μm $\times$ 125-135 μm in surface view. The tetrasporangial features are in agreement with those of the California plants.

Culture study: Unialgal cultures were obtained from excised apical tips of indeterminate branches of tetrasporangial plants. Isolated tips were cultured at 14°C, 14 : 10 LD for first 6 months. They grew well and showed a gross morphology similar to that of young field plants. Six-month-old cultures were divided into 6 groups and grown under three different tem-

peratures and two different light regimes for later 10 months: 5°C, 14 : 10 LD; 5°C, 10 : 14 LD; 10°C, 14 : 10 LD; 10°C, 10 : 14 LD; 14°C, 14 : 10 LD; and 14°C, 10 : 14 LD. However, reporductive structures were not observed on plants cultured at these conditions. Then, all the cultures were removed

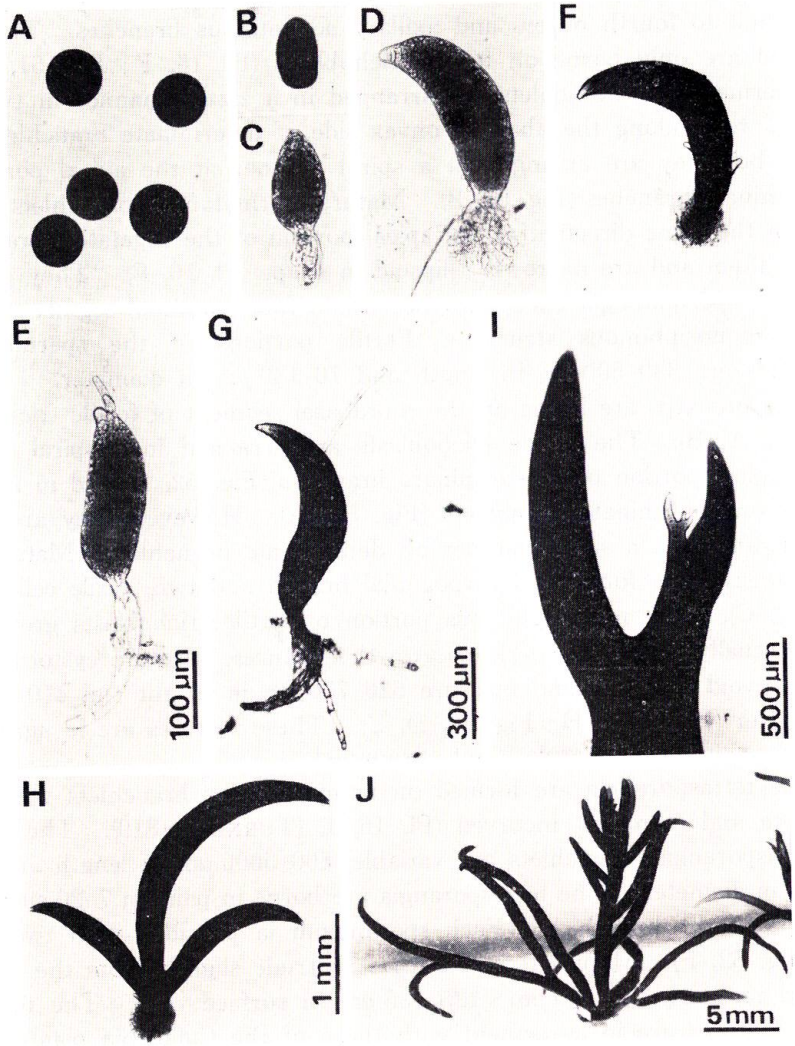

Fig. 53. *Neorhodomela larix*. A. Tetraspores. B–H. Development of tetrasporelings grown at 15°C, 16 : 8 LD: B, attached tetraspore; C, three days old; D, E, seven days old; F, G, fourteen days old; H, one month old. I. Apical portion of a 2-month-old plant. J. Two and a half months old plant.

Scale in E applies also to A–D; scale in G applies also to F.

to the Sapporo laboratory and grown under the following conditions: 5°C, 16 : 8 LD; 5°C, 8 : 16 LD; 10°C, 16 : 8 LD; 10°C, 8 : 16 LD; 15°C, 16 : 8 LD and 15°C, 8 : 16 LD. Several of the plants reached reproductive maturity and bore numerous tetrasporangial branchlets 3 years after transfer at 5°C, 8 : 16 LD; 10°C, 16 : 8 LD and 15°C, 16 : 8 LD.

Liberated tetraspores were globular, dark brownish red in color and 65–82 μm in diameter (Fig. 53, A). Isolated tetraspores quickly attached to the substrate after inoculation (Fig. 53, B). They were cultured at 15°C, 16 : 8 LD and produced colorless rhizoids from one pole of the spore and pigmented upright shoot cells from the other within one day. Sporelings grew first straight (Fig. 53, C) and later bent downward (Fig. 53, D–G;

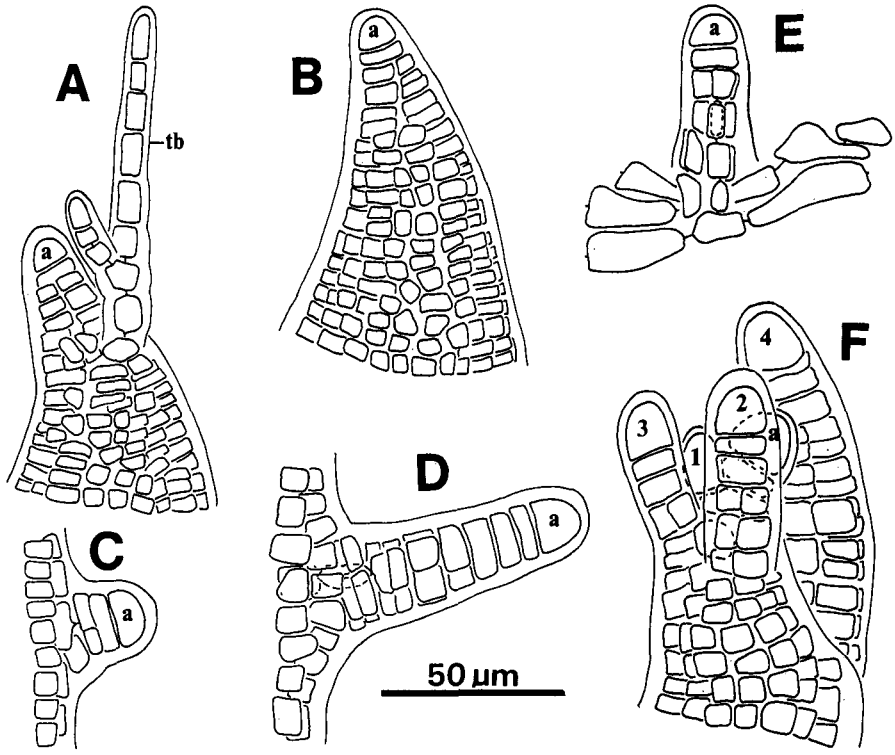

Fig. 54. *Neorhodomela larix.* Cultured plants grown at 15°C, 16 : 8 LD. A, B. Apical portion of 14-day-old plants. C, D. Young adventitious branches borne on the lower portion of primary axes of 21-day-old plants (surface view). E. Young secondary upright axis developed from a superficial cell of basal disc (one month old, surface view). F. Apical portion of a 2-month-old plant forming spirally arranged ordinary branches numbered in their sequence of formation.

54, A, B) After 6 days, several upright shoots formed the first branch which grew into a vegetative trichoblast later (Fig. 53, E, G; 54, A). However, the majority of the upright shoots did not form vegetative trichoblasts, although they bent downward (Fig. 53, D, F; 54, B).

After 14 days, only eleven of the fifty sporelings formed one or two vegetative trichoblasts on the dorsal side (Fig. 53, G; 54, A). Well developed trichoblasts were 1.0–1.5 mm in length and 30–40 μm in diameter at the proximal portion. They were colorless, deciduous and divided once or twice pseudodichotomously. Thus, although the sporelings bend downward and show a characteristic feature of *Neorhodomela*, they differ from those of *N. munita* and *N. aculeata* which bear numerous trichoblasts.

Adventitious branches were formed at the lower portion of the primary axes of the sporelings (Fig. 53, F; 54, C, D). They originated from the outermost cortical cells (Fig. 54, C, D). After 14 days, twenty six of the fifty sporelings bore one or two adventitious branches. The adventitious branches grew in a manner similar to that of the primary main axes.

After one month, the primary axes reached up to 5–6 mm in length, but they did not form ordinary branches of the first order (Fig. 53, H). At this period, secondary axes were formed on the basal discs of the sporelings (Fig. 54, E). They originated from the surface cells of the basal disc.

After 2 months, the primary axes formed ordinary branches of the first order (Fig. 53, I; 54, F). These first order branches were arranged in a spiral manner and the primary axes grew straight (Fig. 53, J). At

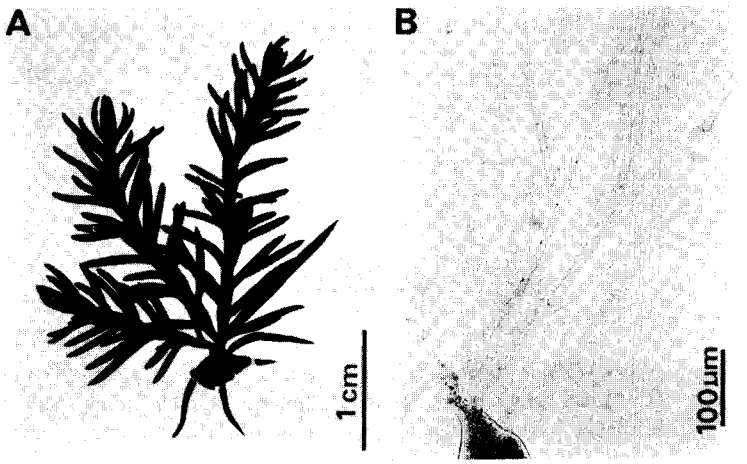

Fig. 55. *Neorhodomela larix.* Cultured plants grown at 15°C, 16:8 LD. A. Five-month-old plant. B. Vigorously developed trichoblasts borne on a 7-month-old plant.

this period, many secondary axes (20-40 on each plant) arose from the basal discs. The secondary axes which were 200-500 μm in length were branched in a spiral manner and bore ordinary branches of the first order. The first order branches of the primary and secondary axes became determinate branches and reached 5-10 mm in length (Fig. 55, A).

After 7 months, the primary axes reached 4-5 cm in length and well developed secondary axes were up to 3 cm in length. Several of the first order branches which were borne on the upper portion of the main axes grew indeterminately. Many adventitious branches were formed in the axils (Fig. 56, C, D). Numerous vegetative trichoblasts were borne at the apical portion of both ordinary and axillary adventitious determinate and indeterminate branches (Fig. 55, B; 56, A, B). On the ordinary determinate branches the trichoblasts originated only from those formed at the upper portion of the main axes. They were arranged in a regularly zigzag manner on the abaxial convex side of the determinate branchlets (Fig. 55, B; 56, A) and in a spiral manner on the indeterminate branches (Fig. 56, B). They grew vigorously, reaching up to 2.5 mm in length and were divided thrice pseudodichotomously (Fig. 55, B).

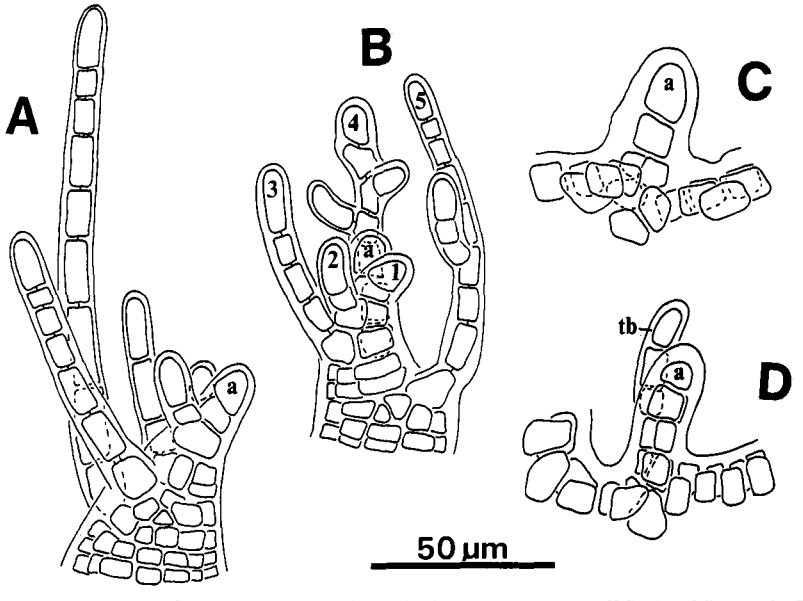

Fig. 56. *Neorhodomela larix.* Cultured plants grown at 15°C, 16 : 8 LD. A, B. Young vegetative trichoblasts borne on 7-month-old plants: A, those arranged in a zigzag manner: B, those arranged in a spiral manner and numbered in their sequence of formation. C, D. Young axillary adventitious branches borne on 7-month-old plants (surface view).

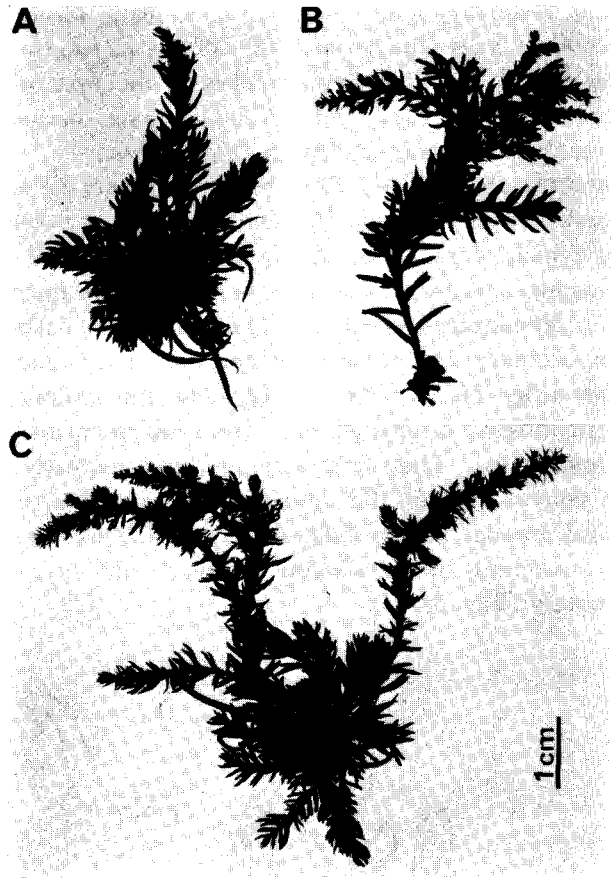

Fig. 57. *Neorhodomela larix.* Cultured plants grown at 15°C, 16 : 8 LD. A. Spermatangial plant (7 months old). B. Procarpic plant (7 months old). C. Tetrasporangial plant (9 months old).
Scale in C applies also to A & B.

Fertile trichoblasts issued at the apical portion of the determinate and indeterminate branches which bore vegetative trichoblasts. The fertile trichoblasts replaced vegetative trichoblasts. On male gametophytes (Fig. 57, A) the fertile trichoblasts bore spermatangia (Fig. 58, A) and on female gametophytes (Fig. 57, B) the trichoblasts produced procarps (Fig. 58, B) in a manner similar to that of field plants described above. Mature cystocarps appeared on female gametophytes one month after starting mixed cultures of male and female plants (Fig. 58, C), although female plants established in single culture did not produce cystocarps. The cystocarps were similar to those of field-collected plants, broadly ovoid in shape and measured 620-

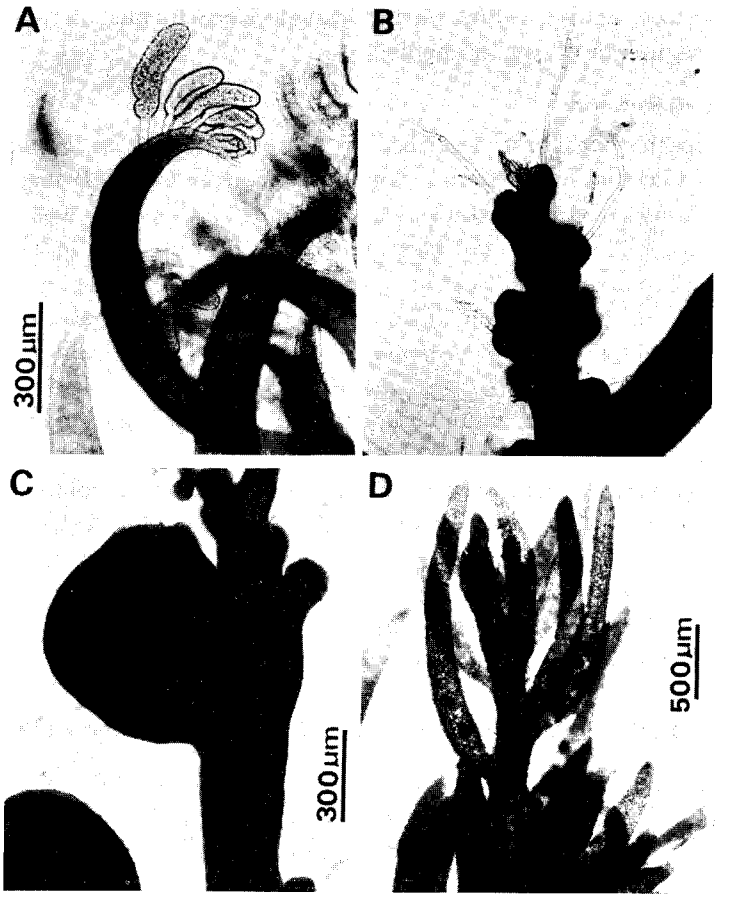

Fig. 58. *Neorhodomela larix.* Cultured plants grown at 15°C, 16 : 8 LD. A. Spermatangial branchlets borne on the plant shown in Fig. 57, A. B. Procarps fromed on the plant shown in Fig. 57, B. C. Mature cystocarp formed on a 8-month-old plant. D. Tetrasporangial branchlets formed on the plant shown in Fig. 57, C.
Scale in C applies also to B.

700 μm in height and 570–640 μm in diameter.

Isolated carpospores germinated and grew into plants similar in morphology to parent gametophytes. The plants reached reproductive maturity 9 months after germination (Fig. 57, C). Tetrasporangia were formed on the ultimate order branchlets of the axillary adventitious branches (Fig. 58, D) and also on the ultimate order ordinary branchlets (the second order) which were borne on the upper portion of the main axes. The tetrasporangial branchlets were not aggregated and differd from those of field-collected

plants described above. The tetrasporangia were formed in pairs in 8-20 successive segments of the branchlets.

Taxonomic discussion

This species was first described by TURNER (1819) as *Fucus larix* on the basis of material from Nootka Sound, Vancouver Island, British Columbia. When C. AGARDH (1822) established *Rhodomela*, this alga was transferred to the genus. This alga has been recorded from various localities of the North Pacific Ocean, the Sea of Okhotsk, the Sea of Japan and Bering Sea. The plant occurring in Japan and adjacent waters was distinguished as an independent species, *Neorhodomela aculeata* (PERESTENKO) MASUDA in this paper.

The aforementioned taxonomic features of the alga under discussion corresponds to the TURNER's (1819) circumscription of genuine *Rhodomela larix*. However, the alga is allied to *Neorhodomela* by the following features: 1) the sporelings with dorsiventrality, 2) vegetative and fertile trichoblasts arranged in a zigzag manner in two longitudinal rows along the abaxial convex side of the determinate branchlets, and 3) the spermatangia produced on specialized fertile branchlets. Thus, the alga under discussion is recognized as the third species of the genus *Neorhodomela*.

Neorhodomela oregona (DOTY) MASUDA, comb. nov.

Basionym: *Odonthalia oregona* DOTY, 1947, p. 196, pl. 13, fig. B; ABBOTT and HOLLENBERG, 1976, p. 744, fig. 700.

Japanese name: Akkeshi-fujimatsumo (MASUDA, 1972)

Materials

The materials examined were collected in Hokkaido from 1970 to 1973. Akkeshi: *Masuda* 9286-9365 (vi-1970, sterile, spermatangial, procarpic & tetrasporangial; vi-1971, ditto). Hamanaka: *Masuda* 13010-13012 (vii-1973, spermatangial, cystocarpic & tetrasporangial, leg. K. MIYAJI). Furthermore, the following specimens were also examined: 1) cystocarpic and tetrasporangial specimens collected from Attu Island, the western Aleutian Archipelago, on July 26, 1975 by members of the Aleutian Research Expedition of Hokkaido University, 1975 (HA-14 in SAP); 2) tetrasporangial specimens collected from Shoya, Hidaka, on July 17, 1970 by M. CHIHARA (TNS-AL 35366, 35367); 3) spermatangial, cystocarpic and tetrasporangial specimens collected at Bodega Head, Sonoma, County, California on February 13, 1977 by J. A. WEST; and 4) spermatangial, cystocarpic and tetrasporangia specimens gathered at Duxbury Reef, Marin County, California on November

22, 1980 by J. A. WEST and M. MASUDA.

Parent plants for culture study were as follows: young sterile plants collected at Akkeshi on June 21, 1970; spermatangial and tetrasporangial plants collected at Akkeshi on June 24, 1971 and tetrasporangial plants collected at Bodega Head on February 13, 1977.

Description

Plants perennial, with several upright thalli arising from a common expanded basal disc; upright thalli terete, branched 3 times in a spiral manner, attaining 5-7 cm high, dark brownish-red, slightly rigid, imperfectly adhering to paper in drying; main axis almost straight, slender, 350-450 μm in diameter in the lowest portion, becoming gradually thicker upward, 600-750 μm in diameter in the lower third to middle portion, tapering toward apex; the first order branches short, up to 2 cm long, bearing progressively shorter and more slender branches; adventitious branches usually formed in the axil, scarce; pericentral cells six, sometimes five in determinate branchlets; vegetative trichoblasts borne on the abaxial convex side of determinate branchlets in two rows in a zigzag manner and on the apical portion of indeterminate branches in a spiral manner, deciduous, rose-colored, divided two times pseudodichotomously; plants dioecious; spermatangial branchlets narrowly ellipsoid, 300-600 μm $\times$ 100-150 μm; cystocarps broadly ovoid, 590-660 μm $\times$ 550-640 μm; tetrasporangia borne in two rows on 8-12 successive segments of ultimate and penultimate order branches, 110-120 μm $\times$ 110-120 μm, divided tetrahedrally; tetraspores 64-81 μm in diameter.

Observations

Habitat: The following information is based on observations at Akkeshi. This alga grows on the vertical face of rocks in the upper intertidal zone, forming dense carpets which reach a vertical height of 20-40 cm. This carpet is mostly made up of the alga mixed with scattered, small clumps of *Pterosiphonia* sp. It grows between the lower part of the *Pelvetia wrightii* belt and the upper edge of the *Corallina pilulifera* belt. Furthermore, this alga is sporadically found on flat rocks lower than the *Corallina* belt together with *Neorhodomela aculeata*, which is dominant there. Although I can not describe the phenology of this species because of the scarcity of field observations, this alga probably has perennial erect thalli judging from its morphology. Namely, several specimens seem to be second year plants, because they have well developed proliferous branches in the lower portion of the old main axes. The secondary upright axes are abundantly observed from the basal disc. Thus, the basal discoid holdfasts are

also apparently perennial. Plants collected in late June had no ripe cystocarps and carpospore liberation was not observed at the time. However, tetrasporangial plants collected at the same time discharged numerous viable spores. Plants collected at Hamanaka by K. MIYAJI on July 3, 1973 had a few well developed cystocarps, which were probably mature.

Morphology of field plants: The following description is based on plants from Akkeshi, unless otherwise indicated. Plants have several upright thalli issuing from a common expanded basal disc, reaching up to 5–7 cm high (Pl. 13, A), and are branched three times in a spiral manner. They are dark brownish-red when living, while they become almost black when fixed in formalin in seawater. They are slightly rigid in texture and adhere imperfectly to paper in drying. Each upright thallus has a consicuous main axis, which is almost straight. The main axes in young plants are denudate below, but they become slightly crowded with several adventitious branches in fully grown plants. They are 350–450 μm in diameter in the lowest portion and become gradually thicker upward up to 600–750 μm in diameter in the lower third to middle portion. The ordinary branches are produced from central cells of the apical portion of the main axis. These first order branches reach 1.5 cm to 2.0 cm in length and are slightly attenuate toward the proximal portion. They are divided into progressively shorter and more slender branches. However, several of the lower branches are not divided, are 5.0–6.5 mm in length, and are usually incurved. The proliferous branches formed adventitiously in the old main axis also have several simple branchlets, which are 2.5–6.0 mm in length in the lower portion.

Adventitious branches are usually formed in the axil sometimes randomly and originate from the outermost cortical cells. However, their number is less fewer than *N. munita*, *N. aculeata* and *N. larix*. The adventitious branches do not grow conspicuously and are less than 1 cm in length. They are attenuate toward the proximal end.

Vegetative trichoblasts are not common in this alga. In young sterile, spermatangial and procarpic plants the vegetative trichoblasts are sometimes borne on the apical portion of the adventitious branches, but they are more commonly found on the apical portion of the determinate branchlets and indeterminate branches in tetrasporangial plants. They reach up to 1 mm long and are divided two times pseudodichotomously. The first branching occurs usually on the suprabasal segment, but it sometimes takes place on the third segment from the base. The longest segment reaches 260 μm long and 20 μm broad. Young trichoblasts are light rose-colored, but they become almost colorless as they grow old. They are arranged in two rows along the abaxial convex side of the determinate branchlets (Fig. 59, A).

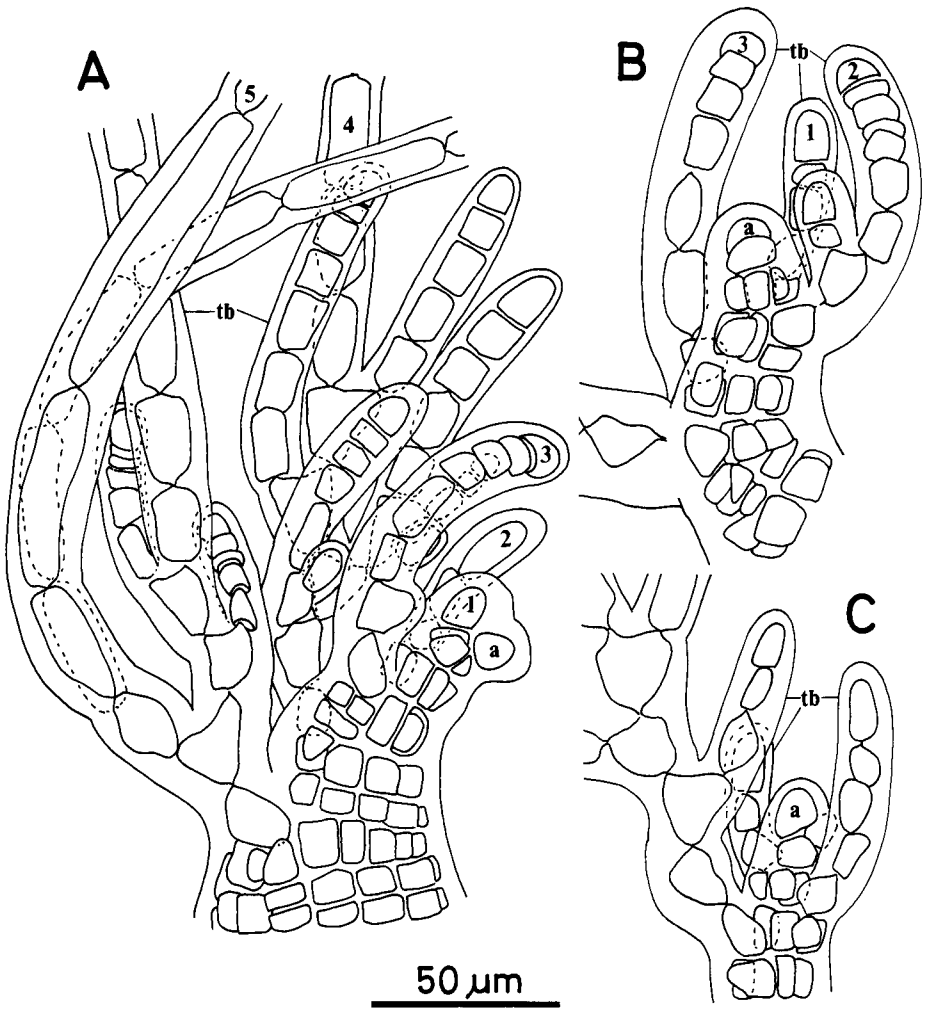

Fig. 59. *Neorhodomela oregona* (DOTY) MASUDA. A, B. Trichoblasts borne on determinate branchlets and arranged in a zigzag manner on the abaxial convex side (A), and in a spiral manner (B) and numbered in their sequence of formation. C. Trichoblasts on a young axillary adventitious branch and arranged in a spiral manner.

However, the arrangement on the indeterminate branches is spiral as in ordinary lateral branches (Fig. 59, C). In a few instances, though, the vegetative trichoblasts are also placed in a spiral manner on the determinate branchlets (Fig. 59, B).

The central cells of the main axis are 300 μm long just above the basal disc, but they increase gradually in length upward. The pericentral cells

are six in the main axis and indeterminate branches (Pl. 17, J, L), but they are sometimes five in the determinate branchlets. Each pericentral cell undergoes a transverse division and is divided into two cells (Pl. 17, K) which cut off cortical cells outward. The main axis possesses 6-7 layers of cortical cells in the middle to lowest portions (Pl. 17, J).

Spermatangia, carpogonia and tetrasporangia are produced on separate individuals. The spermatangia are produced on fertile trichoblasts which are borne on the apical portion of the determinate branchlets of ordinary and axillary adventitious branches. The fertile trichoblasts are also formed on the apical portion of the indeterminate branches. They are located in two rows along the abaxial convex side of the determinate branchlets (Fig. 60, A) and they are arranged in a spiral manner on the indeterminate branches (Pl. 15, G; Fig. 60, B). The fertile trichoblasts become polysipho-

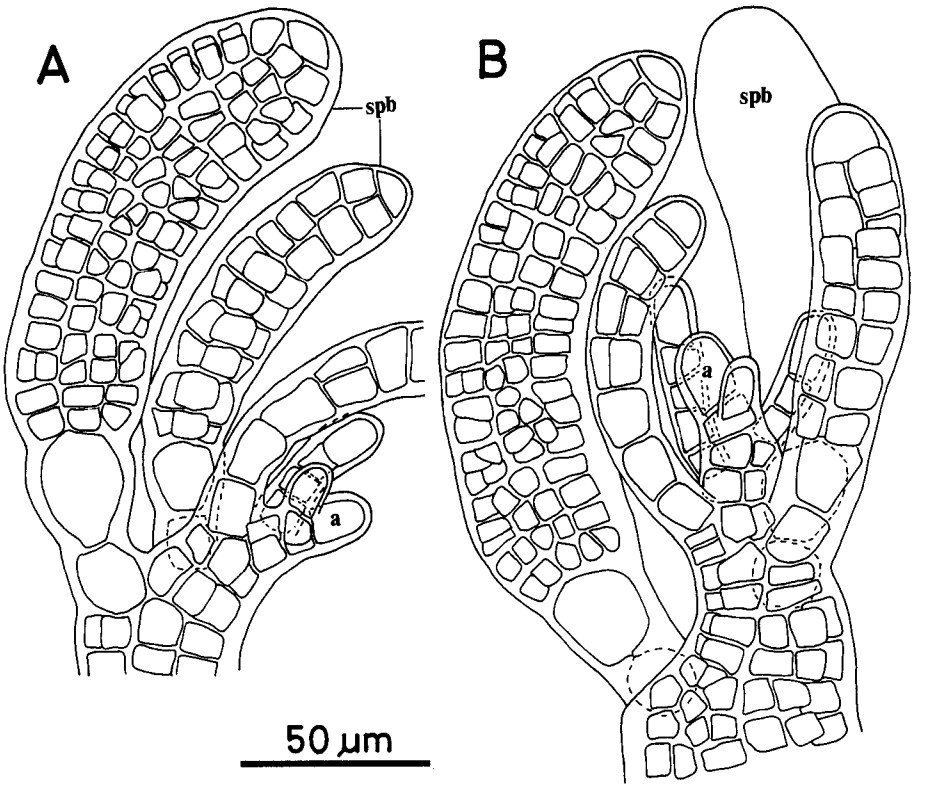

Fig. 60. *Neorhodomela oregona.* A, B. Spermatangial branchlets: A, on a determinate branchlet arranged in a zigzag manner on the abaxial convex side; B, on an indeterminate branch arranged in a spiral manner.

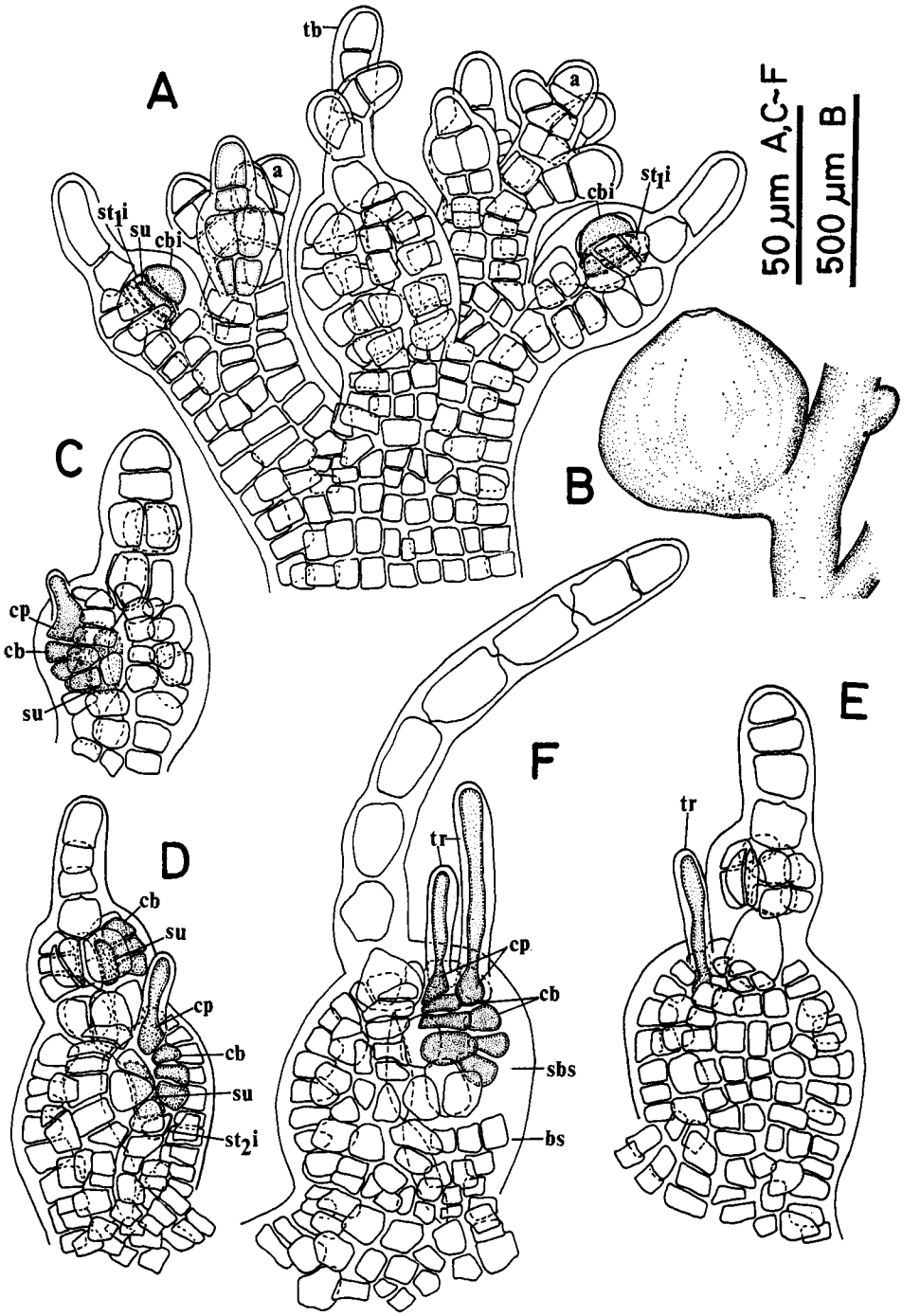

Fig. 61. *Neorhodomela oregona.* A, B, field-collected plants; C–F, cultured plants. A. Apical portion of an indeterminate branch, showing the spiral arrangement of female trichoblasts (right hand) and the zigzag arrangement (left hand). B. Mature cystocarp. C–F. Stage in the development of two procarps on a single trichoblast.

nous and bear numerous spermatangia except in the proximal two or sometimes three segments. Mature spermatangial branchlets are narrowly ellipsoid in shape measuring 300–600 μm in length and 100–150 μm in diameter.

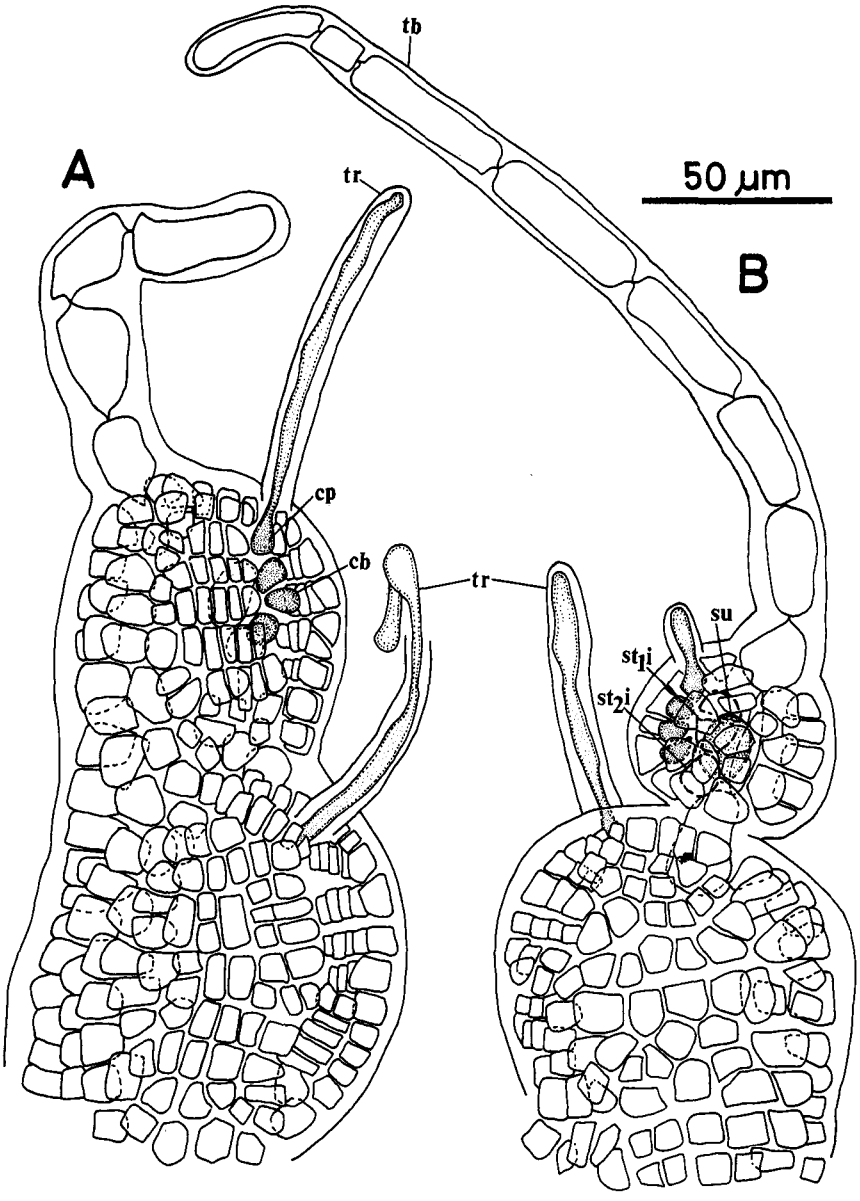

Fig. 62. *Neorhodomela oregona.* A, B. Stage in the development of coupled procarps on a single trichoblast (cultured plants).

The procarps are borne on fertile trichoblasts which are formed on the apical portion of determinate branchlets of the ordinary and axillary adventitious branches. They are arranged in two rows along the abaxial convex side of the branchlets as are vegetative and male trichoblasts (Fig. 61, A). They are also produced on the apical portion of the indeterminate branches and are arranged in a spiral manner (Fig. 61, A). Mature cystocarps have not been encountered in plants collected at Akkeshi. However, plants from Hamanaka possess a few large cystocarps which were probably mature. They are provided with the well developed pericarps, which are broadly ovoid in shape and measure 590–660 μm in height and 550–640 μm in width (Pl. 15, H).

The tetrasporangia are usually formed on ultimate order branchlets and sometimes on penultimate order branches (Fig. 15, I). The tetrasporangial branchlets are not specialized and are identical with vegetative ones. The tetrasporangia are borne in pairs on 8–12 successive segments and provided with two cover cells. They measure 110–120 μm in height and 110–120 μm in diameter and are divided tetrahedrally. Liberated tetraspores are globular, dark brownish-red in color, and measure 64–81 μm in diameter (Pl. 14, A).

Culture study: Unialgal cultures of Akkeshi isolates were obtained from excised apical tips of indeterminate branches of three young sterile plants and a spermatangial plant and from isolated tetraspores. They were first cultured at 14°C, 14 : 10 LD.

All excised apical tips isolated from the three young plants developed into female gametangial plants after 2 months. They produced an expanded discoid holdfast from the lower portion as did the sporelings. Then, they were transferred to stock culture at 10°C, 10 : 14 LD.

Excised apical tips of a male gametophyte grew into mature plants after 2 months. All of the plants produded numerous spermatangial branchlets and a few procarps.

Isolated tetraspores developed into bipolar sporelings within one day after initiation (Pl. 14, B). After 3 days the sporelings became slightly recurved (Pl. 14, C, D). After 7 days the first branch was borne on the dorsal side of the sporelings (Pl. 14, E; Fig. 63, A) and later grew into a vegetative trichoblast. The second one was formed on the same side as the first (Fig. 63, B; 64, A) within 14 days. However, several sporelings did not bear trichoblasts at all at that period. The apical portion of the sporelings recurved whether they bore trichoblasts or not (Fig. 14, F–I). Thus, the very juvenile thallus clearly showed the dorsivenrality which is essentially identical to *N. munita*, *N. aculeata* and *N. larix*. The developmental pattern is very similar to that of *N. larix*.

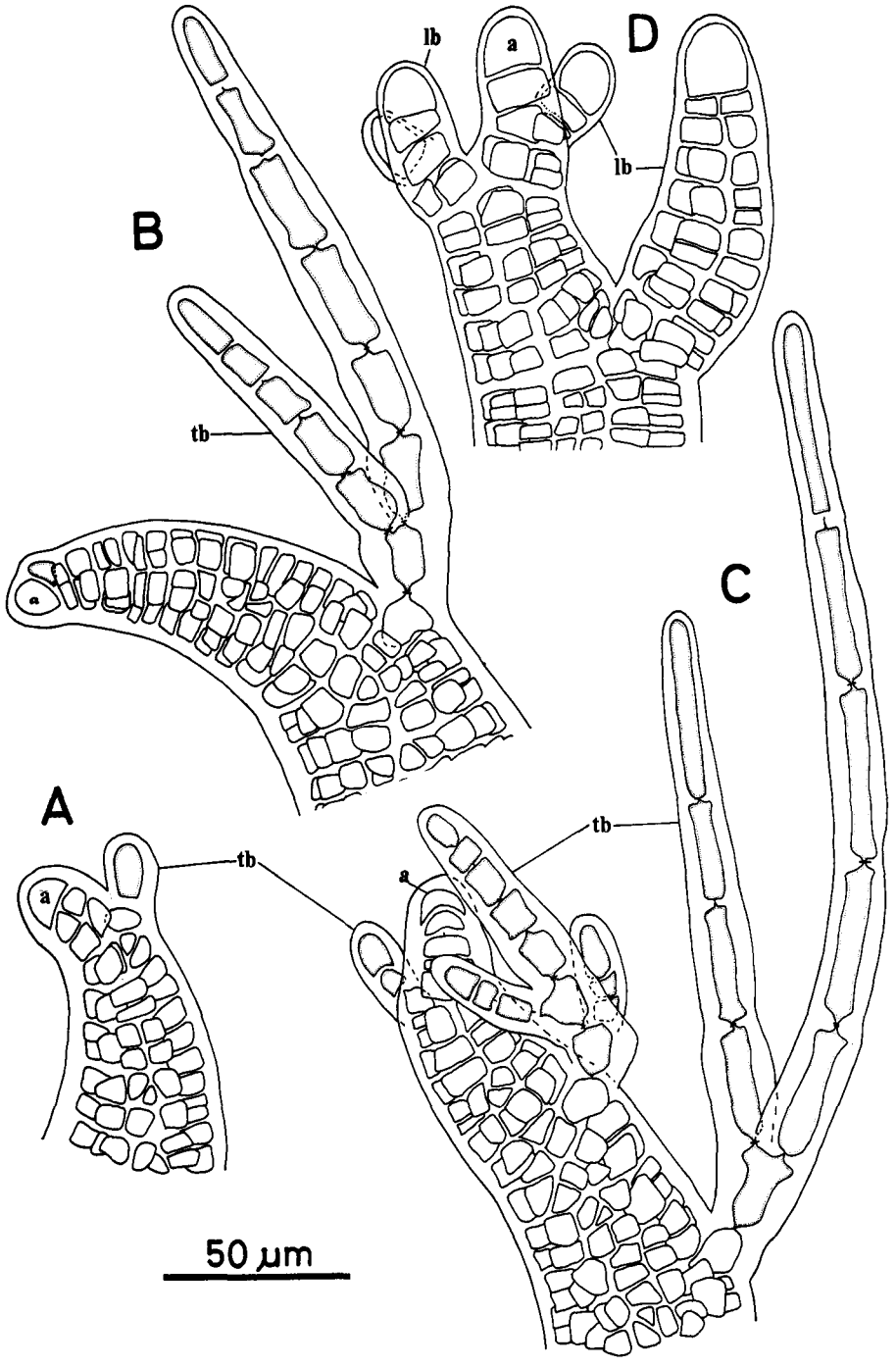

Fig. 63. *Neorhodomela oregona.* A–D. Stages in the development of the apical portion of sporelings: A, seven days old; B, ten days old; C, fourteen days old; D, one month old.

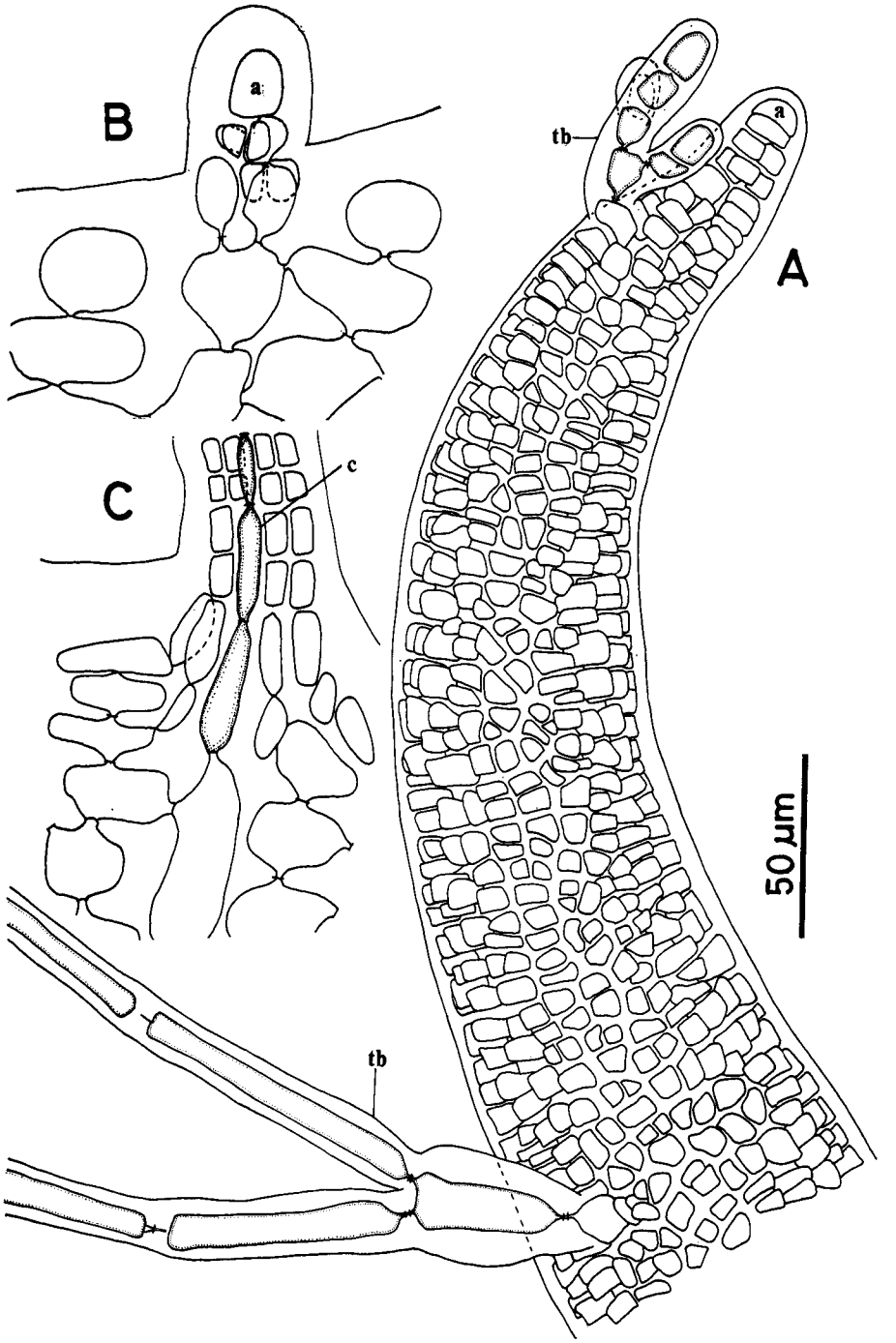

Fig. 64. *Neorhodomela oregona.* Cultured plants. A. Apical portion of a 14-day-old sporeling, showing two trichoblasts on the dorsal side; B, C, longitudinal section of basal discs, showing the secondary upright shoots developed from surface cells of the disc.

Vegetative trichoblasts were not produced regularly. The few observed in 17-day-cultures were as follows: 21 plants had none, 13 plants had only one, 5 plants had two, and 2 plants had three. Of the last mentioned two plants, one produced the third trichoblast on the dorsal side, while the other bore it on the opposite side to the first and second (Fig. 63, C). The trichoblasts were quite similar to those of field-collected plants and reached up to 1 mm in length. However, most trichoblasts were simple or divided only once, and only a few were divided twice.

Both multicellular filamentous and discal rhizoids developed into pseudoparenchymatous basal discs from which secondary axes subsequently issed (Fig. 64, B, C).

After one month, the sporelings reached a length of 1.0–1.2 cm. Then, ordinary branches were produced at the growing apex (Pl. 14, K; Fig. 63, D). They were arranged in a spiral manner. The apex of the primary axis turned upward by this successive formation of the branches. The first order branches developed in a manner similar to that of the main axis.

The plants grew rapidly to a height of 3.5 cm and had 15–20 branches of the first order after 2 months (Pl. 13, B, C; Fig. 65, C). They produced spermatangia and procarps on separate plants. However, only one plant bore both spermatangia and procarps. They were very close as shown in Plate 14, M. The spermatangial branchlets were abundantly produced, but the procarpial trichoblasts were very rare on the plant.

The spermatangia and procarps were borne on the apical portion of

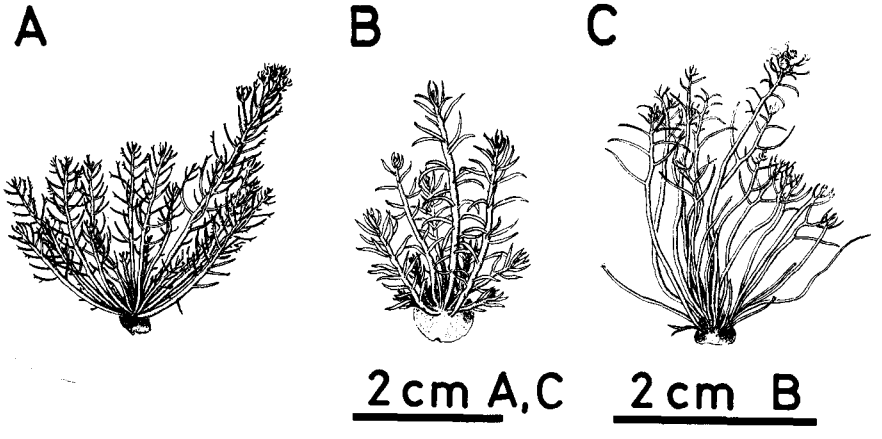

Fig. 65. Habit of cultured plants of *Neorhodomela* grown at 14°C, 14 : 10 LD. A. Tetrasporangial plant of *N. munita* (3 months old). B. Sterile plant of *N. aculeata* (2 months old). C. Spermatangial plant of *N. oregona* (2 months old).

indeterminate branches of the first and second orders as well as on the apical portion of the determinate branchlets (Pl. 14, L, N). The development, structure, and arrangement of the spermatangia and procarps were similar to those of field-collected plants. However, the female gametangial plants in culture often bore two procarps, one on the suprabasal segment and the other on the fourth segment from the proximal end, on the same fertile trichoblast (Fig. 61, C-E; 62, A, B). The segment situated between these two procarps were monosiphonous or polysiphonous. These coupled procarps were often found in considerable number and developed into mature cystocarps later. Two carpogonial branches borne on the same segment was exceptionally rare (Fig. 61, F).

Main axes of the fertile plants were conspicuously denudate in the lower half. The main axes were 250-350 μm across in the lowest portion and 650-800 μm in the lower third to middle portion. The first produced and lowest branch was the longest. Anatomically, the cultured plants differ from field-collected plants. The main axes of the cultured plants have usually five pericentral cells (Pl. 17, M), whereas field-collected plants have six (Pl. 17, J, L). Vegetative trichoblasts were rarely observed on the fertile cultured plans.

Mature cystocarps appeared on female plants in a mixed culture with male plants 21 days after mixture and discharged viable carpospores through the ostioles. However, no cystocarp development was observed on female plants established in single culture. Further, fragments of female gametophytes derived from apical tips of field-collected plants and grown at 10°C, 10 : 14 LD for about one year and male gametophytes derived from the aforementioned tetrasporelings were mixed in the same culture. The female fragments also produced mature cystocarps after 21-30 days. The shape of cystocarps was similar to the description of plants collected at Hamanaka. The cultured cystocarps measured 500-610 μm in height and 480-600 μm in diameter (Pl. 14, O; Fig. 61, B). Liberated carpospores (Pl. 14, P) were similar to tetraspores from field-collected plants, but they had different dimensions from the latter. They were larger than the tetraspores and varied from 77.5 μm to 92.0 μm in diameter.

The germination and development of the carpospores were identical with those of tetraspores described above. After 3 months they developed into mature tetrasporangial plants (Pl. 13, E) that discharged numerous tetraspores, which were generally like those from field-collected plants and measured 64.0-82.5 μm in diameter. The tetrasporangia were produced on the ultimate order branchlets of ordinary and axillary adventitious branches (Pl. 14, Q). They were rarely found on the penultimate order branches.

Although at this stage, the axillary branches formed on the first order laterals were young and sterile, they bore tetrasporangia later.

About one-month-old plants derived from the tetraspores cultured at 14°C, 14 : 10 LD were transferred to the following eight conditions to test the effect of temperatures and photoperiods on the maturation of tetraspore germlings : 5°C, 14 : 10 LD ; 5°C, 10 : 14 LD ; 10°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD ; 18°C, 10 : 14 LD and 22°C, 14 : 10 LD. Five plants were introduced into each condition. The plants became fertile and formed spermatangia and carpogonia on separate plants within 5 months in all conditions tested.

Geographic distribution : In Japan this species has been found at only three localities up to now. The distribution, as shown in Fig. 66, is restricted to the Pacific coast of eastern Hokkaido. The specimens collected from Attu Island, the Aleutians (see materials) are identical with the afore-

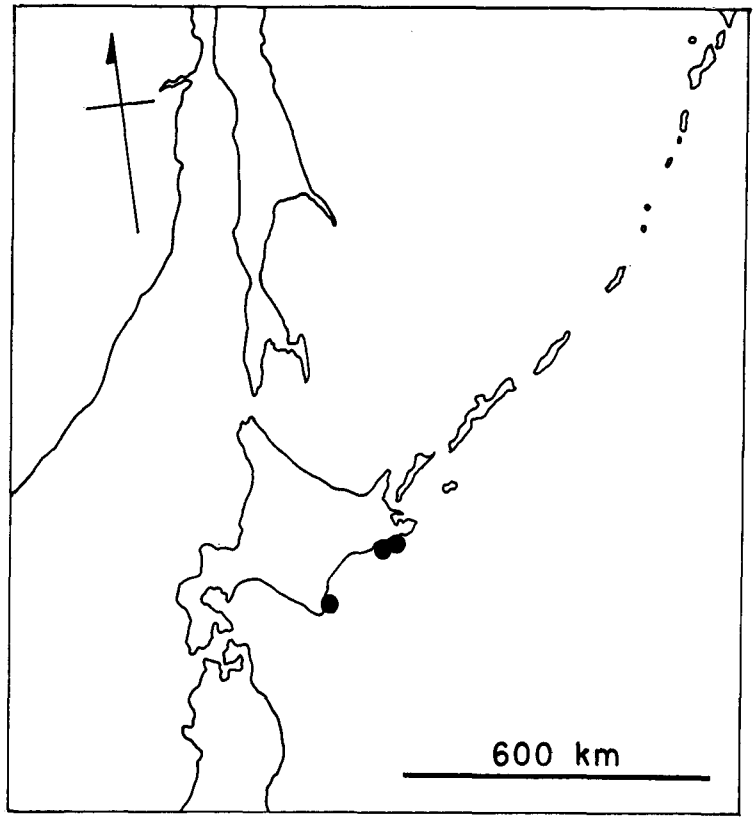

Fig. 66. Distribution of *Neorhodomela oregona* in Japan and adjacent waters.

mentioned alga in every respect. Thus, the distribution of this alga extends northward to the Aleutians, and also eastward to the North America as will be shown in the next section.

Taxonomic discussion

The aforementioned alga had been tentatively recognized as a new species of *Neorhodomela* by me (MASUDA, 1972) until I received living and liquid-preserved materials determined as *Odonthalia oregona* DOTY from Dr. J. A. WEST in February 1977. The specimens including spermatangial, cystocarpic and tetrasporangial plants were collected from a tidal pool in the high intertidal zone at Bodega Head, Sonoma County, California on February 13, 1977 by WEST. The specimens resembled the aforementioned alga in external features. Morphological observations and laboratory culture experiments have been undertaken to clarify whether the Japanese alga and

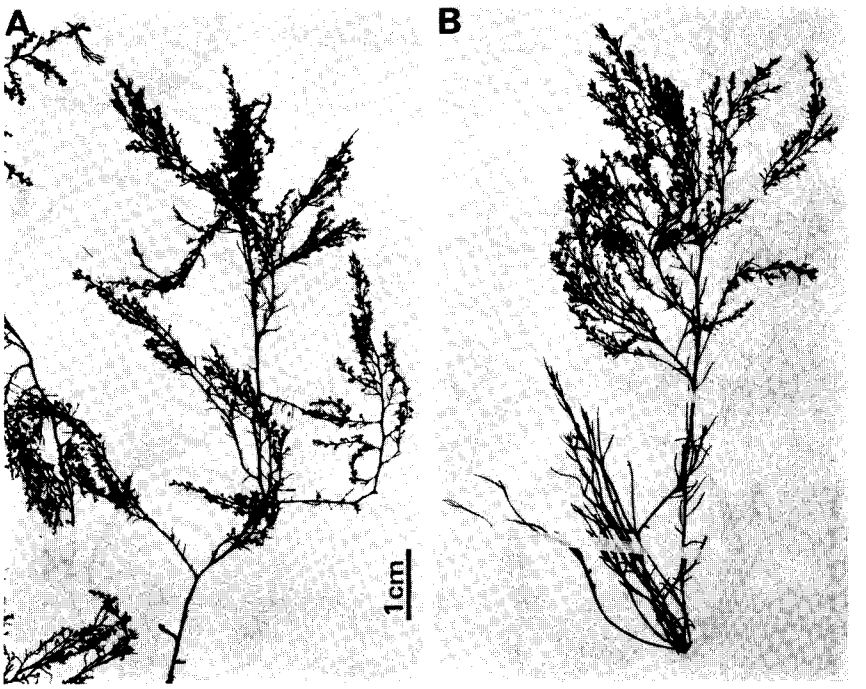

Fig. 67. *Neorhodomela oregona.* A. Holotype specimen of *Odonthalia oregona* DOTY collected from Curry County, Oregon on July 3, 1944 (cystocarpic, DUDLEY Herb. in UC, leg. M. S. DOTY). B. Cystocarpic specimen collected at Duxbury Reef, Marin County, California on November 22, 1980 (SAP, leg. J. A. WEST and M. MASUDA).
Scale in A applies also to B.

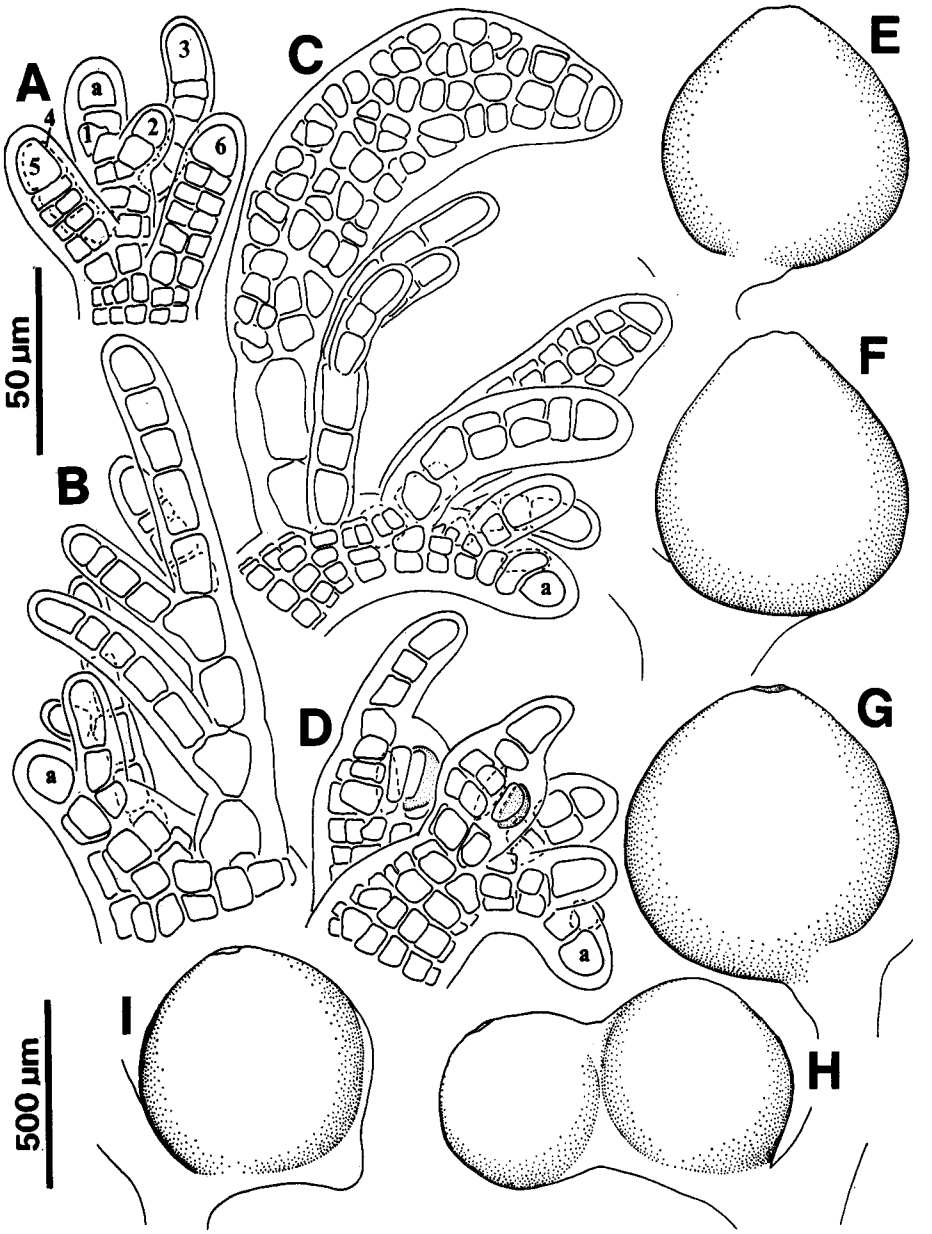

Fig. 68. *Neorhodomela oregona.* A–D, G & I, California; E, F & H, Oregon (holotype specimen). A. Apical tip of young secondary axis forming spirally arranged branches numbered in their sequence of formation. B. Vegetative trichoblasts borne on the abaxial convex side of a determinate branchlet and arranged in a zigzag manner. C. Spermatangial branchlets borne on the abaxial side of a determinate branchlet; note a vegetative trichoblast interspersed with them. D. Female trichoblasts on the abaxial side of a determinate branchlet and arranged in a zigzag manner. E–G. Mature cystocarps. H, I. Coupled cystocarps: H, both of which well developed; I, only one of which developed.

O. oregona are conspeific or not. In addition to the materials collected by WEST, the holotype specimen of *O. oregona* deposited in UC and liquid-preserved specimens collected intertidally at Duxbury Reef, Marin County, California, on November 22, 1980 by WEST and me were examined.

The California specimens are similar to the Japanese alga in many respects. They have terete thalli which are divided spirally (Fig. 68, A). The main axes are up to 1 mm in diameter in the lower third to middle portion. The pericentral cells are six in the main axis (Fig. 69, B) and indeterminate branches and sometimes five in the determinate branchlets. Each pericentral cell undergoes a transverse division and is divided into two cells (Fig. 69, A). The plants bear vegetative and fertile trichoblasts on the uppermost portion of indeterminate and determinate branches. The trichoblasts are arranged in a zigzag manner along the abaxial convex side of the determinate branchlets (Fig. 68, B-D; 69, C) and are arranged in a spiral manner on the indeterminate branches. The spermatangia and procarps are borne on the fertile trichoblasts (Fig. 68, C, D; 69, C). The cystocarps are broadly ovoid and measure 580-730 μm $\times$ 520-740 μm (Fig. 68, G). Coupled cystocarps and procarps are frequently present. The one is borne on the suprabasal segment of the trichoblast and the other on the fourth segment from the proximal end as in the cases of cultured plants of the Japanese alga described previously (Fig. 61, C-E; 62, A, B). Sometimes, the upper cystocarp of these does not develop well (Fig. 68, I). It resembles superficially a calcar formed on cystocarps of several species of *Odonthalia*. The tetrasporangia are borne in two rows on 10-24 successive segments of ultimate order branchlets (Fig. 69, D).

Odonthalia oregona was first described on the basis of material collected from Curry County, Oregon, on July 3, 1944 by DOTY (1947). It is distributed along the Pacific coast of the North America ranging from Whidbey Island, Washington in the north to Bodega Head, California in the south (ABBOTT and HOLLENBERG, 1976). According to DOTY (1947), this species has terete thalli branched in an alternate-distichous manner. The holotype specimen (Fig. 67, A) is very similar in gross morphology to the California plants (Fig. 67, B). Its thallus is entirely terete in accordance with the original description (DOTY, 1947). However, the branching manner is not alternate-distichous but spiral as in the California plants. The specimen is cystocarpic and possesses many well developed cystocarps (Fig. 68, E, F) which are identical with those of the California plants (Fig. 68, G). Coupled cystocarps are also frequently found (Fig. 68, H). The holotype specimen is identical with the California plants in other respects; number of pericentral cells, slender main axis and length of branches. Thus, the California plants

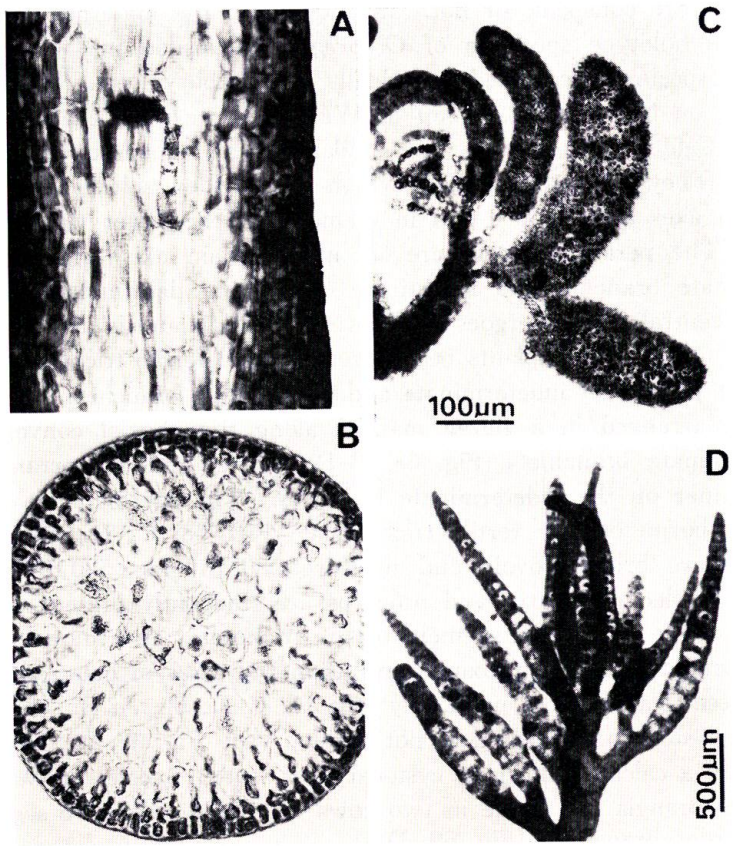

Fig. 69. *Neorhodomela oregona.* California plant. A. Longitudinal section of the lower portion of a main axis. B. Cross section of the lower portion of a main axis. C. Spermatangial branchlets borne on a determinate branchlet. D. Tetrasporangial branchlets.
Scale in C applies also A & B.

are referable to *Odonthalia oregona.* The spiral branching and the presence of vegetative trichoblasts do not ally the alga with *Odonthalia.*

Parent tetrasporangial plants for the culture study were sent to me by air mail from Dr. WEST. The plants received 10 days after collection reached apparently reproductive maturity, but did not discharge tetraspores. They were maintained at 15°C, 16 : 8 LD in crude culture. One month later the tetrasporangial plants discharged many viable spores. The tetraspores were dark brownish-red and 67.5–82.5 μm in diameter (Fig. 70, A). Isolated tetraspores were first cultured at 15°C, 16 : 8 LD. The spores germinated and grew into plants (Fig. 70, B–I) similar in morphology to those of the Japanese

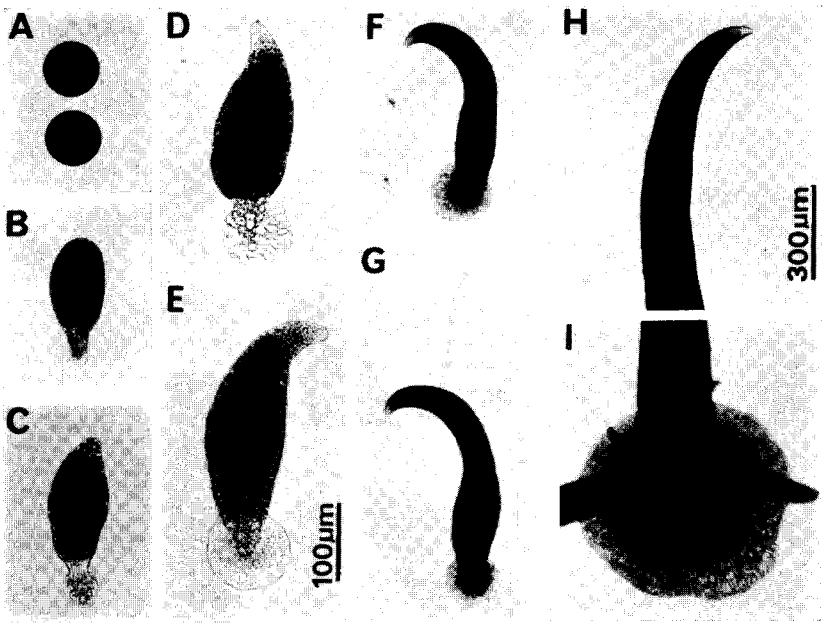

Fig. 70. *Neorhodomela oregona.* Bodega Head isolate. A. Tetraspores. B–I. Development of tetrasporelings grown at 15°C, 16 : 8 LD : B, one day old; C, three days old; D, E, seven days old; F, G, fourteen days old; H, I, one month old.
Scale in E applies also to A–D; scale in H applies also to F, G & I.

alga (Pl. 14, B–I). The plants formed fewer vegetative trichoblasts than the Japanese isolate in the juvenile stage. Of seventy one 14-day-old plants, only six plants bore vegetative trichoblasts. Each produced one trichoblast on the dorsal side (Fig. 70, G). However, the vegetative trichoblasts were formed abundantly, later, just prior to the reproductive maturity (Fig. 71, B).

After 2 months, the plants reached reproductive maturity (Fig. 71, A) and bore spermatangia (Fig. 71, B, C) and procarps (Fig. 71, E) on separate plants. Their arrangement is quite similar to that of field-collected plants. Mature cystocarps appeared on female plants (Fig. 71, D) one month after starting mixed cultures of male and female plants, although female plants established in single culture did not produce cystocarps. The cystocarps were ovoid (Fig. 71, F) and discharged carpospores (Fig. 71, G) which resembled the parent tetraspores in many respects and measured 77.5–92.5 μm in diameter. The carpospores germinated and grew into fertile tetrasporophytes (Fig. 72, A) which bore numerous tetrasporangia (Fig. 72, B) 3 months after inoculation.

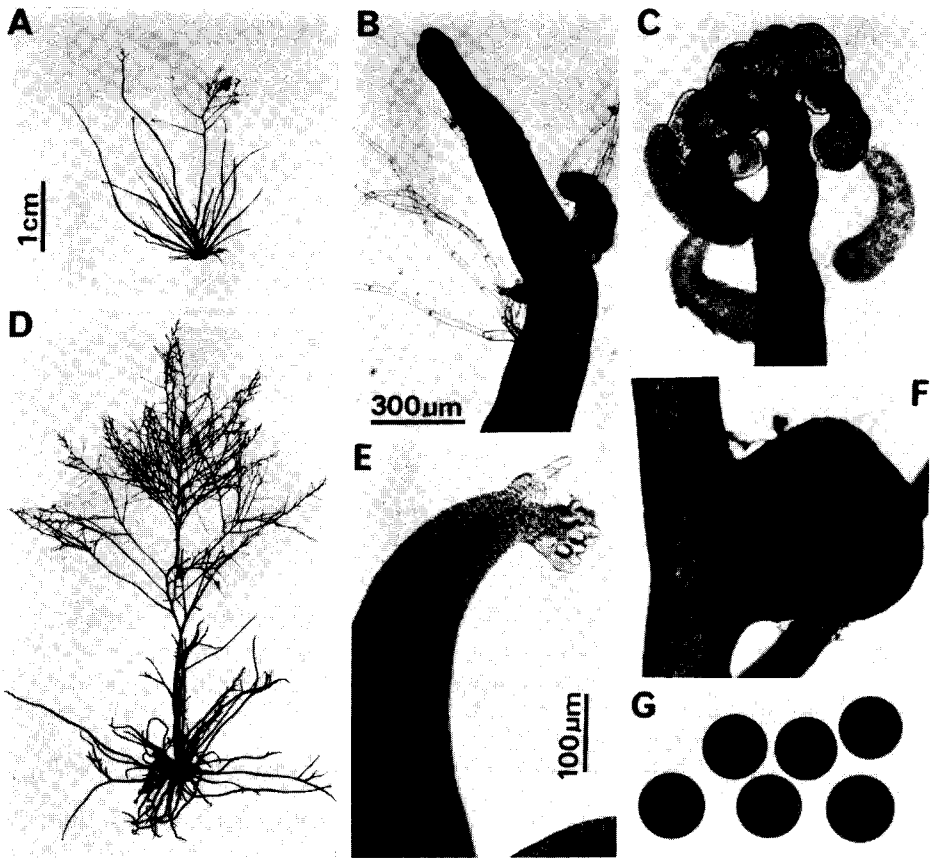

Fig. 71. *Neorhodomela oregona.* Bodega Head isolate grown at 15°C, 16 : 8 LD. A. Spermatangial plant (2 months old). B, C. Spermatangial branchlets borne on the plant shown in A. D. Cystocarpic plant (3 months old). E. Procarps borne on a 2-month-old plant. F. Mature cystocarp formed on the plant shown in D. G. Liberated carpospores from a 3-month-old plant.

Scale in A applies also D; scale in B applies also to C & F; scale in E applies also to G.

Fourteen-day-old plants derived from the carpospores and tetraspores and grown at 15°C, 16 : 8 LD were transferred to the following seven conditions to test the effect of temeratures and photoperiods on the maturation of the plants: 5°C, 16 : 8 LD; 5°C, 8 : 16 LD; 10°C, 16 : 8 LD; 10°C, 8 : 16 LD; 15°C, 8 : 16 LD; 20°C, 16 : 8 LD and 20°C, 8 : 16 LD. The plants reached reproductive maturity under all culture conditions attempted.

Hybridization was attempted with reciprocal crosses between the California isolate and the Japanese isolate at 15°C, 16 : 8 LD by the same pro-

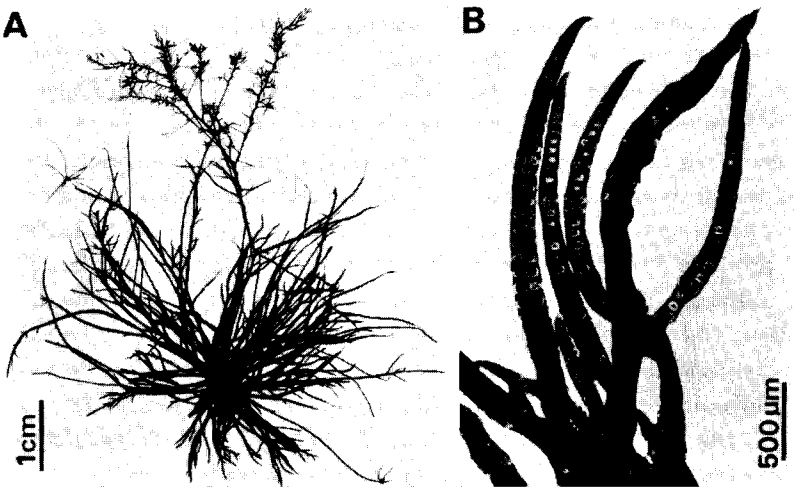

Fig. 72. *Neorhodomela oregona.* Bodega Head isolate grown at 15°C, 16 : 8 LD. A. Tetrasporangial plant (3 months old). B. Tetrasporangial branchlets formed on the plant shown in A.

cedure as that of *Neorhodomela munita* described previously. All the crosses were positive. Cystocarp development and sebsequent carpospore liberation were observed one month after starting each cross. The carpospores germinated and grew into fertile tetrasporophytes 3 months after inoculation.

Thus, morphological observations and laboratory culture experiments reveal that *O. oregona* and the Japanese alga are conspecific. *O. oregona* is transferred to *Neorhodomela* on account of the spiral branching, the dorsiventral arrangement of vegetative and fertile trichoblasts and the spermatangia borne on the trichoblasts.

Discussion of the species of *Neorhodomela*

The genus *Neorhodomela* established in this paper includes four species, *N. munita* (PERESTENKO) MASUDA, the type species, *N. aculeata* (PERESTENKO) MASUDA, *N. larix* (TURNER) MASUDA and *N. oregona* (DOTY) MASUDA. The genus is characterized as follows : (1) the plants with several perennial upright thalli arising from a common expanded basal disc ; (2) the branching manner being basically spiral and partially dorsiventral ; (3) the thalli with six (sometimes five) pericentral cells divided trasversely once ; (4) the vegetative and fertile trichoblasts arranged in a zigzag manner in two longitudinal rows along the abaxial convex side of the determinater branchlets ; (5) the spermatangia and procarps borne on the fertile trichoblasts ; and (6) the plants with a dorsiventrality in the juvenile stage. The possible taxonomic

relationships among the species are discussed below.

N. munita and *N. aculeata* are similar to each other in the juvenile stage of the sporeling (Pl. 10, D–I; 12, C–H). The sporelings produce regularly vegetative trichoblasts, which grow vigorously, from the dorsal side of each segment (Fig. 39, A–D; 45, A–C) and bend strongly downward. On the other hand, *N. larix* and *N. oregona* are also similar to each other in this stage (Pl. 14, B–I; Fig. 53, C–G; Fig. 70, B–G). The sporelings do not produce vegetative trichoblasts regularly (Fig. 54, A, B; 63, A–C; 64, A), although they bend downward. The vegetative trichoblasts formed scarcely on the sporelings do not develop vigorously. The coupled species are not distinguished from each other in this stage. In further developmental stages, the coupled species show also a similarity to each other. The formation of the first order branches in *N. munita* and *N. aculeata* begins at earlier stage than that in *N. larix* and *N. oregona*.

The coupled species show a distinct feature in the development of the first order branches at more advanced stages. The vast majority of the first order branches of *N. aculeata* and *N. larix* do not grow indeterminately and they remain simple or bifurcate (Pl. 11, B–E; 12, K; Fig. 55, A; 57, A–C; 65, B). These branchlets characterize both the species in adult plants. On the other hand, those of *N. munita* and *N. oregona* grow indeterminately (Pl. 9, C–E; 13, B–E; Fig. 65, A, C; 71, A, D; 72, A).

The development of indeterminate adventitious branches except for those produced in the lower portion of the main axes at the juvenile stage characterizes *N. munita* and *N. aculeata* in more developed stage. The adventitious branches of *N. munita* are numerous especially in the axil but common in other region. Those of *N. aculeata* are usually limited to the axil and contribute to the ramification of the plant which bear a few ordinary indeterminate branches. In most advanced stage *N. larix* and *N. oregona* produce adventitious branches usually in the axil. The branches do not grow indeterminately and they bear reproductive structures. In *N. larix* the branches are formed numerously, but in *N. oregona* they are scarce. In this stage, *N. munita* and *N. aculeata* produce also determinate adventitious branches bearing reproductive structures.

In addition, just prior to the formation of reproductive structures, *N. larix* and *N. oregona* begin to produce vegetative trichoblasts. The trichoblasts are more regularly formed in a zigzag manner on the abaxial convex side of the determinate branchlets (Fig. 56, A; 59, A) and in a spiral manner on the apical portion of the indeterminate branches (Fig. 56, B; 59, B, C). On the other hand, *N. munita* and *N. aculeata* continue to produce vegetative trichoblasts on the growing apex of younger branches. Thus, from the

ontogenetic point of view, a parallel developmental pattern is clearly found in the genus.

As to reprodutive feature all the species show a close similarity and only minor differences are present. *N. munita* has pyriform cystocarps (Pl. 10, P; 15, D, E; Fig. 38, D). *N. aculeata* has almost globose to broadly ovoid cystocarps (Pl. 12, Q; 16, D; Fig. 44, D). *N. larix* and *N. oregona* have broadly ovoid cystocarps (Pl. 16, G, H; Fig. 52, D, E; 58, C; 68, E-G; 71, F). *N. oregona* bears frequently coupled cystocarps (Fig. 68, H, I). The coupled cystocarps are found in *O. dentata* (ROSENVINGE, 1923-24) and in *O. corymbifera* (present author). This feature seems to be more primitive as is discussed later.

Interspecific hybridization was attempted with reciprocal crosses among three isolates of *N. munita* (Rausu, Akkeshi and Muroran), two isolates of *N. aculeata* (Nemuro and Muroran), one isolates of *N. larix* (Vancouver), and two isolates of *N. oregona* (Akkeshi and Bodega Head). All the crosses were negative except intraspecific controls which released viable carpospores in one month. A sterility barrier is present among the species and augments the aforementioned morphological differences. On the basis of the similarity of developmental morphology *N. munita* and *N. aculeata* are closely related to each other and *N. larix* and *N. oregona* are also closely related.

Odonthalia LYNGBYE, 1819, nom. cons.

The genus *Odonthalia* was established by LYNGBYE (1819) on the basis of *O. dentata*, which was first named *Fucus dentatus* LINNAEUS (1767). However, *O. dentata* (LINNAEUS) LYNGBYE was transferred to *Rhodomela* by C. AGARDH (1822). Later, GREVILLE (1830) re-established *Odonthalia* as an independent genus. According to the International Code of Botanical Nomenclature (STAFLEU *et al.*, 1978), the genus *Odonthalia* has been conserved against *Fimbriaria* STACKHOUSE (1809) which synonymized *Atomaria* STACKHOUSE (1816).

In addition to the characters of the tribe Rhodomeleae mentioned previously, *Odonthalia* is characterized by having compressed to flat thalli branched repeatedly in an alternate-distichous manner and by the absence of vegetative trichoblasts. DE TONI (1903) listed ten species including two doubtful species* as follows: 1) *Odonthalia corymbifera* (GMELIN) GREVILLE (1830), 2) *O. lyallii* (HARVEY) J. AGARDH (1863), 3) *O. floccosa* (ESPER) FALKENBERG (1901), 4) *O. aleutica* (MERTENS ex C. AGARDH) J. AGARDH (1841), 5) *O. kamtschatica* (RUPRECHT) J. AGARDH (1863), 6) *O. ochotensis* (RUPRECHT) J. AGARDH (1863), 7) *O. semicostata* MERTENS ex J. AGARDH

(1863), 8) *O. dentata* (LINNAEUS) LYNGBYE (1819), 9)* *O. furcata* REINSCH (1875), and 10)* *O. obtusangula* HARVEY (1859). Later, the following six species were described in this genus: *O. washingtoniensis* KYLIN (1925), *O. japonica* OKAMURA (1942), *O. oregona* DOTY (1947), *O. teres* PERESTENKO (1973), *O. annae* PERESTENKO (1973), and *O. kawabatae* MASUDA (1981 b). However, *O. obtusangula* was reduced to the synonymy with *O. corymbifera* by YAMADA (1934). *O. japonica* was transferred to the genus *Pleuroblepharidella* (family Bonnemaisoniaceae) by WYNNE (1980 b). *O. semicostata* was reduced to the synonymy with *O. ochotensis* by PERESTENKO (1977). *O. oregona* and *O. teres* were transferred to *Neorhodomela* and *Rhodomela*, respectively, in this paper. PERESTENKO (1977) proposed a new combined name, *O. setacea* (RUPRECHT) PERESTENKO on the basis of *Atomaria setacea* RUPRECHT (1850). *O. furcata* seems to be identical with *O. dentata* f. *angusta* HARVEY (1853), judging from the original description and illustration (REINSCH, 1875) as well as from the specimen distributed in P. B. A. (No. 1297, COLLINS *et al.*, 1905). Thus, eleven species are presently recognized in the genus *Odonthalia*, although the status of *O. aleutica* is uncertain whether it is an independent species or synonymous with *O. floccosa* (MASUDA and YAMADA, 1980).

In Japan and adjacent waters, *Odonthalia corymbifera*, *O. ochotensis*, *O. aleutica*, *O. lyallii*, *O. kamtschatica* and *O. floccosa* have been reported by OKAMURA (1902, 1912, 1923, 1932, 1933 a, 1933 b, 1934, 1936), TOKIDA (1932, 1934, 1950, 1954), YAMADA (1934), KAWABATA (1936), NAGAI (1941), YAMADA and TANAKA (1944 a), YAMADA and KINOSHITA (1948, 1950), TAZAWA (1975) and others. Of these, the following reports were recently reviewed by re-examination of their voucher specimens (MASUDA, 1981 a, 1981 b; MASUDA and YAMADA, 1980, 1981). *O. ochotensis* reported by OKAMURA (1923, 1933 a) is identical with *O. kamtschatica*, and *O. ochotensis* reported by NAGAI (1941) is nothing but *O. annae* (MASUDA and YAMADA, 1981). *O. aleutica* reported by OKAMURA (1932, 1936) and others is identical with *O. annae* (MASUDA and YAMADA, 1980). *O. lyallii* recorded by OKAMURA (1933 b, 1934) and NAGAI (1941) is identical with *O. setacea* (MASUDA, 1981 a). On the basis of *O. lyallii* reported by KAWABATA (1936), which differs from genuine *O. lyallii*, a new species, *O. kawabatae* was described (MASUDA, 1981 b). In this paper vegetative and reproductive structures of the Japanese *O. annae* and *O. corymbifera* are described based on field and cultured materials. Furthermore, two new species, *O. macrocarpa* which has been confused with *O. corymbifera* by earlier workers and *O. yamadae* which has been confused with *O. kamtschatica* are erected on the basis of specimens collected from Hokkaido.

Odonthalia annae PERESTENKO

PERESTENKO, 1973, p. 65, fig. 3; GUSSAROVA, 1975, p. 118; KLOCZCOVA and BYVALINA, 1979, p. 14; MASUDA and YAMADA, 1980, p. 183, figs. 6–13.

Synonyms: *Odonthalia aleutica* auct. non J. AGARDH; OKAMURA, 1932, p. 75, pl. 286, 1936, p. 904; TOKIDA, 1934, p. 23, pl. 3, pl. 4, fig. a, 1954, p. 149; YAMADA, 1934, p. 39; KAWABATA, 1936, p. 212; NAGAI, 1941, p. 240; YAMADA and TANAKA, 1944 a, p. 76; YAMADA and KINOSHITA, 1950, p. 12, pl. 60; SEGAWA, 1956, p. 121, pl. 72 (591).

Odonthalia ochotensis auct. non J. AGARDH; NAGAI, 1941, p. 239.

Japanese name: Aryushan-nokogirihiba (OKAMURA, 1932).

Materials

The materials examined were collected from Hokkaido from 1967 to 1981. Monbetsu: *Masuda* 14345 & 14356 in SAP (vii–1981, sterile). Rausu: *Masuda* 6841–6940 (i–1969, procarpic & young tetrasporangial; iii–1969, cystocarpic & tetrasporangial; v–1968, ditto; vi–1969, sterile; vii–1968, ditto; viii–1968, ditto; x–1968, ditto). Nemuro: *Masuda* 9692–9703 (Hanasaki, iv–1972, cystocarpic & tetrasporangial; ix–1970, sterile). Akkeshi: *Masuda* 9658–9691 (vi–1967, sterile; vi–1970, ditto; vi–1971, sterile & old tetrasporangial).

In addition, the herbarium specimens deposited in the herbaria listed below were also examined. KURILES Shumsh Island: NAGAI Herb. (Kataoka-wan, vii–1930). Paramshir Island: NAGAI Herb. (Murakami-wan, vii–1930; Kakumabetsu, vii–1932). Urup Island: SAP 15145 & 22056 (Mishima, viii–1935, Iema, viii–1933); NAGAI Herb. (Mishima, viii–1935; Kobune, viii–1935). Etorof Island: NAGAI Herb. (Moyoro, viii–1931, Nos. 2186–2189 & 2191; Chikohai, viii–1931, Nos. 2183, 2185; Uebetsu, vii–1934, No. 3981; Iriribushi, non date, No. 4015). Kunashiri Island: NAGAI Herb. (Atoiya, vii–1929, No. 404; Pontomari, vii–1929, No. 467). Shikotan Island: SAP 15500, 15501, 22825 & 22830 (vii–1934; viii–1936); NAGAI Herb. (Shakotan, vii–1934, Nos. 5431, 5435; Aimizaki, non date, Nos. 4010, 4013). SAKHALIN TOKIDA Herb. (Yoman, vii–1935, No. 6; Kaihyoto, vii–1930, cystocarpic & tetrasporangial; Nobori, viii–1926, No. 128; Chishiya, iv–1937, cystocarpic & tetrasporangial; Nishinotoro, iv–1937, cystocarpic; vii–1932). Hokkaido Nemuro: KUROGI in SAP (Nosappu-misaki, iv–1970; vi–1970; viii–1969; xii–1969). Hamanaka: OKAMURA Herb. in SAP (Kiritappu, viii–1918). Akkeshi: SAP 24637, 25565 & 25702 (vi–1933, vi–1949); OKAMURA in SAP (1923).

Parent plants for culture study were as follows: three sterile plants collected at Rausu on June 13, 1971; and two cystocarpic and two tetraspo-

rangial plants collected at Hanasaki, Nemuro, on April 15, 1972.

Description

Several perennial upright thalli arising from a common expanded basal disc; each thallus monopodial, alternate-distichously branched, up to 25 cm high, dark brownish-red in color and turning to almost black in drying, rather rigid to the touch, adhering imperfectly to paper in drying; main axis almost terete below, 850–1000 μm in diameter just above the basal disc, becoming gradually compressed upward and reaching 1300–1400 μm in breadth in the lower third portion, without midribs; the first order branches usually growing indeterminately and divided into progressively shorter branches up to the sixth order; adventitious branches usually in the axil sometimes randomly; pericentral cells six in the main axis; plants dioecious; spermatangia borne on the apical portion of branches and covering the surface; procarps originating from the suprabasal segments of simple fertile trichoblasts; cystocarps arranged in a flexuose-racemose manner, semiglobose, 950–1150 μm × 975–1200 μm, usually with calcars of 175–400 μm in length; carpospores 95–108 μm in diameter; tetrasporangial branchlets 1.2–2.5 mm in length, sometimes arranged in a spiral manner; tetrasporangia borne in two rows on 9–18 successive segments of the branchlets, each provided with two cover cells, 120–130 μm × 130–140 μm; tetraspores 80–95 μm in diameter.

Observations

Habitat and phenology: This alga grows on rocks in the upper sublittoral zone. The following phenological information is based on observations at Rausu from 1968 to 1969. This alga can be found throughout the year. Small, apparently first year plants are found in July. They develop into fertile plants during the next winter. In addition, sterile plants with proliferous branches which develop on the old main axis are seen at the same time (Fig. 77, A). Young upright thalli which originate from the basal disc are found in all seasons. Procarpic and young tetrasporangial plants are found in January. Mature plants with cystocarps and tetrasporangia are collected in March to May (Pl. 18, A, B). The plants reach the most luxuriant growth in May and become up to 25 cm high. Unfortunately, I could not find spermatangial plants at any locality in Hokkaido. The fertile season of this alga is from winter to spring.

Morphology of field plants: The following account is given on the basis of plants gathered from Rausu unless otherwise indicated. Plants consist of several upright thalli issuing from a common expanded basal disc.

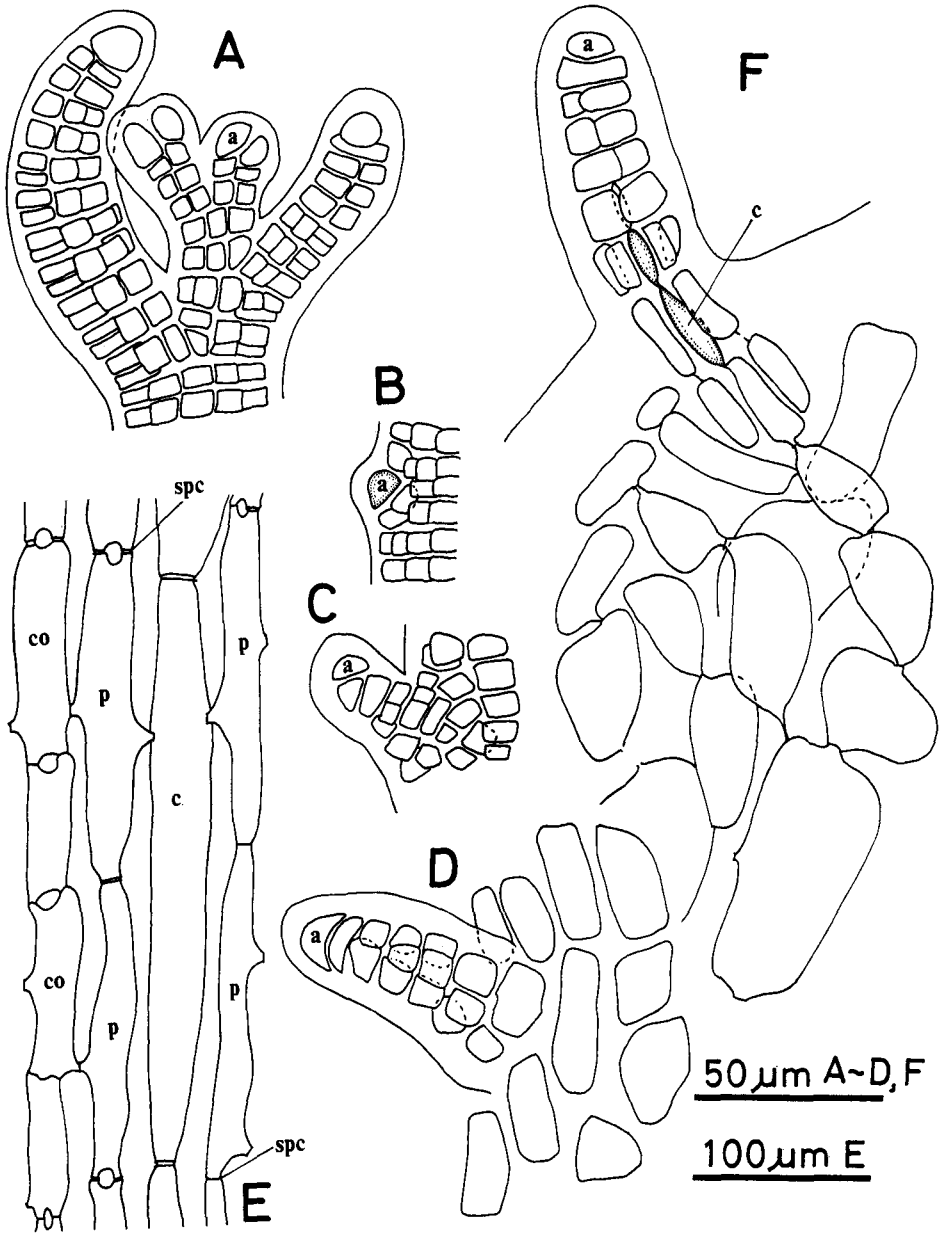

Fig. 73. *Odonthalia annae* PERESTENKO. A & E, field-collected plants; B–D & F, cultured plants. A. Apical portion of a main axis showing the alternate-distichous branching. B–D. Stages in the development of adventitious branches from outermost cortical cells. E. Longitudinal section of the lower portion of a main axis, showing a central cell, pericentral cells and cortical cells. F. Longitudinal section of a basal disc, showing the secondary upright shoot developed from a superficial cell of the disc.

They are dark brownish-red and turn to almost black in drying. They are rather rigid in texture and imperfectly adhere to paper in drying except for old plants. Each erect thallus is monopodial and decompound-pinnate, as a rule, in a single plane. It has a conspicuous main axis which is straight. The main axes are almost terete below and become gradually compressed upward. They are 850–1000 μm in diameter just above the base and 1300–1400 μm in breadth in the lower third portion. Ordinary branches of the first order are produced from the central cells of the apical portion of the main axis. They are regularly formed in an alternate-distichous manner from every third segment (Fig. 73, A). The first order branches usually grow indeterminately in a manner quite similar to the main axis and are divided into progressively shorter branches up to the sixth order. However, they sometimes cease their growth early and become determinate branchlets. They are sporadically present among the indeterminate branches. The first order indeterminate branches become longer upward and reach up to 12 cm long in the middle portion of the main axis. In second year plants the branches fall off leaving their proximal portions and proliferous branches are developed from the cortical cells (Pl. 18, B; Fig. 77, A).

Adventitious branches are produced from the cortical cells of the ordinary branches as illustrated for cultured plants (Fig. 73, B–D). They usually issue from the axillary portion, but sometimes arise from other portions. Vegetative trichoblasts are entirely lacking.

The thallus is of uniaxial construction composed of a central cell, six pericentral cells and several layers of cortical cells. Of the six pericentral cells, four are situated on the flat face of the thallus and the other two are situated on the flanks (Pl. 28, D). Each pericentral cell is divided transversely one or two times. The upper pericentral cell retains the pit-connection with the central cell, while the lower one becomes linked with a pericentral cell of the underlying segment by a secondary pit-connection (Pl. 28, C; Fig. 73, E). Each pericentral cell cuts off 2 or 3 cortical cells outward which are also divided once transversely. This process is repeated several times so that there is a 8–10 layered cortex in the middle portion of the main axis and a 10–18 layered cortex in the lower portion. The central cells of the main axes are 280–300 μm in length just above the base, becoming gradually longer upward, and reach up to 1 mm in the middle portion.

Midribs are not discernible in any region of the upright thalli, although OKAMURA (1932) stated as follows: "for the most part of the frond ecostate or the midribs quite indistinct, in the inferior part costa gradually formed by the evolution of cortical layer on either-one side or on both sides." This OKAMURA's description does not correspond to the formation of midribs

but to the thickening growth of the perennial main axis. His illustration (OKAMURA, 1932, pl. 286, fig. 6) shows clearly this feature.

Procarps and tetrasporangia are borne on separate plants. As I have been unable to collect spermatangial plants in the field, it will be described later on the basis of cultured plants. The development of the procarps is also described in cultured plants later. The cystocarps are borne on unmodified branches and are arranged in a flexuose-racemose manner. Mature

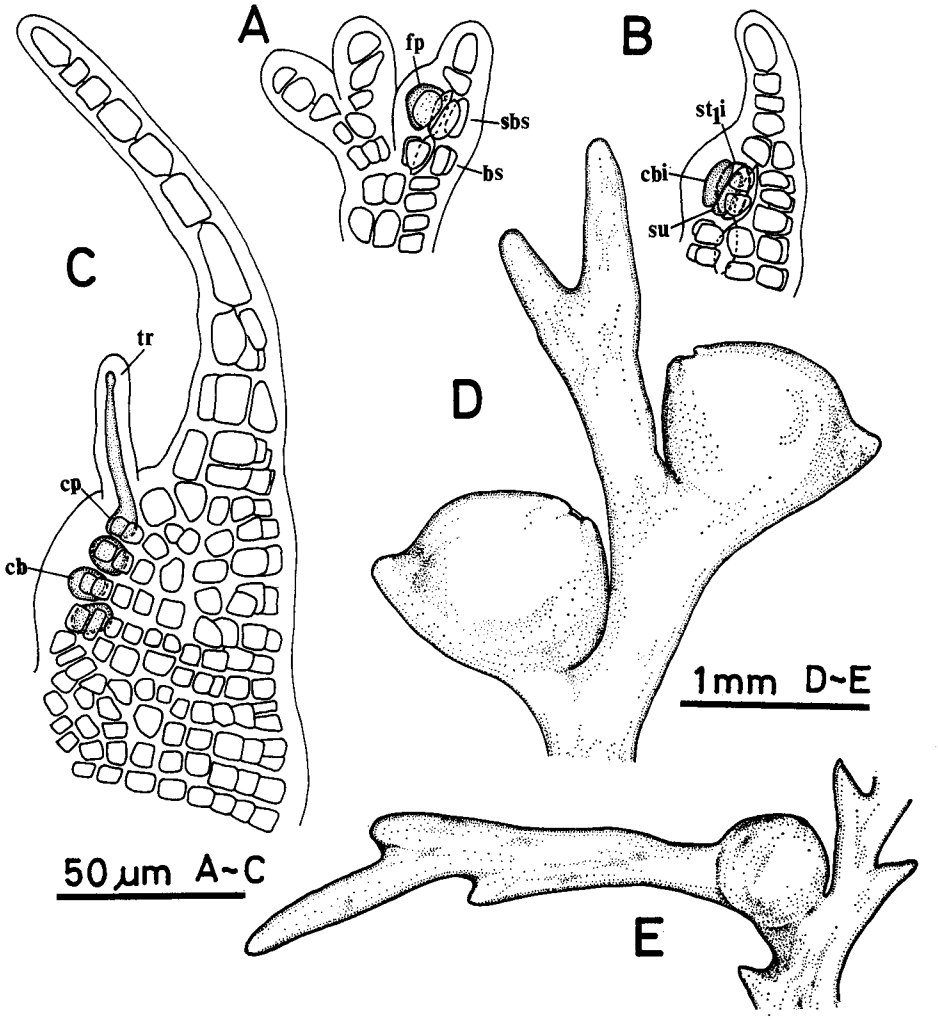

Fig. 74. *Odonthalia annae.* A-C, cultured plants; D. E, field-collected plants. A-C. Stages in the development of procarps. D. Mature cystocarps with calcars. E. Cystocarp with a branched calcar.

cystocarps are semiglobose and measure 950–1150 μm in height and 975–1200 μm in diameter (Pl. 26, A; Fig. 74, D). They prossess usually simple calcars which are 175–400 μm in length. Branched calcars are sometimes formed (Fig. 44, E). According to OKAMURA (1932), the cystocarps of this alga lack the calcars. However, his illustration (OKAMURA, 1932, pl. 286, figs. 8, 9) clearly shows ecalcarate cystocarps as well as calcarate ones. Liberated carpospores were observed from plants collected at Hanasaki, Nemuro on April 15, 1972. They are globular, dark brownish-red in color and measure 95–108 μm in diameter (Pl. 19, A).

The tetrasporangia are produced on the determinate branchlets of ordinary and adventitious branches. These fertile branchlets are somewhat specialized than the vegetative branches (Pl. 27, A). They are placed in alternate-distichous manner as illustrated by OKAMURA (1932), but they often shift to a spiral arrangement. The tetrasporangial branchlets are 1.2–2.5 mm in length and slightly compressed measuring 200 μm × 170 μm across. The tetrasporangia originate from pericentral cells as in *Odonthalia dentata* (KYLIN, 1934) and they are protected by two cover cells. Two tetrasporangia are formed on 9–18 successive segments of the fertile branchlets. Tetrahedrally divided sporangia are 120–130 μm × 130–140 μm in surface view.

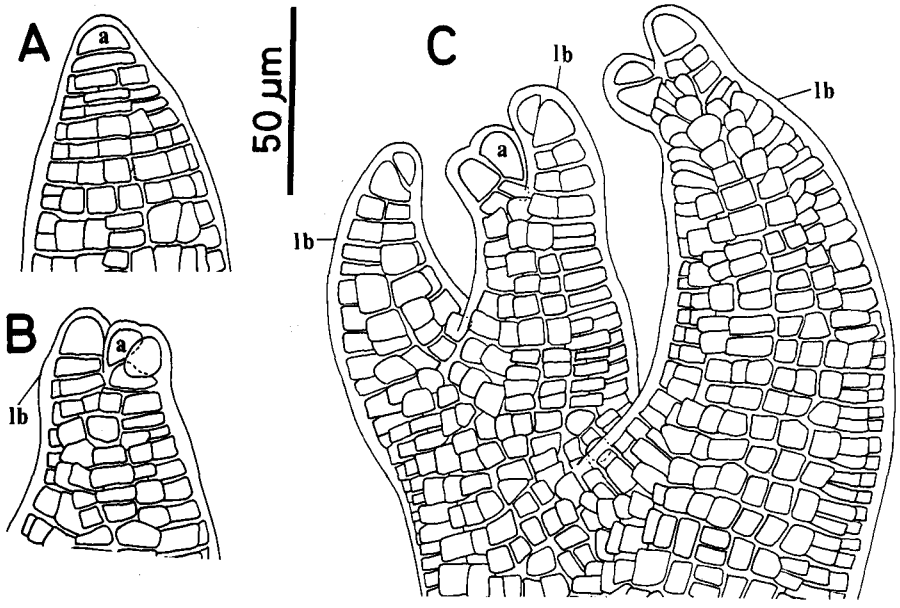

Fig. 75. *Odonthalia annae.* A–C. Development of the apical portion of sporelings, showing the branching manner: A, seven days old; B, fourteen days old; C, twenty-one days old.

Liberated tetraspores were observed from plants collected at Hanasaki, Nemuro on April 15, 1972. They resemble, in many respects, carpospores except in their size (Pl. 19, B). They are smaller than the latter and measure 80–95 μm in diameter.

Culture study: Unialgal cultures were obtained from both isolated carpospores and tetraspores (the Nemuro plants) as well as from excised apical tips of the indeterminate branches (the Rausu plants). Isolated spores and excised tips were first cultured at 10°C, 14 : 10 LD. The following account is based on observations on the development of the tetraspores.

Islated tetraspores divided into bipolar sporelings within one day. However, sporelings did not conspicuously produce rhizoids at that time (Pl. 19, C), although they attached to the substrate by one pole and stood upright. After 3 days, the sporelings distinctly differentiated into a colorless rhizoidal portion and a pigmented upright shoot (Pl. 19, D, E). The rhizoids were divided repeatedly to form either a discoid holdfast (Pl. 19, F) or a monosiphonous one (Pl. 19, G), both of which were multicellular. Forty were discoid and 41 were monosiphonous in 5-day-old sporelings. Both types of rhizoids eventually developed into pseudoparenchymatous basal discs. The basal discs grew both concentrically and upward producing secondary axes from the superficial cells (Fig. 73, F). The sporelings increased by means of a large apical cell from which pericentral cells were subsequently cut off. Each pericentral cell simultaneously cut off cortical cells so that the polysiphonous structure was entirely obscured except in the uppermost portion of the sporelings (Fig. 75, A–C). The sporelings grew rapidly and became slightly recurved (Pl. 19, I). The first lateral branch was observed in 14-day-old plants (Fig. 75, B). Subsequently, several branches were produced from the central cells in an alternate-distichous manner from every third segment (Fig. 75, C). These first order laterals were as a rule indeterminate branches and developed in a manner quite similar to that of the main axis. Then, plantlets grew straight and showed bilateral symmetry. After one month, plants reached up to 6 mm high and produced 5–6 ordinary branches from the upper portion (Pl. 19, L) and 1 or 2 adventitious branches, which issued from the cortical cells (Fig. 73, B–D), from the lower portion. Several secondary upright axes issued from the basal disc. As growth advanced, cultured plants bore a close resemblance to field-collected plantlets.

Two months after inoculation, several of plants maintained at 10°C, 14 : 10 LD were transferred to 5°C, 10 : 14 LD ; 5°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 14 : 10 LD and 18°C, 14 : 10 LD. Of these, the plants cultured at 5°C, 10 : 14 LD reached reproductive maturity 4 months after transfer and bore spermatangia and procarps on separate plants. The spermatangia

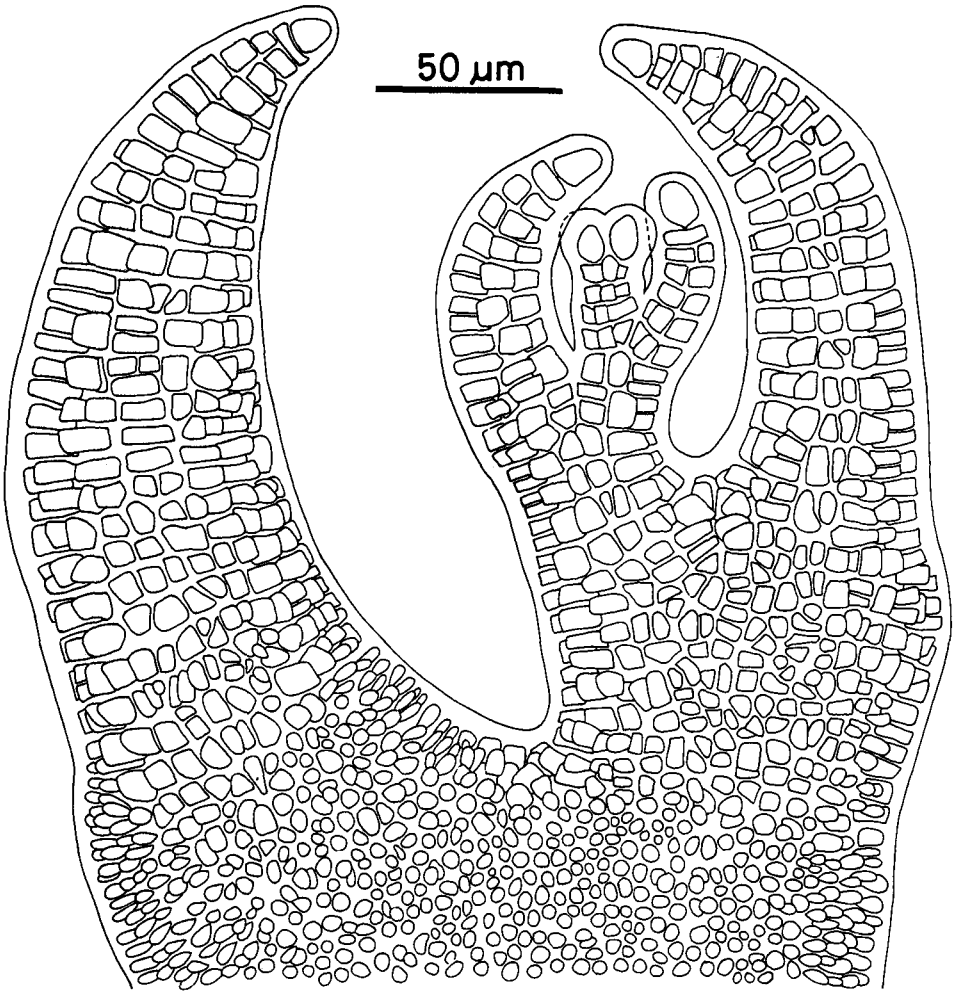

Fig. 76. *Odonthalia annae.* Apical portion of a spermatangial branch (cultured plant).

and procarps were produced on the first to fourth order branches and on the adventitious branches (Pl. 19, M, N). The spermatangia originate only from the cortical cells of unspecialized branches (Pl. 19, M; Fig. 76) as in *O. dentata* (FALKENBERG, 1901; KYLIN, 1934) and *Rhodomela.*

The procarps originate from the suprabasal segment of simple fertile trichoblasts which arise at the apical portion of indeterminate branches of the first to fourth order. The trichoblasts are arranged in an alternate-distichous manner replacing vegetative branches. The fertile segment produces five pericentral cells as does *O. dentata* (KYLIN, 1934). The carpogonial branches

are formed from the last formed pericentral cell (the fifth), which functions as the supporting cell, and are borne on the adaxial side of the trichoblasts (Fig. 74, A, B). The carpogonial branches consist of four cells and before fertilization are surrounded by well developed pericarps (Fig. 74, C). Hence, the sterile cell groups are not clearly detected. The basal segment of the trichoblast becomes similar in structure to the vegetative branches bearing it. As the pericarp develop, the trichoblast elongates as does that of *Rhodomela* and *Neorhodomela*. However, one to four segments of the trichoblasts change into a polysiphonous calcar prior to fertilization. So far as examined, only the suprabasal segment contributes to reproductive activity.

Both the male and female gametangial plants were transferred together to a large glass vessel (14.5 cm × 11.0 cm) containing 1200 *ml* of medium at 5°C, 10 : 14 LD. However, no cystocarp development was observed. The plants grown at other culture conditions did not produce reproductive structures.

The carpospores isolated from the Nemuro plants germinated and developed in a pattern quite similar to that of the aforementioned tetraspores. However, the plants did not produce any reproductive organs in one year old cultures under the following conditions : 5°C, 10 : 14 LD ; 5°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 10°C, 14 : 10 LD ; 14°C, 14 : 10 LD and 18°C, 14 : 10 LD.

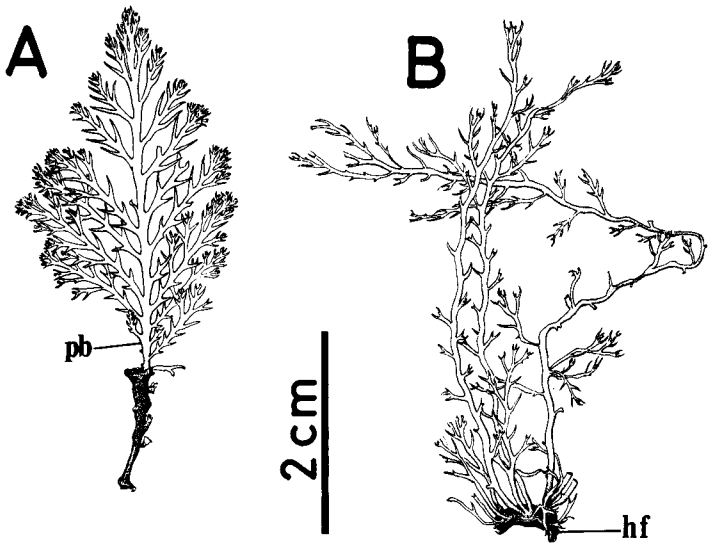

Fig. 77. *Odonthalia annae*. A. Habit of a field-collected plant with proliferous branches. B. Habit of a cultured plant derived from an excised apical tip grown at 10°C, 14 : 10 LD (8 months old).

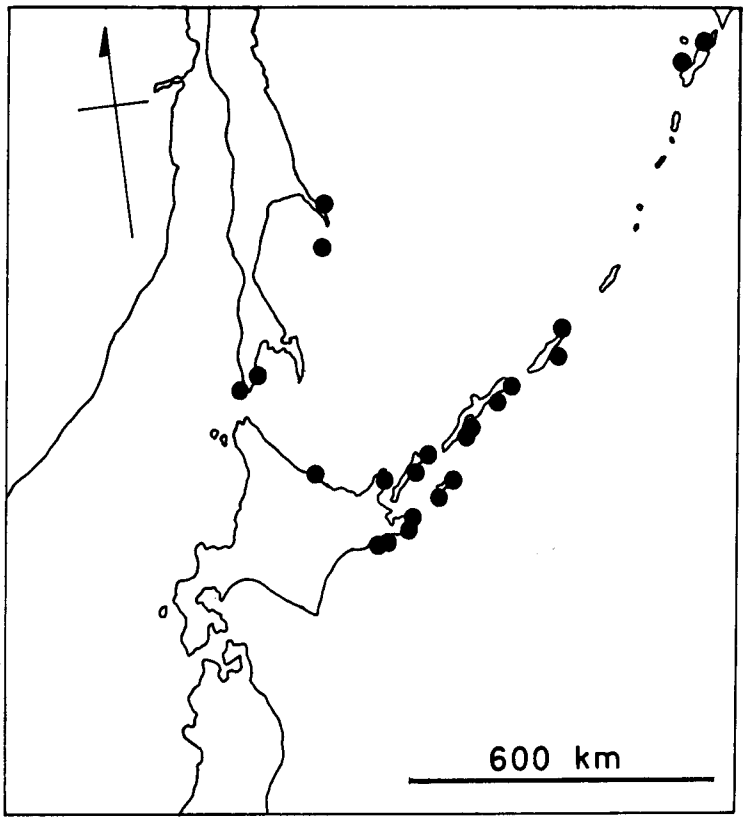

Fig. 78. Distribution of *Odonthalia annae* in Japan and adjacent waters.

One-month-old cultures derived from excised apical tips of the Rausu plants were divided into eight groups. One was maintained at 10°C, 14 : 10 LD and the others were transferred to the following seven culture conditions : 5°C, 10 : 14 LD ; 5°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 10 : 14 LD ; 14°C, 14 : 10 LD ; 18°C, 10 : 14 LD and 18°C, 14 : 10 LD. These plants developed in a pattern quite similar to that of the sporelings. The rhizoids sprouted from their lower portion and grew into the pseudoparenchymatous discoid holdfast (Fig. 77, B) from which several secondary upright shoots were produced. Reproductuve organs were observed only in the plants cultured at 5°C, 10 : 14 LD 7 months after transfer. The plants produced only spermatangia in a manner similar to that described previously for male plants derived from tetraspores.

Geographic distribution : The present known range of this species in

Japan and adjacent waters is shown in Fig. 78 on the basis of examination of the specimens cited in materials. These areas are strongly washed by the Oyashio and the East Sakhalin Current, both of which are cold currents.

Taxonomic discussion

As mentioned in an earlier paper (MASUDA and YAMADA, 1980), this alga which has been called *Odonthalia aleutica* in Japan is distinguished from genuine *O. aleutica* described by C. AGARDH (1822) under the *Rhodomela aleutica* in that the latter has terete main axes and ovoid cystocarps. This alga is identical with *O. annae* PERESTENKO (1973) in vegetative and reproductive features (MASUDA and YAMADA, 1980). *O. annae* was described on the basis of materials collected in Kassatka Bay, Etorof Island, on July 19, 1967 by PERESTENKO. Re-examination of the type specimen on loan from LE and cystocarpic specimens presented to SAP from LE, which were collected from Bering Island, Commander Islands, on June 30, 1972, reveals that *O. annae* is similar in having narrow thalli without midribs, semiglobose cystocarps measuring 875–1225 μm × 1000–1300 μm and tetrasporangial branchlets of 950–2600 μm in length forming two sporangia on 6–23 successive segments to the Japanese alga and they are conspecific (MASUDA and YAMADA, 1980).

Odonthalia corymbifera (GMELIN) GREVILLE

GREVILLE, 1830, p. 1; J. AGARDH, 1863, p. 894; OKAMURA, 1902, p. 66; 1912, p. 143, pl. 91, 1916, p. 81, 1936, p. 902; YAMADA, 1934, p. 48; KAWABATA, 1936, p. 212, 1959 (*pro parte*), p. 295; NAGAI, 1941 (*pro parte*), p. 237; YAMADA and TANAKA, 1944 a (*pro parte*), p. 123; TOKIDA, 1954, p. 223; SEGAWA, 1956, p. 121, pl. 72 (590); CHIHARA, 1970, p. 114, pl. 67 (5), 1972 (*pro parte*), p. 158; KANEKO and NIIHARA, 1970, p. 177; TAZAWA, 1975, p. 160, fig. 43, A, B; PERESTENKO, 1977, p. 38, 1980, p. 119, figs. 243, 244.

Basionym: *Fucus corymbiferus* GMELIN, 1768, p. 124, pl. 9.

Synonyms: *Rhodomela corymbifera* (GMELIN) C. AGARDH, 1822, p. 371.
Odonthalia gmelini POSTELS et RUPRECHT, 1840, p. 14, pl. 28; KÜTZING, 1849, p. 847.
Atomaria corymbifera (GMELIN) RUPRECHT, 1850, p. 213.
Odonthalia obtusangula HARVEY, 1859, p. 329; 1959 (in Dawson), p. 13, pl. 6 (A).

Japanese name: Hakesaki-nokogirihiba (OKAMURA, 1902).

Materials

The materials studied were collected from Hokkaido from 1968 to 1979. Rishiri Island: *Masuda* 14347-14351 (iv-1979, sterile). Rausu: *Masuda* 6763-6840 (i-1969, sterile; v-1968, ditto; vii-1968, ditto; viii-1968, cystocarpic & tetrasporangial; x-1968, ditto). Akkeshi: *Masuda* 9653-9657, 13281 & 13282 (vi-1971, sterile). Muroran: *Masuda* 10047-10245 (ii-1971, sterile; iii-1971, ditto; iv-1971, ditto; v-1971, ditto; vii-1970, sterile, cystocarpic & tetrasporangial; vii-1971, ditto; vii-1972, spermatangial, cystocarpic & tetrasporangial; viii-1970, ditto; ix-1970, ditto; x-1970, cystocarpic & tetrasporangial; xi-1970, ditto; xii-1970, sterile, old cystocarpic & old tetrasporangial; xii-1972, ditto). Usujiri: *Masuda* 10293-10310 (iv-1973, sterile). Esan-misaki: *Masuda* 10311-10317 (iv-1973, sterile). Shirikishinai: *Masuda* 10278-10292 (iv-1973, sterile).

The following herbarium specimens were also examined. KURILES Shumsh Island: NAGAI Herb. (Horokawa, non date). Paramshir Island: NAGAI Herb. (Murakami-wan, vii-1930; Kurosaki, vii-1932; Suribachi-wan, viii-1932). Shimshir Island: NAGAI Herb. (Broughton Bay, vii-1930, cystocarpic). Urup Island: SAP 15113 & 15136-15138 (Iema, viii-1933); NAGAI Herb. (Kobune, viii-1935, tetrasporangial). Etorof Island: NAGAI Herb. (Uenbetsu, vii-1934, Nos. 3816-3818 & 3820; Rubetsu, vi-1903). Kunashiri Island: NAGAI Herb. (Furukamappu, viii-1930, No. 2350). Shikotan Island: SAP 15515, 15516 & 22828 (vii-1934); NAGAI Herb. (Shakotan, vii-1934; Chiboi, vii-1934; Notoro, non date; Aimizaki, non date). SAKHALIN TOKIDA Herb. (Notoro, iv-1937, sterile; Chisha, viii-1906, cystocarpic; Rorei, viii-1932, tetrasporangial). HOKKAIDO Rebun Island: YENDO Herb. (vii-1910, tetrasporangial). Rishiri Island: SAP 22827 (viii-1934). Akkeshi: SAP 12376 (ix-1931); Hidaka: SAP 22829 (Horoizumi, v-1934); TNS-AL 31568-31579, 31589, 31590 & 31592 (Shoya, vii-1970; Aburakoma, vii-1970; Enrumu-misaki, vii-1970). Muroran: SAP 28560 (vii-1954, spermatangial). Shirikishinai: KAWABATA Herb. (x-1956, tetrasporangial).

The following plants were used for culture experiments: cystocarpic plants collected at Muroran on November 20, 1970 and December 18, 1972 and tetrasporangial plants collected at Muroran on October 5, 1970, November 20, 1970, and December 18, 1972.

Description

Several perennial upright thalli arising from a common expanded basal disc; each thallus monopodidal, alternate-distichously branched, up to 35 cm in height, dark red in color, rather rigid, adhering imperfectly to paper in drying; main axis almost terete only just above the basal disc, 1.2-1.5 mm

in diameter, becoming abruptly flat and reaching up to 4.5 mm in breadth in the upper portion, without distinct midribs; the first order branches growing indeterminately and divided into progressively shorter branches up to the sixth order; numerous short adventitious branches borne randomly at the marginal portion of the main axis and indeterminate branches; pericentral cells six in the main axis; plants dioecious; spermatangia borne on short fertile branchlets arising from the uppermost portion of ordinary and adventitious branches or directly from the margin of branches, covering the surface; procarp-bearing branchlets polysiphonous, short, borne on narrow and densely ramified short branches; procarps originating from the suprabasal segments of the branchlets, often coupled procarps borne on the single branchlets; cystocarps arranged in a corymbose manner, ovoid, 360–420 μm × 270–350 μm, usually with calcars of 70–155 μm in length; carpospores deep red, 80–98 μm in diameter; tetrasporangial branchlets borne on narrow and densely ramified short branches, 550–900 μm in length, aggregate; tetrasporangia borne in two rows on 5–7 successive segments of the branchlets, each provided with two cover cells, 115–120 μm × 120–125 μm; tetraspores 68–90 μm in diameter.

Observations

Habitat and Phenology: The following account is based on observations at Muroran from 1970 to 1972. This species grows on rocks in the upper sublittoral zone. It inhabits places exposed to wave action and forms a large community, often together with *Rhodomela teres*. It is sometimes found in places moderately sheltered from waves, where it does not form a conspicuous community. It can be found throughout the year. Plants achieve their most luxuriant growth in June to early July attaining a height of 35 cm. Mature spermatangial plants appear in July and can be found in late September (Pl. 20, A). Mature cystocarpic and tetrasporangial plants are found from late July and discharge carpospores and tetraspores until at least the end of December (Pl. 20, B). After discharging spores, the upper part of plants are lost leaving only their lower portion. However, proliferous branches issuing from the lower portion of the plants develop from winter to spring. Thus, this species is perennial. Only sterile plants are found from late winter to early summer.

Morphology of field plants: The following description is given on the basis of plants gathered at Muroran unless otherwise indicated. Plants consist of several upright thalli arising from a common basal disc. The plants are dark red and have a rather rigid texture. Young plants adhere to paper in drying fairly well, but old ones imperfectly adhere to paper. Each upright thallus is monopodial and decompound-pinnate in a single plane. It has a

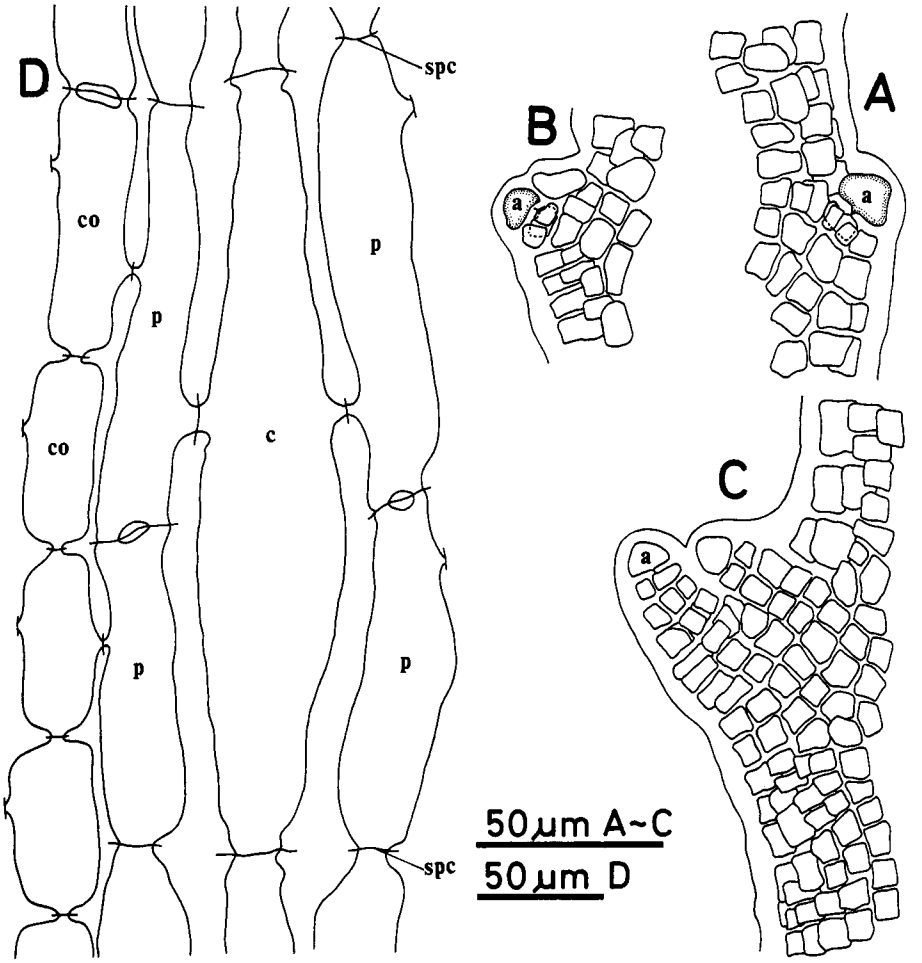

Fig. 79. *Odonthalia corymbifera* (GMELIN) GREVILLE. A–C. Stages in the development of adventitious branches from outermost cortical cells. D. Longitudinal section of the lower portion of a main axis showing a central cell, pericentral cells and cortical cells.

main axis from which many indeterminate branches issue. The main axes are almost terete just above the base and measure 1.2–1.5 mm in diameter. They become abruptly flattened and reach up to 4.5 mm in breadth in their upper portion. Congenitally-fused portions of the main axes are up to 7.5 mm in breadth in the upper portion. The flat portion of the main axes is 480–780 μm in thickness at its median portion and becomes gradually thinner toward the flanks (Pl. 28, H). In the upper portion, evanescent midribs are faintly discernible in surface view as descrived by OKAMURA

(1912). However, the midribs are not anatomically manifest (Pl. 28, H). Ordinary branches of the first order are regularly formed in an alternate-distichous manner in the apical portion of the main axis. The first order branches grow indeterminately in a manner quite similar to the main axis and are divided into progressively shorter branches up to the sixth order.

Adventitious branches are formed from the cortical cells in the marginal portion of the main axis and indeterminate branches (Fig. 79, A-C). They usually issue in large numbers on the upper half portion of the plants and are near to each other (Fig. 84, C). This abundant occurrence of adventitious branches characterizes the alga under study. The adventitious branches are not developed so well in comparison with ordinary branches, but they contribute to reproductive activity. The adventitious branches also issue from the lower portion of the main axis. They are almost terete in the proximal portion and develop in a manner quite similar to the main axis. In late summer to winter they are produced as proliferous branches and may grow into fertile branches in the following season. Vegetative tricho-

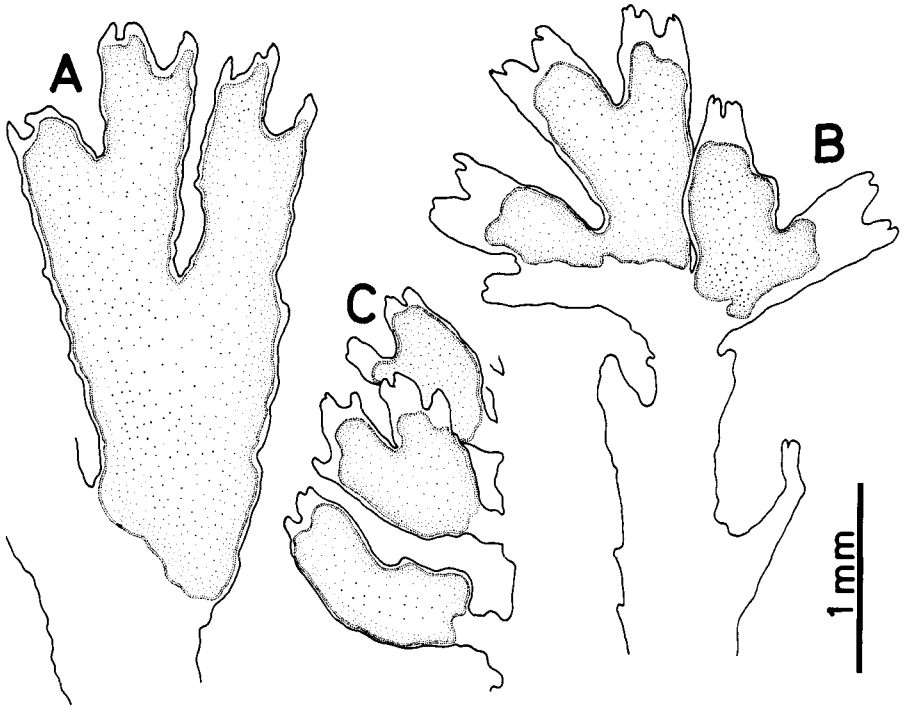

Fig. 80. *Odonthalia corymbifera.* Spermatangial branches: A, formed on the apical portion of an ordinary branch; B, C, formed on adventitious branches.

blasts are entirely absent.

The upright thallus is uniaxial and consists of a central cell, six pericentral cells and several layers of cortical cells. Of the six pericentral cells, the two are situated on the flat faces of the thallus and the other four are situated on the flanks. However, in many cases the pericentral cells and central cell are scarecely discernible and they are indistinguishable from the inner cortical cells. Each pericentral cell is divided transversely one or two times (Pl. 28, F; Fig. 79, D). The upper pericentral cell retains a pit-connection with the central cell, but the lower one becomes linked with a pericentral cell of the underlying segment by a secondary pit-connection (Fig. 79, D). Each pericentral cell cuts off cortical cells in a pattern similar to that of *O. annae*. In consequence, there are 4-7 layers of cortical cells in the middle portion of the main axes in mature plants (Pl. 28, H) and 24-28 layers in the lowest terete portion (Pl. 28, E). The cortical cells develop well in small young plants (4.7-6.5 mm in height) consisting of 10-12 layers in the lowest terete portion of their main axes (Pl. 28, G).

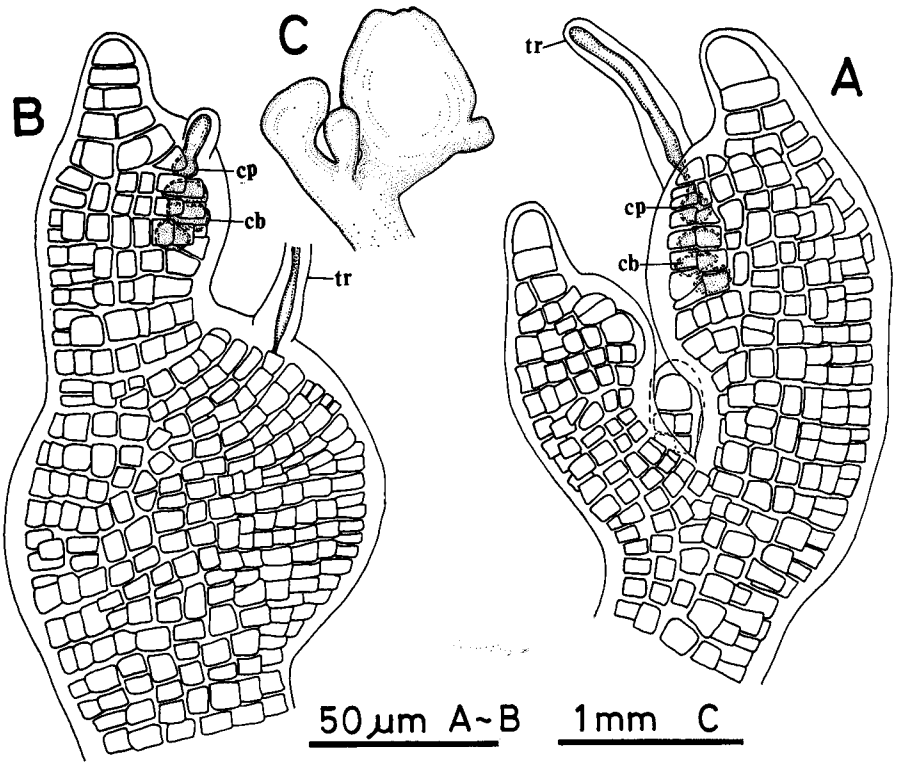

Fig. 81. *Odonthalia corymbifera*. A, B. Procarps (B shows two procarps borne on a single procarp-bearing branchlet). C. Cystocarps.

Spermatangia, carpogonia and tetrasporangia are formed on separate plants. The spermatangia of this species was recently described by TAZAWA (1975) based on plants collected at Muroran. The spermatangia originate only from the cortical cells of short fertile branches. The fertile branches arise from the uppermost portion of ordinary and marginal adventitious branches (Fig. 80, A, B). They are also frequently borne directly on the margin of the branches (Fig. 80, B). The spermatangia are borne on almost the whole spermatangial branches exclusive of the lowest and uppermost portions (Fig. 50, A–C). According to TAZAWA (1975), the spermatangial development is as follows. The spermatangial mother cells are formed by means of transverse or oblique divisions of the superficial cells of the spermatangial branches. The spermatangia issue from the distal end of these spermatangial mother cells as a narrow beak-like protuberance. Then, they are cut off by an oblique annular ingrowth of the cell wall.

The procarps originate from short fertile branchlets which are polysiphonous and simple. Prior to the formation of these procarp-bearing branchlets, narrow and densely ramified short branches are formed on the uppermost portion of ordinary and adventitious branches. The procarp-bearing branchlets are borne on the narrow branches (Pl. 26, B). They are not placed regularly in an alternate-distichous manner and they are densely aggregated. The procarps are produced from the suprabasal segment of the branchlets (Fig. 81, A). However, two procarps are often borne on the same branchlet (Fig. 81, B) as in *Odonthalia dentata* (ROSENVINGE, 1923–24). The carpogonial branch is composed of four cells and surrounded by a conspicuously developed pericarp (Fig. 81, A, B). Hence, the sterile cell groups are indistinguishable from the vegetative cells of the pericarps. The basal segment of the branchlet becomes structured quite similar to the vegetative branch bearing it. The upper sterile portion of the procarp-bearing branchlets grows into a calcar (Fig. 81, C). Mature cystocarps are ovoid in shape and measure 360–420 μm in height and 270–350 μm in diameter (Pl. 26, B; Fig. 81, C). The cystocarps are usually provided with calcars which are 70–155 μm in length. They are arranged in a corymbose manner. Liberated carpospores are globular, deep red in color and measure 80–98 μm in diameter (Pl. 21, A).

The tetrasporangial branchlets are borne on narrow and densely ramified short branches which are produced on the uppermost portion of ordinary and adventitious branches. The branchlets are slightly compressed and measure 180–200 μm $\times$ 130–140 μm in cross section and 550–900 μm in length. They are not arranged regularly in an alternate-distichous manner and are densely aggregated (Pl. 27, B). The tetrasporangia originate from the peri-

central cells and are protected by two cover cells as illustrated by OKAMURA (1912). Two tetrasporangia are formed on 5–7 successive segments of the branchlets. Mature sporangia are 115–120 μm × 120–125 μm in surface view. Liberated tetraspores resemble in many respects the carpospores except in their dimensions (Pl. 21, B). They are smaller than the latter and measure 68–90 μm in diameter.

Culture study: Unialgal cultures were obtained from both isolated carpospores and tetraspores. They were first cultured at 14°C, 14 : 10 LD. There was no essential difference in their germination. The following description is given on the basis of carpospore germination.

Isolated carpospores soon attached to the substrate at one pole and became vertically obovoid in shape (Pl. 21, C). They were divided into bipolar sporelings within one day and differentiated into a colorless rhizoidal portion produced from one pole of the spore and a pigmented upright shoot portion from the other (Pl. 21, D). The rhizoids were divided repeatedly so as to form either a discoid holdfast or a monosiphonous one (Pl. 21, E), both of which were multicellular. The former type was dominant. Sixty-one were discoid and 18 were monosiphonous in 5-day-old sporelings. Both types of rhizoids eventually developed into pseudoparenchymatous basal discs (Pl. 21, H, J). The basal discs continued development growing both concentrically and upward and produced new upright shoots from the superficial cells. The sporelings developed in a pattern similar to that of *O. annae*, but grew less rapidly than those of *O. annae*.

The first branch was observed in 14 days. Subsequently, several branches were produced from the central cells of the growing apex in an alternate-distichous manner. These first order branches were indeterminate and developed in a manner quite similar to the primary axis. The lateral branches were congenitally fused to the main axis (Pl. 21, I). Simultaneously, adventitious branches were produced from cortical cells in the lower portion of the sporeling (Pl. 21, H). After one month, plantlets reached up to 2 mm high and 400–430 μm broad in the upper portion. After 2 months the plants reached up to 6 mm high and produced numerous secondary upright shoots from the basal disc (Pl. 21, J). The lowest portion of these cultured plants were terete and 300 μm across. As growth advanced, the plants clearly showed gross morphology and thallus color similar to those of field-collected plants.

Several of six-month-old plants maintained at 14°C, 14 : 10 LD were transferred to the following conditions : 5°C, 14 : 10 LD ; 5°C, 10 : 14 LD ; 10°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD and 18°C, 10 : 14 LD. The plants maintained at 14°C, 14 : 10 LD became up to 2 cm

high and produced tetrasporangia after 9 months (Pl. 21, K). The plants transferred to 18°C, 14 : 10 LD also reached reproductive maturity 3 months after transfer. Prior to the formation of tetrasporangial branches, these plants formed narrow and densely ramified short branches first on the uppermost portion of ordinary branches, later on marginal adventitious branches. The tetrasporangial branchlets were quite similar to those of field-collected plants (Pl. 21, L). Subsequently, the plants discharged many viable tetraspores which were identical with those from field-collected plants. However, the plants transfered to the other six culture conditions did not produce any reproductive organs.

Liberated tetraspores germinated in a pattern quite similar to that of the aforementioned carpospores. To test the effect of temperatures and photoperiods on the growth and maturation of tetrasporelings, one-month-old plants grown at 14°C, 14 : 10 LD were cultured under four different temperatures and two different light regimes: 5°C, 14 : 10 LD; 5°C, 10 : 14 LD; 10°C, 14 : 10 LD; 10°C, 10 : 14 LD; 14°C, 14 : 10 LD; 14°C, 10 : 14 LD; 18°C, 14 : 10 LD and 18°C, 10 : 14 LD. Ten plants were introduced into each condition. They grew more rapidly at 10–18°C than at 5°C and they grew best in long day conditions. After 8 months, the plants maintained at 14°C, 14 : 10 LD produced spermatangia and carpogonia in a manner quite similar to that of field-collected plants. The plants transferred to 18°C, 14 : 10 LD also reached reproductive maturity 7 months after transfer and formed spermatangia and carpogonia on separate plants. However, no cystocarp development was observed, although female and male gametophytes were cultured in a single vessel. The plants transferred to the other conditions did not produce any reproductive organs.

Geographic distribution: A search of the literature revealed this alga to be a cold water species of the west coast of the North Pacific. As *Odonthalia corymbifera* reported by Japanese phycologists has been confused with *O. macrocarpa* described in the next part, the geographic records of this species published previously must be reviewed. On the basis of a study of this alga in the field in Hokkaido and northern Honshu and a re-examination of herbarium specimens, all the confirmed records of *O. corymbifera* in Japan and adjacent waters are described in materials and shown in Fig. 82.

As described above, *O. corymbifera* in laboratory culture experiments became fertile under conditions, 14°C, 14 : 10 LD and 18°C, 14 : 10 LD, which correspond to summer conditions at Muroran. According to NAGAI (1941), however, in the middle to northern Kuriles ranging from Urup Island in the south to Shumsh Island in the north, seawater temperatures in summer

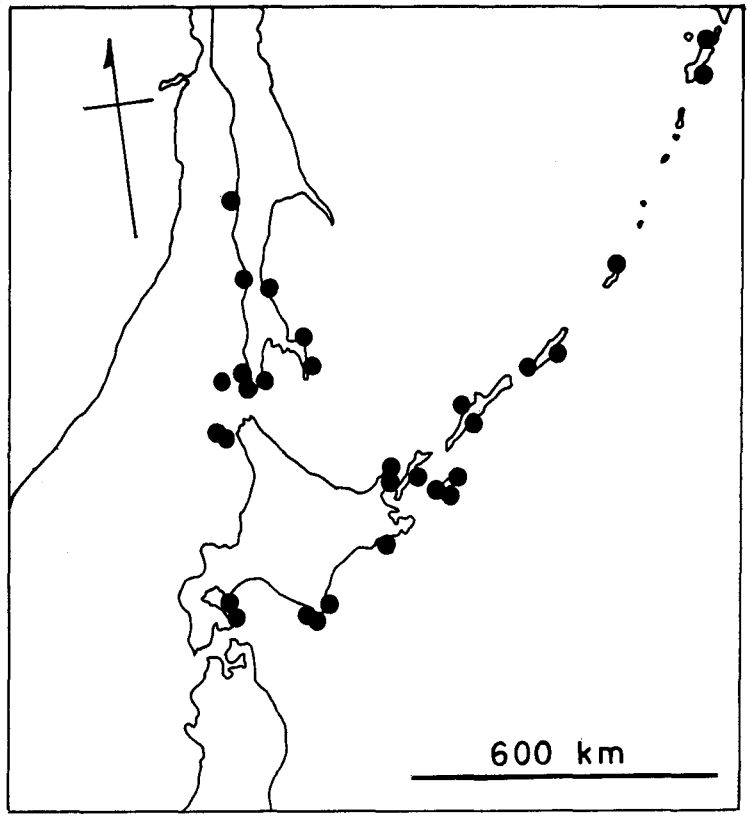

Fig. 82. Distribution of *Odonthalia corymbifera* in Japan and adjacent waters.

during July 20-August 11, 1930 were 3.8-8.0°C. His mature cystocarpic plants were collected at Broughton Bay, Shimshir Island where seawater temperature was 5.9°C on July 22, 1930. These temperatures are very different from the temperatures at which the *O. corymbifera* collected from Muroran became fertile. Thus, the plant from the northern part of its range must respond to much lower temperatures or it may be of a different taxon. Further study is required to elucidate this problem on the basis of plants from the middle to northern Kuriles.

Taxonomic discussion

This species was first described by GMELIN (1768) as *Fucus corymbiferus* on the basis of material from the Kamchatka Peninsula. When *Rhodomela* was established, this alga was transferred to that genus by C. AGARDH

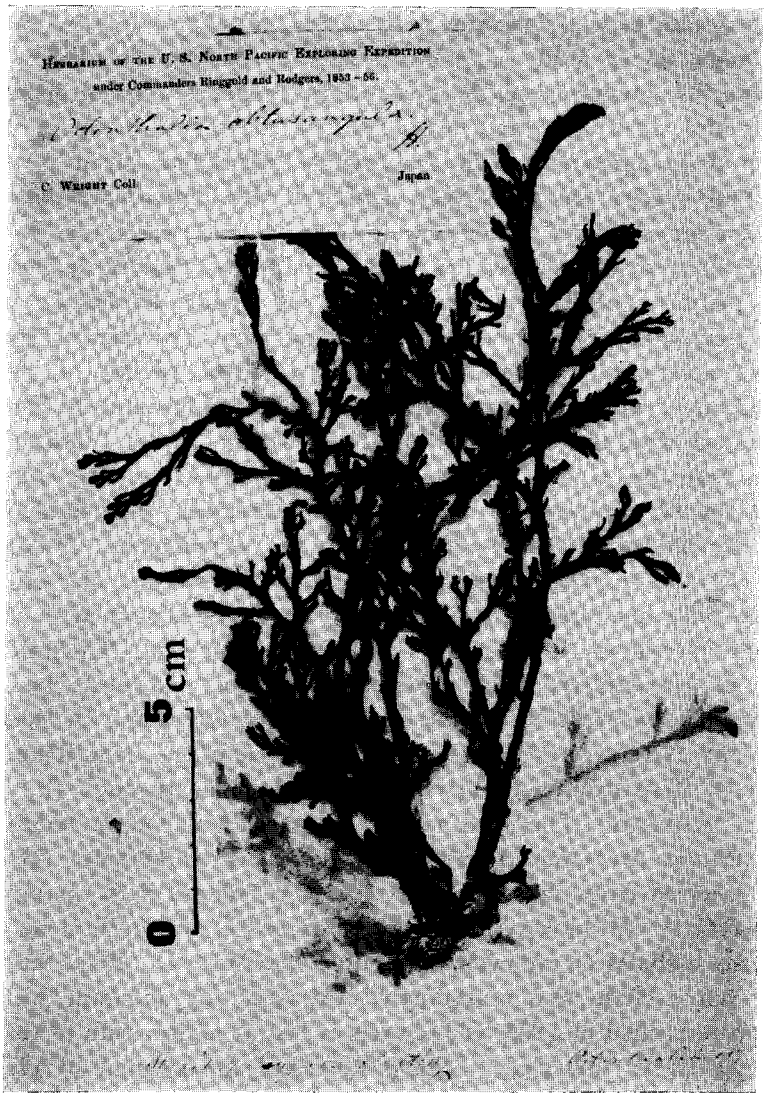

Fig. 83. Sterile specimen of *Odonthalia obtusangula* HARVEY collected from Tsugaru Straits (TCD, leg. C. WRIGHT).

(1822). In re-establishment of the genus *Odonthalia*, GREVILLE (1830) transferred this alga to *Odonthalia*. This species was first reported in Japan by OKAMURA (1902). Then, this alga has been recorded from various localities in Japan and adjacent waters. As pointed out earlier (MASUDA, 1973 b), however, these reports have included two different species. One is genuine *O. corymbifera* described above and the other is *O. macrocarpa* described

as a new species in the following part.

The alga under study is characterized by having flat thalli without distinct midribs, numerous short adventitious branches bearing reproductive structures, and small cystocarps arranged in a corymbose manner. In these features it is in agreement with the original description given by GMELIN (1768). This species has been often confused with *Odonthalia macrocarpa* by Japanese phycologists. A check of their voucher specimens is needed, because in many cases their reports lacked detailed descriptions or illustrations.

The plant reported from Urup Island, the middle Kuriles by YAMADA (1934) is assignable to *O. corymbifera* judging from his voucher specimens, which are now contained in SAP (15113 & 15136–15138). KAWABATA's (1936) specimens collected from Shikotan Island, the southern Kuriles are quite identical with this alga (SAP 15515, 15516 & 22827). NAGAI's (1941) specimens from the Kuriles include both *O. corymbifera* and *O. macrocarpa*. Those of the *O. corymbifera* were cited in materials. The Sakhalin plant recorded by TOKIDA (1954) is referable to *O. corymbifera*. YAMADA and TANAKA (1944 a) reported *O. corymbifera* from Akkeshi, but of their voucher specimens, only one specimen (SAP 12376) is in agreement with this alga. The other specimens are identical with *O. macrocarpa*. CHIHARA (1972) recorded *O. corymbifera* from Hidaka, Hokkaido. However, his voucher specimens preserved in TNS include both *O. corymbifera* and *O. macrocarpa*. KANEKO and NIIHARA (1970) recorded *O. corymbifera* from Rishiri Island, Hokkaido. I have examined their voucher specimens through the kindness of Mr. T. KANEKO. They are actually identical with *O. corymbifera*.

Odonthalia obtusangula was briefly described by HARVEY (1859) from material received from Japan. YAMADA (1934) reduced it to synonymy with *O. corymbifera*. However, the plant treated as *O. corymbifera* by Japanese phycologists includes *O. corymbifera* and *O. macrocarpa*. HARVEY's description did not include the reproductive features. In addition, his original illustration published in 1959 by DAWSON is just as appropriate to *Odonthalia macrocarpa* as to this alga. I have examined a specimen of *Odonthalia obtusangula* deposited in the HARVEY Herbarium (TCD), which was kindly lent to me by Dr. D. A. WEBB. It was collected by C. WRIGHT floating in Tsugaru Straits between Honshu and Hokkaido during 1853–56. This specimen consists of several young upright thalli arising from a common basal disc (Fig. 83) and is quite in agreement with young plants of *Odonthalia corymbifera* described above in all respects. I recognize *O. obtusangula* and *O. corymbifera* to be conspecific.

Odonthalia macrocarpa MASUDA, sp. nov.

Synonym : *Odonthalia corymbifera* auct. non GERVILLE ; NAGAI, 1941 (*pro parte*), p. 237 ; YAMADA and TANAKA, 1944a (*pro parte*), p. 123 ; YAMADA and KINOSHITA, 1948, p. 17, pl. 20 ; KAWABATA, 1959 (*pro parte*), p. 295 ; CHIHARA, 1972 (*pro parte*), p. 158.

Japanese name : O-nokogirihiba (nom. nov.)

Materials

The materials examined were collected from Hokkaido from 1970 to 1973. Nemuro : *Masuda* 13523-13627 (Hanasaki, iv-1972, spermatangial, cystocarpic & tetrasporangial ; ix-1970, sterile). Akkeshi : *Masuda* 13435-13522 (vi-1970, sterile, cystocarpic & tetrasporangial ; vi-1971, ditto). Muroran : *Masuda* 12283-13434 (i-1972, sterile & young tetrasporangial ; ii-1971, tetrasporangial ; iii-1971, cystocarpic & tetrasporangial ; iii-1972, ditto ; iv-1971, ditto ; v-1971, sterile & tetrasporangial ; v-1973, ditto ; vii-1971, ditto ; ix-1973, sterile ; xii-1971, sterile & young tetrasporangial). Usujiri : *Masuda* 13628-13644 (iv-1973, spermatangial, cystocarpic & tetrasporangial). Esanmisaki : *Masuda* 13645-13681 (iv-1973, cystocarpic & tetrasporangial). Shirikishinai : *Masuda* 13682-13731 (iv-1973, sterile, spermatangial, cystocarpic & tetrasporangial).

In addition, the following herbarium specimens were also examined. KURILES Etorof Island : SAP 21984 (Moyoro, viii-1931, sterile) ; NAGAI Herb. (Moyoro, viii-1931, sterile ; Chikohai, viii-1931, sterile, Nos. 2163-2165 ; Iriribushi, vii-1934, sterile, Nos. 3824, 3825). Kunashiri Island : NAGAI Herb. (Atoiya-misaki, viii-1929, sterile & old cystocarpic, Nos. 469-475 ; Rebun-iso, vii-1929, sterile & old tetrasporangial, Nos. 470-474 ; Furukamappu, viii-1930, sterile, Nos. 2362-2364). HOKKAIDO Nemuro : KUROGI in SAP (Nosappu, iv-1970, cystocarpic & tetrasporangial ; v-1969, tetrasporangial ; vi-1970, ditto ; vii-1969, sterile ; Hanasaki, iii-1969, cystocarpic ; iv-1970, cystocarpic & tetrasporangial ; vi-1970, ditto ; vii-1969, sterile ; viii-1969, ditto ; x-1969, ditto ; xii-1969, ditto). Akkeshi : SAP 24631, 24656 & 26630 (vi-1933) ; TNS-AL 31598 (v-1971). Kushiro : SAP 25397 (Konbumori, v-1945, tetrasporangial) ; YENDO Herb. (Shireto, v-1897, leg. T. KAWAKAMI). Hidaka : SAP 25405, 25493 (Okoshi, viii-1943 ; Samani, vii-1943) ; TNS-AL 31584, 31586-31588, 31594-31596 & 31599 (Erimo-misaki, vii-1970 ; Aburakoma, v-1971, cystocarpic ; vii-1970, sterile ; Enrumu-misaki, iv-1958 ; v-1971, cystocarpic & tetrasporangial). Muroran : SAP 23347, 23348 (iii-1936, tetrasporangial ; iv-1935, cystocarpic). Shirikishinai : KAWABATA Herb. (iv-1955, tetrasporangial). Hakodate : SAP 24546 (non date).

The following plants were used for culture experiments: cystocarpic plants collected at Muroran on March 19, 1971, April 28, 1971 and March 21, 1972, and at Hanasaki, Nemuro, on April 15, 1972; tetrasporangial plants collected at Muroran on February 19, 1971, February 26, 1971, March 20, 1971 and March 17, 1972; and at Hanasaki on April 15, 1972.

Description

Thalli plures recti perennes e disco basali communi effecti, omnino monopodiales, alterne-distiche ramosi, usque ad 21 cm in altitudine, in colore brunneolo-rubri, ad tactum aliquantum rigidi, exsiccatione chartae adhaerentes; axis principalis fere teres supra discum basalem et 500–1000 μm in diametro, abrupte comprescens et extensus usque ad 3.8–4.3 mm in latitudine ad partem superam, sine costis distinguibilibus vel evanescentibus; rami plures ordinis primae bene cresentes et in ramos sensim breviores usque ad ordinem quintum divisi; rami adventitii nec vulgares; cellulae pericentrales sex in axe principali; plantae dioeciae; spermatangia in ramis fertilibus latis formata, paginam tegentia; ramuli procarpiferi polysiphonii, breves; cystocarpia in ramis anguste contractis portata, racemosa, ovoidea, 1600–2000 μm in altitudine et 1300–1600 μm in diametro, calcaribus (100–500 μm in longitudine), pedicellis longis (usque ad 1.0–1.5 mm in longitudine); carposporae brunneolo-rubrae, 85–105 μm in diametro; ramuli tetrasporangiferi in parte summa ramorum portati, fasciculati, leviter compressi, 1.5–2.5 mm in longitudine; tetrasporangia in series longitudinales duas ad 12–17 segmenta successiva ramulorum formata, omnino cellulis obtectis duabus 125–130 μm × 145–150 μm, tetraedrice divisa; tetrasporae 75–100 μm in diametro.

Holotypus: SAP 032079 (*Masuda* 13334), specimen cystocarpiis.

Several perennial upright thalli issuing from a common basal disc, each thallus monopodial, alternate-distichously branched, up to 21 cm in height, brownish-red in color, rather rigid to the touch, adhering to paper in drying; main axis almost terete above the basal disc and 500–1000 μm in diameter, becoming abruptly flattened and reaching up to 3.8–4.3 mm in breadth in the upper portion, without distinct or evanescent midribs; several branches of the first order growing well and divided into progressively shorter branches up to the fifth order; adventitious branches not common; pericentral cells six in the main axis; plants dioecious; spermatangia formed on broad fertile branches, covering the surface; procarp-bearing branchlets polysiphonous, short; cystocarps borne on narrowly tapering branches, racemose, ovoid, 1600–2000 μm in height and 1300–1600 μm in diameter, with calcars (100–500 μm in length) with long stalks (up to 1.0–1.5 mm in length); carpospores brownish-red, 85–105 μm in diameter; tetrasporangial branchlets borne on

the uppermost portion of branches, fasciculate, slightly compressed, 1.5–2.5 mm in length; tetrasporangia formed in two longitudinal rows on 12–17 successive segments of the branchlets, each provided with two cover cells, 125–130 μm × 145–150 μm, divided tetrahedrally; tetraspores 75–100 μm in diameter.

Holotype: SAP 032079 (*Masuda* 13334), cystocarpic specimen collected at Muroran, Hokkaido, on March 20, 1971 by M. MASUDA (Pl. 22, A).

Observations

Habitat and Phenology: This species occurs attached to rocks in places exposed to wave action in the upper sublittoral zone. At Hanasaki, Nemuro this alga forms a rather large community. It does not form a conspicuous community at Muroran where it often associates with *Odonthalia corymbifera* and their holdfasts sometimes combine into one another. The following phenological information is given on the basis of observations executed at Muroran from 1971 to 1972. This alga can be found throughout the year. Plants achieve their most luxuriant growth in March and grow up to 21 cm high. Young tetrasporangial plants appear in mid-December. Mature tetrasporangial plants are found from mid-February to July (Pl. 22, B). Mature cystocarpic plants are seen from mid-March to April (Pl. 22, A). After discharging spores, the upper portions of the cystocarpic and tetrasporangial plants are lost leaving only their lower portion. However, proliferous branches issue from the lower portion in summer to autumn and develop into fertile branches in the following season. Thus, this species is perennial. Only sterile plants are found from late July to November. Spermatangial plants have not been collected at Muroran, but old ones were found at Hanasaki, Usujiri and Shirikishinai in April.

Morphology of field plants: The following account is given based on plants gathered at Muroran unless otherwise indicated. Plants consist of several upright thalli issuing from a common expanded basal disc which adheres firmly to the rocky substrate. They are brownish-red, which is less conspicuously tinged with red than *O. corymbifera*. This alga is easily distinguished in the field from *O. corymbifera* by its color. This alga has a rather rigid texture and adhere to paper in drying fairly well. Each upright thallus is monopodial and decompound-pinnate in a single plane. It has a visible main axis which is slightly flexuous. The main axes are almost terete just above the base and measure 500–1000 μm in diameter (Pl. 28, I). They become immediately flattened and reach 3.8–4.3 mm in breadth in the upper portion. Congenitally-fused portions of the main axis are up to 6 mm in breadth in the upper portion. The flat portion of the main axes is

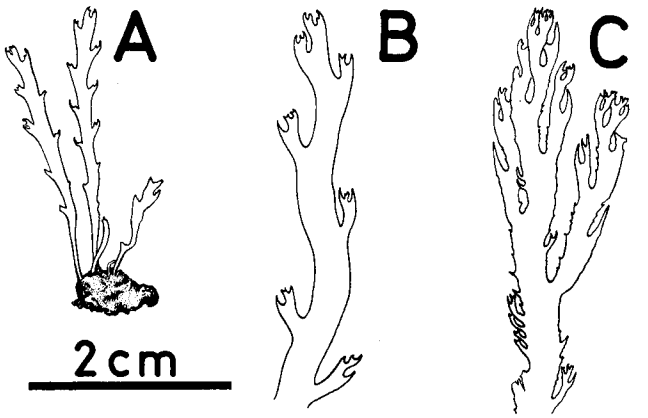

Fig. 84. Habit of *Odonthalia macrocarpa* MASUDA (A, B) and *O. corymbifera* (C). Field-collected plants. A. Young secondary upright thalli issuing from an old basal disc. B, C. Apical portion of the main axes in young plants.

480–600 μm in thickness at the median region and becomes gradually thinner toward both flanks (Pl. 28, K). Distinct or evanescent midribs are not present.

Ordinary branches of the first order are produced from central cells of the apical portion of the main axis. They are regularly formed in an alternate-distichous manner (Fig. 84, A, B). The first order branches are as a rule indeterminate branches except for the lower ones. However, only several of them develop well as does the main axis. These well developed laterals are sporadically present among short branches (Pl. 22, A, B). They reach up to 12 cm long in the middle portion of the main axis and are divided into progressively shorter branches up to the fifth order.

Adventitious branches are sometimes produced from cortical cells in the marginal portion of the main axis and indeterminate branches. They bear reproductive structures. Vegetative trichoblasts are entrely absent. The thallus structure is basically similar to that of *O. corymbifera* (Pl. 28, I–K; Fig. 85, A).

Spermatangia, procarps and tetrasporangia are borne on separate individuals. The spermatangia originate from the cortical cells of short fertile branches, which issue from indeterminate branches. These spermatangial branches are divided regularly in an alternate-distichous manner and consist of three orders of branches (Fig. 85, B, C). They are somewhat broader than sterile branches of the same order and are distinguished from the latter by their light color. The spermatangia are borne on almost the whole branch

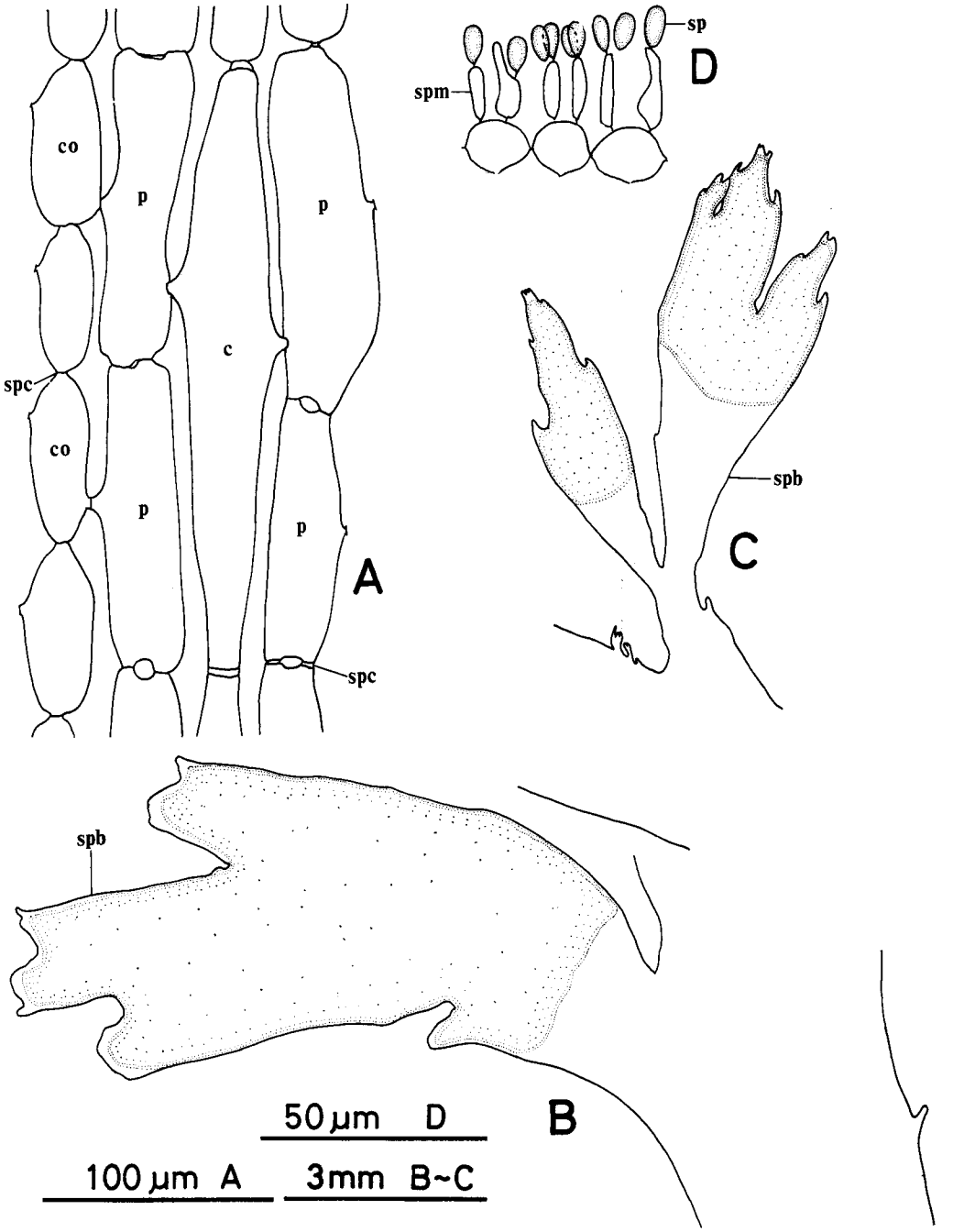

Fig. 85. *Odonthalia macrocarpa.* A, B & D, field-collected plants; C, cultured plant. A. Longitudinal section of the lower portion of a main axis in a young plant, showing the arrangement of a central cell, pericentral cells, and cortical cells. B, C. Spermatangial branches. D. Cross section of a spermatangial branch, showing the spermatangia and spermatangial mother cells.

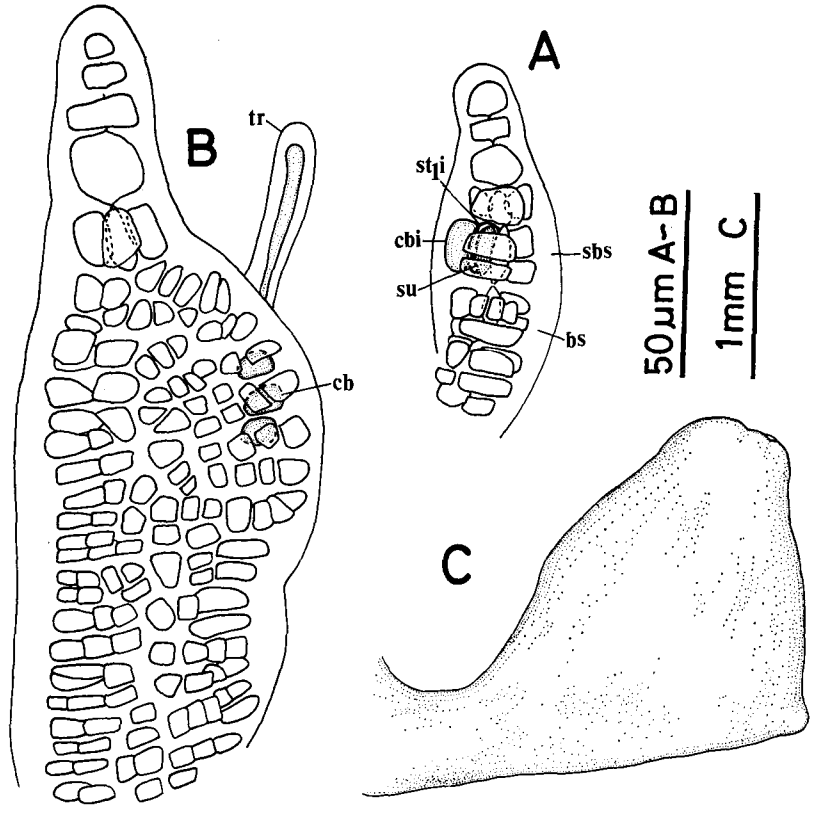

Fig. 86. *Odonthalia macrocarpa.* A, B. Procarps. C. Cystocarp.

exclusive of the lowest and uppermost portions (Fig. 85, B, C). The development of spermatangia is identical with *O. corymbifera.* The spermatangial mother cells are usually formed by means of an oblique division of the outermost cortical cells. The spermatangia are cut off from the distal end of the spermatangial mother cell. Two spermatangia are usually borne on each mother cell (Fig. 85, D).

The procarps are produced on short fertile branchlets. These procarp-bearing branchlets arise from narrowly tapering branches which are transformed from the distal portion of broad ordinary and adventitious branches (Pl. 22, A). Rarely, the narrow branches are directly formed adventitiously on the margin of broad branches. The procarp-bearing branchlets are not arranged regularly in an alternate-distichous manner but irregularly in a spiral manner (Pl. 23, S). The procarp originates from the suprabasal segment of the branchlets. The carpogonial branch consists of four cells and is surrounded by a well developed pericarp (Fig. 86, A, B). Hence, the

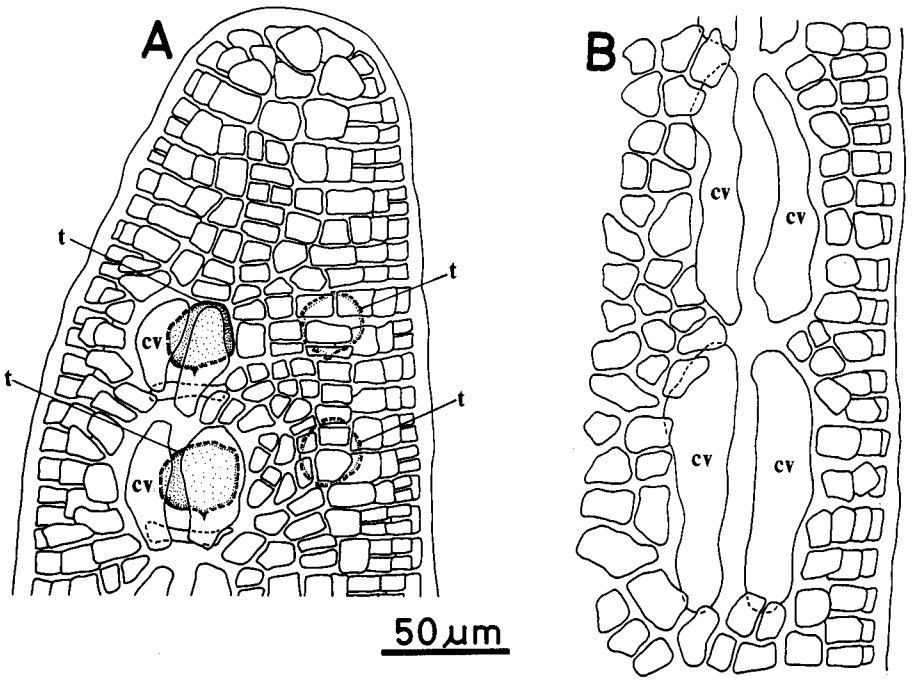

Fig. 87. *Odonthalia macrocarpa*. A. Apical portion of a tetrasporangial branch. B. Portion of a tetrasporangial branch, showing two cover cells.

sterile cell group is indistinguishable from the vegetative cells of the pericarp. The basal segment of fertile branchlets becomes a structure quite similar to that of vegetative branches bearing it and becomes elongated as growth advances. It is up to 1.0-1.5 mm in length in mature cystocarps. The upper sterile portion of the procarp-bearing branchlets becomes polysiphonous and gives rise to a calcar which reaches 100-500 μm in length. Mature cystocarps are situated in conspicuously developed ovoid pericarps (Pl. 26, C; Fig. 86, C) and arranged in a racemose manner. They are much larger than those of *O. corymbifera* and measure 1600-2000 μm in height and 1300-1600 μm in diameter. Liberated carpospores are brownish-red and measure 85-105 μm in diameter (Pl. 23, A). The carpospores from plants colletced at Hanasaki, Nemuro are similar to those from the Muroran plants in every respects.

The tetrasporangia are produced on aggregate simple branchlets borne on the apical portion of ordinary and adventitious branches. When young, these tetrasporangial branchlets are strongly incurved, but they become straight and slightly compressed measuring 240-250 μm × 200-220 μm across

and 1.5–2.5 mm long. They are narrow at the proximal end and become gradually attenuated to the distal end (Pl. 27, C). These slender tetrasporangial branchlets contrast strikingly with broad vegetative branches. The tetrasporangia originate from pericentral cells. Two tetrasporangia are formed on 12–17 successive segments of the fertile branchlets (Pl. 27, C; Fig. 87, B). Each is provided with two cover cells (Fig. 87, B). The mature portion protrudes slightly and tetrahedrally divided sporangia are 125-130 μm by 145–150 μm in surface view. Liberated tetraspores resemble in many respects the carpospores except in their dimensions (Pl. 23, B). They are smaller than the latter at 75–100 μm in diameter. The tetraspores from plants collected at Hanasaki and Akkeshi are quite similar to those from Muroran.

Culture study: Unialgal cultures were obtained from both isolated carpospores and tetraspores from the Muroran and the Nemuro plants. They were first cultured at 10°C, 14 : 10 LD. There was no essential difference in their germination. The following account is given on the basis of germination of carpospores derived from the Muroran plants.

Isolated carpospores developed in a pattern similar to those of *Odonthalia corymbifera* as shown in Plate 23, C–N, although these carposporelings grew more rapidly and the first lateral branch appeared at 17 days. Subsequently, several lateral branches were produced from central cells and arranged in an alternate-distichous manner. Adventitious branches were sometimes produced from cortical cells in the lower portion of the sporeling.

After 2 months plantlets reached up to 15 mm in height and 1.9 mm in breadth in the upper portion. They produced 5–6 lateral branches, which are congenitally fused with the main axis (Pl. 23, O). They also produced several secondary upright axes from the basal disc (Pl. 23, P). They clearly showed a gross morphology (Pl. 23, Q) and thallus color similar to field-collected plants.

After 3 months, several plants maintained at 10°C, 14 : 10 LD were transferred to the following five conditions: 5°C, 10 : 14 LD; 5°C, 14 : 10 LD; 10°C, 10 : 14 LD; 14°C, 10 : 14 LD and 14°C, 14 : 10 LD. The plants transferred to 10°C, 10 : 14 LD reached reproductive maturity 8 months after transfer (Pl. 22, C; 23, T). The plants transferred to 5°C, 10 : 14 LD reached reproductive maturity 12 months after transfer. These plants produced tetrasporangia in a manner similar to that of field-collected plants, but tetrasporangial branchlets of cultured plants were longer than those of field-collected plants. They were up to 5 mm in length and produced tetrasporangia on 20–50 successive segments. Subsequently, the plants discharged viable tetraspores which were identical with those from field-collected plants. However, the plants transferred to 5°C, 14 : 10 LD, 14°C, 10 : 14 LD and

14°C, 14 : 10 LD and the plants maintained at 10°C, 14 : 10 LD did not produce any reproductive organs.

To test the effect of temperatures and photoperiods on the growth and maturation of tetrasporelings, one-month-old plants grown at 10°C, 10 : 14 LD were cultured under four different temperatures and two different light regimes : 5°C, 14 : 10 LD ; 5°C, 10 : 14 LD ; 10°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 14 : 10 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD and 18°C 10 : 14 LD. Ten plants were introduced into each situation. They grew at first more rapidly at 10°C–18°C than at 5°C and they grew best in long day conditions. Later, however, plants cultured at 18°C grew less rapidly than those at 5–14°C. Six months after transfer plants cultured at 5°C were comparable in size to those cultured at 18°C. The plants maintained at 10°C, 10 : 14 LD became fertile after 8 months (Pl. 22, D, E ; 23, R, S). The plants transferred to

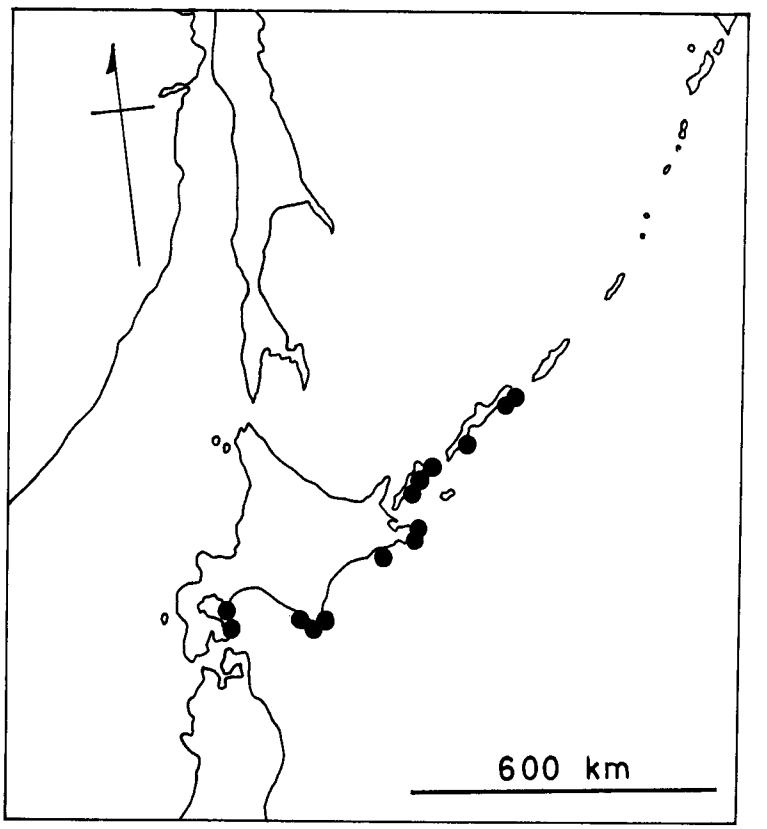

Fig. 88. Distribution of *Odonthatia macrocarpa* in Japan and adjacent waters.

5°C, 10 : 14 LD reached also reproductive maturity 10 months after transfer. These plants produced spermatangia or carpogonia on separate individuals in a manner similar to field-collected plants. The female and male gametangial plants cultured at 5°C, 10 : 14 LD were transferred together to large glass culture vessels (14.5 cm × 11.0 cm) containing 1200 *ml* of medium at 5°C, 10 : 14 LD and 10°C, 10 : 14 LD. However, cystocarp development was not observed. The plants cultured under the other five situations attempted did not produce any reproductive organs.

Tetraspores isolated from field-collected plants from Muroran and cultured at 10°C, 14 : 10 LD developed in a pattern quite similar to that of the carpospores described above. After 3 months, several germlings were transferred to the five other conditions : 5°C, 10 : 14 LD ; 5°C, 14 : 10 LD ; 10°C, 10 : 14 LD ; 14°C, 10 : 14 LD and 14°C, 14 : 10 LD. Only plants transferred to 5°C, 10 : 14 LD and 10°C, 10 : 14 LD became fertile as in the tetrasporelings obtained from cultured plants.

Both the carpospores and the tetraspores of the Nemuro isolates developed in a pattern quite similar to that of the Muroran isolates. The plants were quite similar to those of the latter isolates in gross morphology, environmental responses and reproductive structures.

Geographic distribution : An examination of the algae *in situ* in Hokkaido and northern Honshu and a check of herbarium specimens deposited in several herbaria, all of which were quoted previously (see materials), resulted in the present known range of this species (Fig. 88). The geographic distribution is confined to the west coast of the Northern Pacific ranging from Etorof Island in the north to the coast of southern Hokkaido in the south. Thus, this species is less widely distributed than *O. corymbifera*. These areas are strongly washed by the Oyashio (cold current) but not by the East Sakhalin Current.

Taxonomic discussion

As mentioned already, this alga has been confused with *O. corymbifera* by previous investigators. Both the algae show a close similarity to each other in having broad thalli without conspicuous midribs by which they are distinguished from the other species of *Odonthalia*. However, the alga under discussion differs strikingly from *O. corymbifera* both in vegetative features, the absence of minute adventitious branches, absence of indistinct midribs and brownish-red color of thalli ; and in reproductive features, larger spermatangial branches, cystocarps and tetrasporangial branchlets. Furthermore, breeding discontinuity between the two algae is maintained by a seasonal isolation of gametogenesis. In Hokkaido the gametogenesis

of the alga under discussion occurs in winter, whereas that of *O. corymbifera* does in summer.

Odonthalia yamadae MASUDA, sp. nov.

Synonym: *Odonthalia kamtschatica* auct. non J. AGARDH; YAMADA and TANAKA, 1944 a, p. 77; YAMADA and KINOSHITA, 1950, p. 13, pl. 61; SEGAWA, 1956, p. 121, pl. 72 (592).

Japanese name: Akkeshi-nokogirihiba (nom. nov.)

Materials

The materials used for this study were collected at Akkeshi from 1970 to 1974: *Masuda* 9724-9804, 13259-13268 & 13780-13785 (iv-1974, cystocarpic & tetrasporangial; vi-1970, sterile & cystocarpic; vi-1971, sterile, cystocarpic & tetrasporangial). In addition, the herbarium specimens deposited in SAP and TNS were also examined: SAP 12354, 12446, 12447, 25022 & 25704 (Akkeshi, vii-1940, sterile; ix-1931, sterile); TNS-AL 31529 (Nemuro, v-1971, leg. M. CHIHARA) 31527, 31528 & 31530 (Akkeshi, v-1971, sterile & cystocarpic, leg. M. CHIHARA).

Parent plants for culture experiments were collected at Akkeshi as follows: sterile plants on June 23, 1971; a cystocarpic & tetrasporangial plants on Apirl 8, 1974.

Description

Thalli plures recti perennes e disco basali communi effecti, omnino monopodiales, alterne-distiche ramosi, usque ad 30 cm in altitudine, in colore profunde rubri, ad tactum molles, exsiccatione chartae adhaerentes; axis principalis infra fere teres et 1.0-1.2 mm in diametro, gradatim comprescens, extensus usque ad 2-4 mm in latitudine ad partem superam, costis conspicuis; rami multi ordinis primae bene cresentes et in ramos sensim breviores usque ad ordinem quintum divisi; rami adventitii plerumque ad axillam portati; spermatangia in ramis fertilibus latis formata, paginam tegentia; ramuli procarpiferi monosiphonii; cystocarpia in ramis leviter anguste contractis portata, flexuoso-racemosa, cupiformia vel late ovoidea, ostiolis paulo latis, 500-750 μm in longitudine et 460-700 μm in diametro, interdum calcaribus brevibus (40-110 μm in longitudine); carposporae in colore profunde rubrae, 90-110 μm in diametro; tetrasporangia in series longitudinales duas ad 5-15 segmenta successiva ramulorum immutorum formata, extensa versus partes congentice coalitas, omnino cellulis obtectis duabus, 150-170 μm $\times$ 140-160 μm, tetraedrice divisa; tetrasporae 75-85 μm in diametro.

Holotypus: SAP 032116 (*Masuda* 13781), specimen cystocarpiis.

Several perennial upright thalli issuing from a common basal disc, each thallus monopodial, alternate-distichously branched, up to 30 cm in height, deep red in color, soft to the touch, adhering to paper in drying; main axis almost terete below and 1.0–1.2 mm in diameter, becoming gradually flattened, reaching up to 2–4 mm in breadth in the upper portion, with conspicuous midribs; many branches of the first order growing well and divided into progressively shorter branches up to the fifth order; adventitious branches usually borne in the axil; spermatangia formed on broad fertile branches, covering the surface; procarp-bearing branchlets monosiphonous, cystocarps borne on slightly narrowly tapering branches, flexuose-racemose, barrel-shaped or broadly ovoid, with rather wide ostioles, 500–750 μm in length and 460–700 μm in diameter, sometimes with short calcars (40–110 μm in length); carpospores deep red in color, 90–110 μm in diameter; tetrasporangia formed in two longitudinal rows on 5–15 successive segments of unmodified branchlets, extended to congenitally-fused portions, each provided with two cover cells, 150–170 μm $\times$ 140–160 μm, divided tetrahedrally; tetraspores 75–85 μm in diameter.

Holotype: SAP 032116 (*Masuda* 13781), cystocarpic specimen collected at Akkeshi, Hokkaido, on April 8, 1974 by M. MASUDA (Pl. 24, B).

Observations

Habitat: This species grows on rocks in depths between 3 and 5 m judging from its frequent occurrence in dredges at Akkeshi as does *Rhodomela lycopodioides* f. *tenuissima* mentioned previously. It is sometimes found in the upper sublittoral zone occurring together with *O. macrocarpa* in the *Laminaria-Alaria* forest. It inhabits deeper water than other *Odonthalia* species found in Hokkaido. Although I can not describe the phenology of this species because of the scarcity of field observations, it probably has perennial upright thalli on the basis of its morphology. Plants, which possess the stout main stem, seem to be second year plants and have numerous well developed proliferous branches. Mature cystocarpic and tetrasporangial plants are found from early Apirl to early June. However, the plants collected in early June had only a few cystocarps and tetrasporangia. This alga may become fertile in winter to spring.

Morphology of field plants: The following description is based on materials collected at Akkeshi. Plants consist of several upright thalli arising from a common expanded basal disc and reaching up to 30 cm high. The thalli are deep red and have a rather soft texture. They adhere to paper in drying fairly well. Each upright thallus is monopodial and decompound-

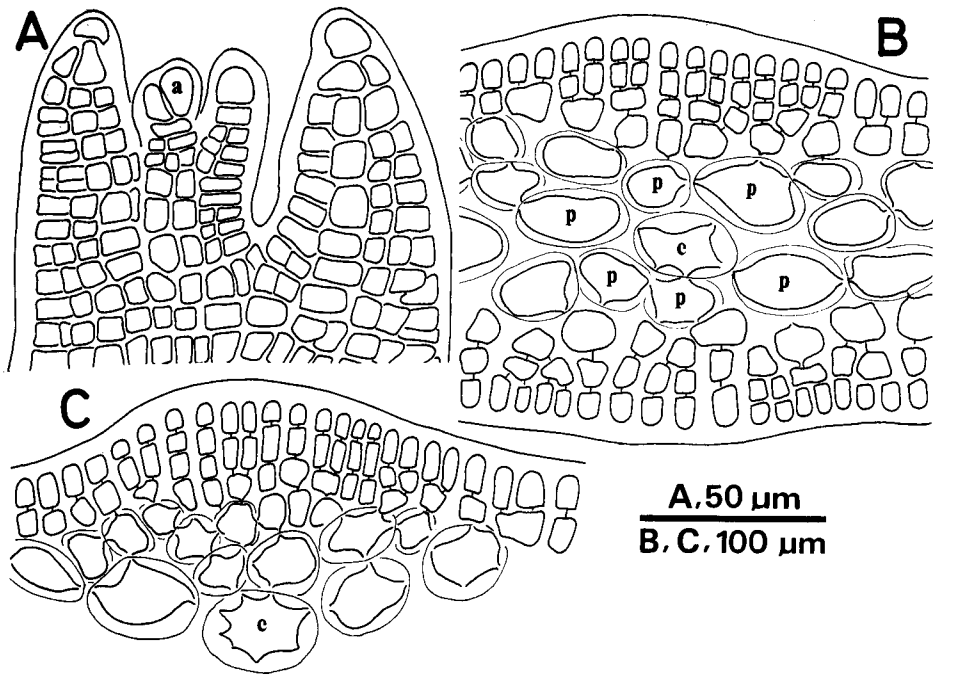

Fig. 89. *Odonthalia yamadae* MASUDA. A. Apical tip of an indeterminate branch forming lateral branches arranged in an alternate-distichous manner. B, C. Stages in the development of midribs.

pinnate in a single plane, showing a bilateral symmetry (Pl. 24, A, B). It has a main axis from which lateral branches issue regularly in an alternate-distichous manner (Fig. 89, A). The main axes of first year plants are almost terete below, becoming gradually compressed upward, are eventually flat in the middle to upper portions, and are provided with a conspicuous midrib. The main axes are 1.0–1.2 mm in diameter just above the base and 2–4 mm in breadth in the upper portion. Congenitally-fused portions are up to 5–6 mm in breadth in the uppermost portion of the main axes. The first order branches are as a rule indeterminate and reach up to 15 cm long in the middle portion of the main axis. They are attenuated toward their proximal portion, but not terete. They develop exactly in the same manner as in the main axis and are divided into progressively shorter branches up to the fifth order (Pl. 24, A, B). The main axes of the second year plants are stout and almost terete even in the middle portion. They are up to 2.5 mm in diameter just above the base, and are covered with numerous proliferous branches.

Adventitious branches are produced from cortical cells of main axes and

indeterminate branches (Fig. 90, B–E). In many cases, they are formed in the axil, but sometimes are produced on the marginal portion. In second year plants, the adventitious branches sometimes issue from the mediam portion. The adventitious branches are almost terete in the proximal portion and become gradually flattened toward the upper portion, resembling main

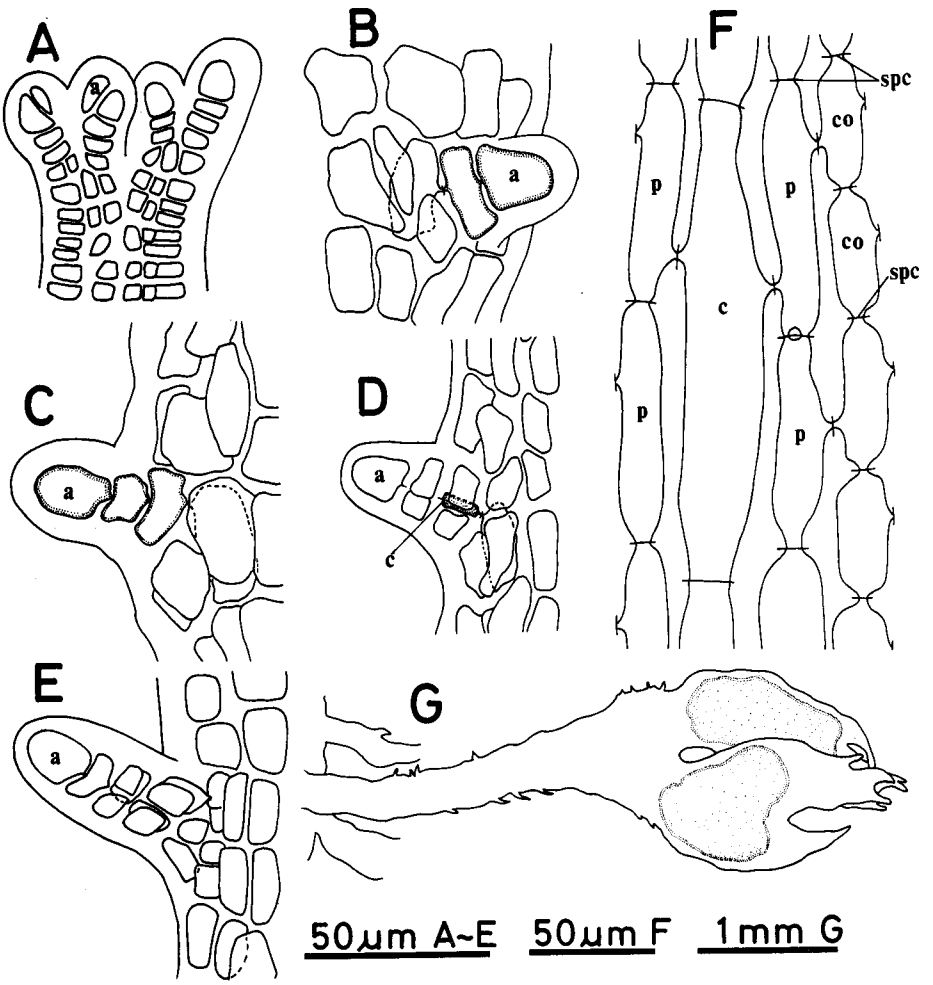

Fig. 90. *Odonthalia yamadae.* A–D & G, cultured plants; E, F, field-collected plants. A. Apical portion of a main axis, showing the alternate-distichous branching. B–E. Stages in the development of adventitious branches from outermost cortical cells. F. Longitudinal section of the lower portion of a main axis, showing the arrangement of a central cell, pericentral cells and cortical cells. G. Spermatangial branch formed adventitiously on the main axis.

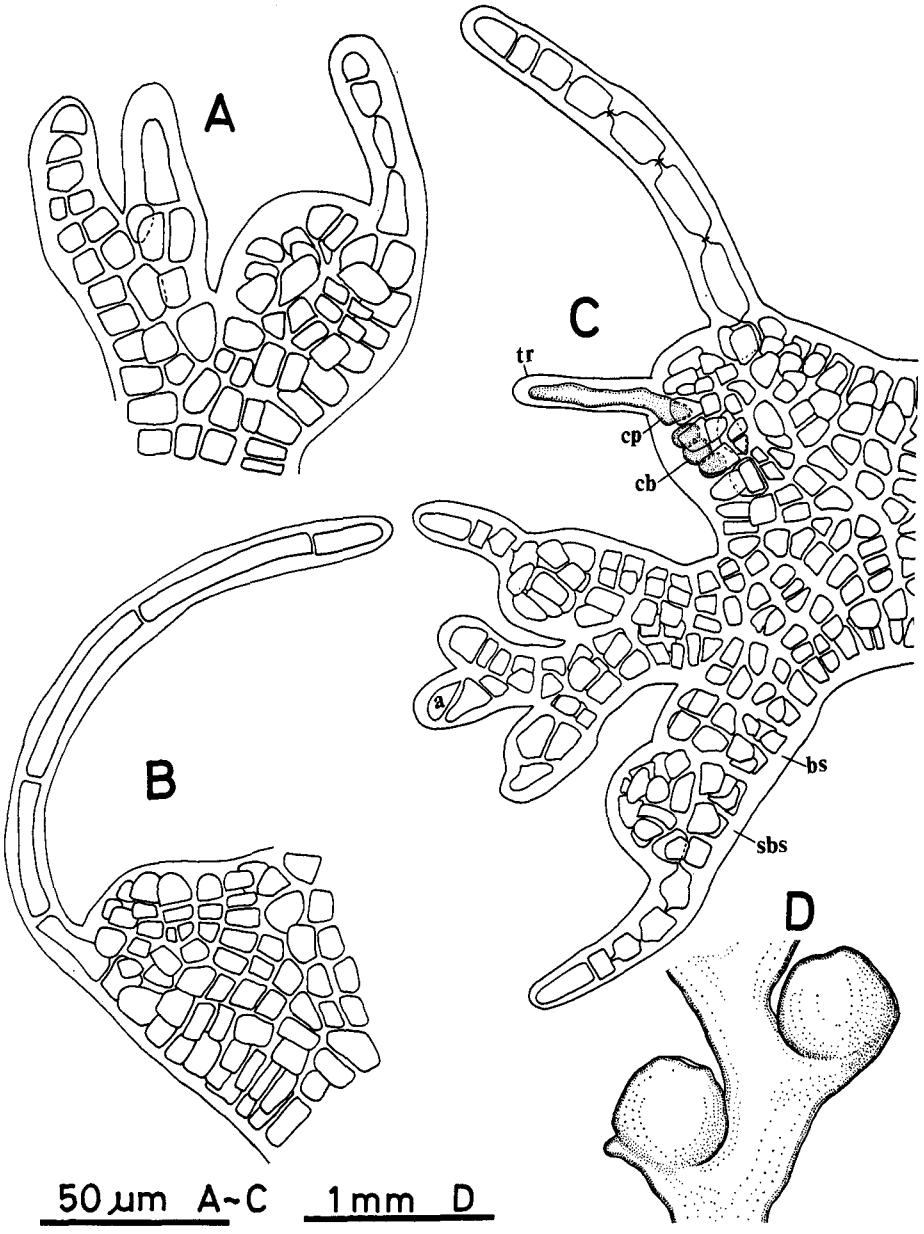

Fig. 91. *Odonthalia yamadae.* A, B & D, field-collected plants; C, cultured plant. A–C. Development of procarps. D. Cystocarps.

axes of the first year plant. Most of them bear reproductive structures, while the others remain vegetative and may become reproductive in the following season. Vegetative trichoblasts are entirely lacking.

The thallus structure is essentially in agreement with that of the preceding three species exclusive of the formation of conspicuous midribs (Pl. 28, A, B; Fig. 89, B, C; 90, F).

The midribs are formed by successive divisions of cortical cells which are situated near the central cell (Fig. 89, B, C). They appear as narrow longitudinal thickenings in the lower portion of the main axis of young plants and elongate upward as the main axis grows. The thickenings appear usually on both the sides of the main axis at the same time (Fig. 89, B, C), but they appear sometimes on one side. These thickenings gradually become thicker and broader assuming a very conspicuous midrib in mature plants (Pl. 28, B). Later, in lateral branches longitudinal thickenings appear from

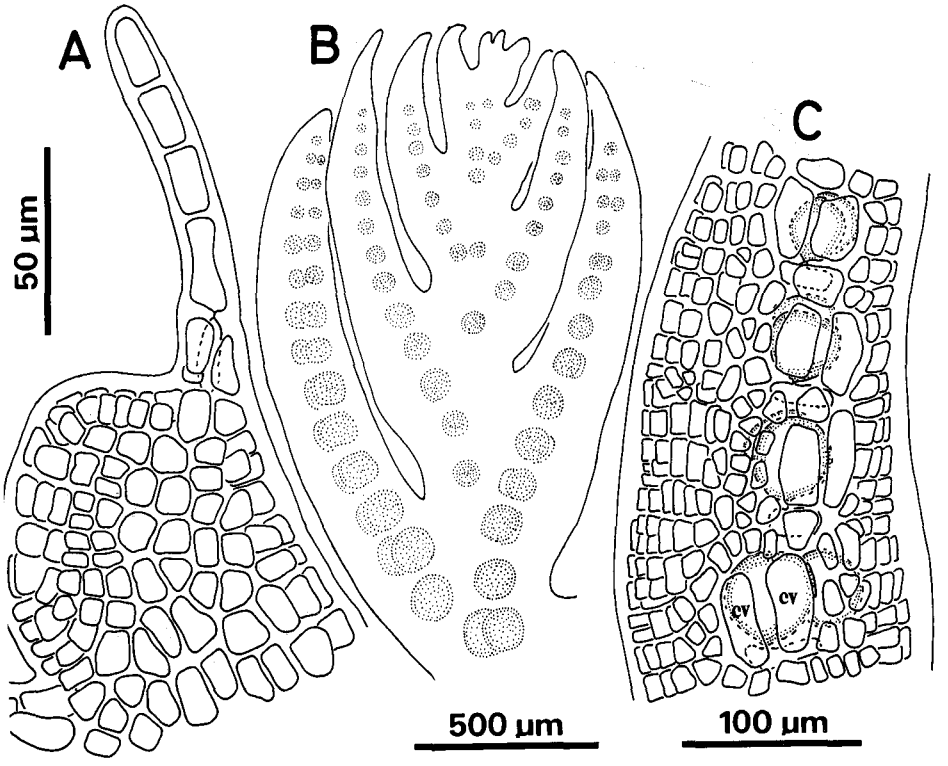

Fig. 92. *Odonthalia yamadae.* A. Procarp probably after fertilization; note the third segment of the trichoblast from the proximal end becoming polysiphonous. B. Tetrasporangial branches. C. Portion of a young tetrasporangial branchlet.

the proximal portion and develop into a midrib like that on the main axis. The midrib continues in the development and eventually becomes a stout main stem of old plants.

No spermatangial plants have been collected and they will be described later based on cultured plants. No adequately preserved procarpic material has been available for examination. A few procarps were formed in fertile field-collected plants. They are borne on fertile trichoblasts (Fig. 91, A, B). The upper sterile portion of the trichoblast falls usually off as the cystocarp develops. At times, the third segment from the proximal end becomes polysiphonous and grows into a calcar (Fig. 92, A). The development of the procarps is described in more detail for cultured plants later.

The cystocarps are borne on slightly narrow tapering branches which are transformed from the distal portion of ordinary and adventitious branches (Pl. 24, B). At times, the slightly narrow branches are directly formed adventitiously on the main stem of second year plants. The cystocarps are arranged regularly in an alternate-distichous manner (Pl. 26, D; Fig. 91, D). Mature cystocarps are barrel-shaped or broadly ovoid with rather large ostioles (Pl. 26, D; Fig. 91, D) and measure 500–750 μm in length and 460–700 μm in diameter. They are sometimes provided with short calcars which are 40–110 μm long. Liberated carpospores are deep red and 90–110 μm in diameter (Pl. 25, A).

Tetrasporangia are formed on short branchlets which issue from the upper portion of ordinary and adventitious branches. These tetrasporangial branchlets are not more specialized than the vegetative branches and are up to 2 mm in length and 300 μm in breadth (Pl. 27, D). They are placed in an alternate-distichous manner as are the vegetative branches. The tetrasporangia originate from pericentral cells and are provided with two cover cells (Fig. 92, C). Two tetrasporangia are formed on 5–15 successive segments of the branchlets and they are extended to congenitally-fused regions (Pl. 27, D; Fig. 92, B). This feature has not been observed in other species of *Odonthalia*. Tetrahedrally divided sporangia measure 150–170 μm $\times$ 140–160 μm. Liberated tetraspores are similar to the aforementioned carpospores except in size and measure 75–85 μm in diameter (Pl. 25, B).

Culture study: Unialgal cultures were obtained from excised apical tips of the indeterminate branches of sterile plants. Isolated tips were first cultured at 10°C, 14 : 10 LD for 6 months. They produced from their lowest portion rhizoids which grew into pseudoparenchymatous basal discs and their upper portion developed in a pattern quite similar to sporelings of *O. annae*, *O. corymbifera* and *O. macrocarpa*. Indeterminate lateral branches of the first order were regularly formed in an alternate-distichous manner from

every fourth segment of the primary axis (Fig. 90, A). Thus, the apical tips grew into plants similar in morphology to the parent plants. Secondary upright shoots were subsequently produced from the basal discs. However, reproductive organs were not observed on these plants. The effect of temperatures and photoperiods on the maturation was tested. The apices of the indeterminate branches of plants maintained at 10°C, 14 : 10 LD were cut into nearly uniform lengths of about 5 mm and transferred to seven other conditions : 5°C, 14 : 10 LD ; 5°C, 10 : 14 LD ; 10°C, 10 : 14 LD ; 14°C, 14 : 10 LD ; 14°C, 10 : 14 LD ; 18°C, 14 : 10 LD and 18°C, 10 : 14 LD. Five apices were placed under each condition These plants developed well under all conditions tested. The plants produced many secondary upright shoots, which developed in a pattern quite similar to the primary axis.

The plants cultured at 5°C, 10 : 14 LD and 5°C, 14 : 10 LD became mature and bore spermatangia and procarps on separate plants 8 months after transfer. Prior to the formation of the reproductive structures the plants produced many adventitious branches which issued usually from the marginal portion (PL. 25, M), sometimes from the flat portion. The spermatangia and procarps were borne on the uppermost portion of ordinary (Pl. 25, N, O) and adventitious branches (Fig. 90, G). The spermatangial branchlets were slightly broader than the parent branches (Pl. 25, N) and became yellowish white when mature. The spermatangia originated from the cortical cells of the branchlets.

The procarps were borne on fertile trichoblasts which were rose-colored. The fertile trichoblasts issued from the apical portion of narrower branches than the vegetative branches regularly in an alternate-distichous manner (Pl. 25, O ; Fig. 91, C). The procarps originated from the suprabasal segment of the trichoblasts. The carpogonial branch was formed from the last produced pericentral cell, which functioned as the supporting cell, on the adaxial side of the fertile branchlets. It consisted of four cells and was surrounded by well developed pericarp before fertilization (Fig. 91, C). The sterile cell groups were indistinguishable from the vegetative cells of pericarps. The basal segment of the fertile branchlets becomes structured quite similar to the vegetative branches bearing it. As the pericarp developed, the monosiphonous portion of the fertile trichoblast elongated as in *O. annae*.

Both male and fermale gametangial plants cultured at 5°C, 10 : 14 LD and 5°C, 14 : 10 LD were transferred together to a large culture vessel (14.5 cm × 11.0 cm) containing 1200 *ml* of medium at the same conditions. However, carposporophyte development was not observed.

The plants cultured under the other conditions attempted did not form reproductive organs. This indicates that this alga at least requires a low

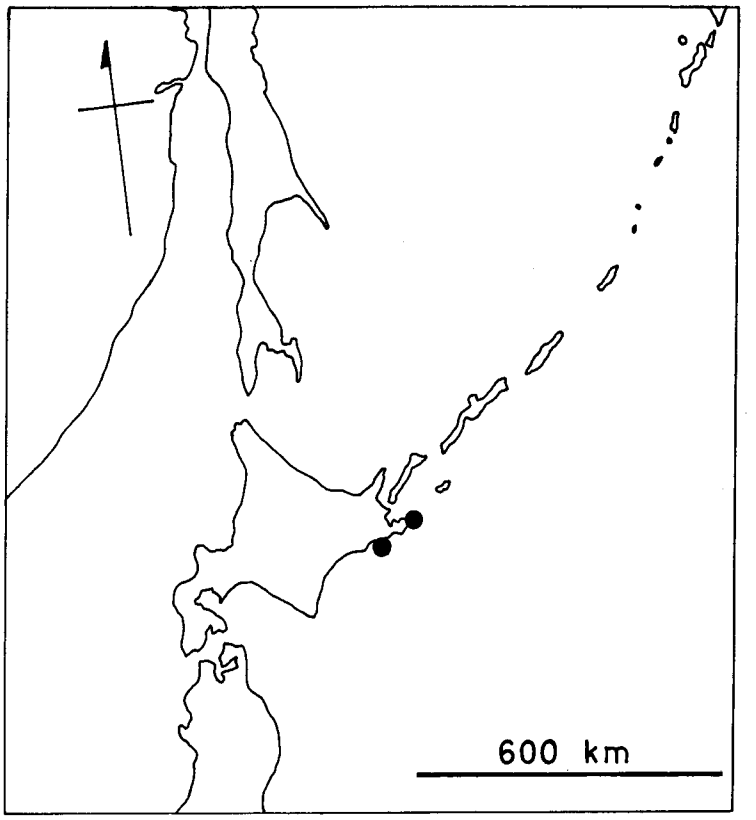

Fig. 93. Distribution of *Odonthalia yamadae* in Japan and adjacent waters.

seawater temperature for the formation of reproductive organs.

Isolated tetraspores and carpospores derived from field-collected plants were grown at 5°C, 14 : 10 LD and 10°C, 14 : 10 LD. The ontogeny of the tetrasporelings are shown in Plate 25, C-L. The developmental pattern is similar to those of *O. annae*, *O. corymbifera* and *O. macrocarpa*. After 2 months, the cultures were heavily contaminated by a species of *Ulva*. Then, the cultures were terminated.

Geographic distribution: In Hokkaido this alga is found along the east coast where it is under the influence of the Oyashio Current. Fig. 93 is based on our collections and represents the present known range of this alga.

Taxonomic discussion

In Japan this alga has been confused with *Odonthalia kamtschatica* (RUPRECHT) J. AGARDH (YAMADA and TANAKA, 1944 a ; YAMADA and KINO-

SHITA, 1950; SEGAWA, 1956). The latter alga was described by RUPRECHT (1850) on the basis of material collected at Petropavlovsk (St. Petri et Pauli), Awacha Bay, south-east coast of Kamchatka Peninsula under the name *Atomaria kamtschatica*. It was transferred to *Odonthalia* by J. AGARDH (1863). That species is characterized by having many expansive branches with conspicuous midribs, urceolate cystocarps with long calcars borne on narrowly tapering branches and arranged in a flexuose-racemose manner (RUPRECHT, 1850; MASUDA and YAMADA, 1981). Although the alga in question is closely related to *O. kamtschatica* on the basis of these taxonomic features, it differs from the latter in having barrel-shaped or broadly ovoid cystocarps without conspicuous calcars. In addition, procarp-bearing branchlets of *O. kamtschatica* are polysiphonous (MASUDA, 1981 a), whereas those of the alga are monosiphonous and can be called fertile trichoblasts. These reproductive features have taxonomic significance at the species level as pointed out earlier (MASUDA and YAMADA, 1981).

The alga under discussion is somewhat similar to *O. lyallii* in that they possess monosiphonous procarp-bearing branchlets and ovoid cystocarps arranged in a flexuose-racemose manner (HARVEY, 1862; MASUDA, 1981 a). However, the alga is distinguished from *O. lyallii* in that the latter has neither narrowly modified branches bearing cystocarps nor tetrasporangia of which formation extended to congenitally-fused regions. Thus, the alga in question is different from all the known species of this genus and is erected into a new species, *Odonthalia yamadae*. This specific epithet memorializes the late Professor Emeritus Yukio YAMADA of Hokkaido University.

Discussion of the species of *Odonthalia*

In this paper two new species are added to the genus. At present twelve species[1] are assignable to *Odonthalia*: 1) *O. dentata* (LINNAEUS) LYNGBYE (1819), the type species, 2) *O. corymbifera* (GMELIN) GREVILLE (1830), 3) *O. lyallii* (HARVEY) J. AGARDH (1863), 4) *O. ochotensis* (RUPRECHT) J. AGARDH, 5) *O. kamtschatica* (RUPRECHT) J. AGARDH (1863), 6) *O. floccosa* (ESPER) FALKENBERG (1901), 7. *O. washingtoniensis* KYLIN (1925), 8) *O. annae* PERESTENKO (1973), 9) *O. setacea* (RUPRECHT) PERESTENKO (1977), 10) *O. kawabatae* MASUDA (1981 b), 11) *O. macrocarpa* MASUDA (present paper), and 12) *O. yamadae* MASUDA (present paper). In addition to the last mentioned two species, *O. corymbifera* and *O. annae* are described in this paper. Furthermore, I have examined herbarium or liquid-preserved specimens of

1) *Odonthalia aleutica* (MERTENS ex C. AGARDH) J. AGARDH (1841) is excluded from the list on account of its uncertain status (see, p. 342).

other eight species (MASUDA, 1981 a, 1981 b; MASUDA and YAMADA, 1980, 1981). The possible taxonomic relationships among the species are discussed below.

O. annae, *O. corymbifera*, *O. macrocarpa* and *O. yamadae* are similar to each other in the juvenile stage of the sporelings (Pl. 19, C–K; 21, D–I; 23, D–P; 25, C–L). The sporelings produce regularly first order branches in an alternate-distichous manner. Thus, from the ontogenetic point of view, their developmental patterns of the sporelings are closely related to each other. In more advanced stage the species are characterized as follows. In *O. annae* the sporelings do not grow wide and become narrowly compressed thalli, whereas in *O. corymbifera*, *O. macrocarpa* and *O. yamadae* the sporelings grow wide and become flat thalli. In further advanced stages *O. macrocarpa* is characterized by insufficient development of the first order branches. The majority of the branches do not grow indeterminately, whereas those of the other three species grow expansively. In more developed stages *O. yamadae* is characterized by formation of midribs which develop conspicuously and grow into stout stems. In *O. corymbifera* evanescent midribs, which are faintly discernible in surface view, are formed, but they are not anatomically manifest. *O. annae* and *O. macrocarpa* do not form conspicuous or evanescent midribs. In further developed stages *O. corymbifera* is characterized by abundant formation of short adventitious branches.

Of the aforementioned vegetative features, the nature of midribs is taxonomically most important. The species of *Odonthalia* can be divided into two groups on the basis of this feature (MASUDA, 1981 b). One group is chracterized by conspicuously developed midribs. Eight species are included in this group: *O. dentata*, *O. lyallii*, *O. ochotensis*, *O. kamtschatica*, *O. setacea*, *O. washingtoniensis*, *O. kawabatae* and *O. yamadae* (the costate group). The other group has evanescent midribs or no midribs. For species are included in this group: *O. corymbifera*, *O. floccosa*, *O. annae* and *O. macrocarpa* (the ecostate group). *O. corymbifera* which possesses evanescent midribs may link the ecostate group to the costate group.

Although each species of the two groups is characterized by thallus breadth, developmental grade of branches, frequency of adventitious branches, thallus color and thallus substance, it is clearly characterized by the reproductive features. As to the position of cystocarps three distinct grades can be recognized in the two groups. (1) The cystocarps are borne on unmodified branches as found in *O. lyallii*, *O. ochotensis*, *O. setacea*, *O. kawabatae*, *O. floccosa* and *O. annae*. Those of *O. ochotensis* and *O. kawabatae* are restricted to the uppermost portion of branches and so they are arranged

in a corymbose manner. Those of the other four species are arranged in a flexuose-racemose manner. (2) The cystocarps are formed on narrowly tapering branches which are transformed from the distal portion of unmodified branches and they are arranged in flexuose-racemose manner in *O. kamtschatica* and *O. yamadae* or in a racemose manner in *O. macrocarpa*. (3) The cystocarps are borne on narrow and short modified branches and are arranged in a corymbose manner as found in *O. dentata*, *O. washingtoniensis* and *O. corymbifera*.

Similarly, as to tetrasporangial features, the following characterization is possible. (1) The tetrasporangial branchlets are borne on the uppermost portion of unmodified branchlets and are frequently aggregated as found in *O. lyallii* (MASUDA, 1981 a), *O. ochotensis* (RUPRECHT, 1850), *O. yamadae*, *O. setacea* (MASUDA, 1981 a), *O. kawabatae* (MASUDA, 1981 b), *O. floccosa*, *O. annae* and *O. macrocarpa*. These eight species are included in the first and second groups defined by the cystocarpic features. Of these, *O. yamadae* is characterized by the tetrasporangial branchlets of which the sporangium formation is extended to congenitally-fused region. (2) The tetrasporangial branchlets are borne on narrow and short modified branches in *O. dentata*, *O. washingtoniensis* and *O. corymbifera*. This group corresponds to the third group defined by the cystocarpic features. As to spermatangial features, at present a clear characterization is impossible on account of insufficient information.

According to these characterization, three pairs of species closely similar to each other are recognized in the costate group: *O. dentata* and *O. washingtoniensis*, *O. lyallii* and *O. setacea*, *O. ochotensis* and *O. kawabatae*; and one pair in the ecostate group: *O. floccosa* and *O. annae*. Each species of the three pairs in the costate group is characterized by the shape and dimension of cystocarps (MASUDA, 1981 a; MASUDA and YAMADA, 1981). The cystocarps of *O. dentata* are pitcher-shaped and provided with calcars, whereas those of *O. washingtoniensis* are almost globose and not provided with calcars. The cystocarps of *O. lyallii* are ovoid, but those of *O. setacea* are urceolate and more larger than the former. The cystocarps of *O. ochotensis* are urceolate and small, whereas those of *O. kawabatae* are broadly ovoid and about twice the size of the former. However, *O. lyallii* and *O. setacea* are closely related to each other in other respects. Further experimental analysis of the taxonomic features of the two species is necessary (MASUDA, 1981 a). *O. floccosa* and *O. annae* have large semiglobose cystocarps both of which show similar ranges of dimension. They only recognizable difference between the two cystocarps is the presence of calcars in *O. annae*. Furthermore, *O. floccosa* differs from *O. annae* in having

fasciculate spermatangial branchlets (SETCHELL and GARDNER, 1903).

Systematic remarks of the tribe Rhodomeleae

The tribe Rhodomeleae now includes four genera, *Rhodomela* C. AGARDH (1822), *Odonthalia* LYNGBYE (1819), *Beringiella* WYNNE (1980) and *Neorhodomela* MASUDA (present paper). The possible taxonomic relationships among the genera are discussed below.

The branching manner in *Rhodomela*, *Beringiella* and *Neorhodomela* is spiral, whereas that in *Odonthalia* is alternate-distichous. In this connection upright thalli of *Odonthalia* are compressed to flat, but those of the other three genera are terete. This is the most conspicuous feature distinguishing *Odonthalia* from the other genera. However, in the fertile branchlets of *Odonthalia* the transition from alternate-distichous to spiral branching is present and it shows an affinity to the other three genera. This type of transition occurs in *Pterosiphonia* belonging to the Polysiphonioideae, in which the branching is primarily alternate-distichous but the spermatangial branchlets produced at the tip of branches are mostly generated in a spiral manner (HOMMERSAND, 1963; MASUDA, 1973 a). A tendency to shift from an alternate-distichous to a spiral branching is not an uncommon occurrence in closely allied genera of the Rhodomelaceae (HOMMERSAND, 1963). It is supposed that the spiral branching may appear to be a secondary condition derived from an alternate-distichous branching.

Vegetative trichoblasts are present in *Rhodomela* and *Neorhodomela*, but they are entirely lacking in *Odonthalia* and *Beringiella*. The vegetative trichoblasts of *Rhodomela* and *Neorhodomela* are formed on the main axis at the sporeling stage and later, on the growing apex of younger branches. They are regularly formed on every segment and ultimately replaced by lateral branches. The trichoblasts of *Rhodomela* are arranged in a spiral manner, whereas those of *Neorhodomela* are arranged in a zigzag manner in two rows along the abaxial convex side of the main axis and lateral branches. However, their occurrence is somewhat variable and characterizes each species of the genera.

Spermatangia are produced on unmodified branches in *Rhodomela* and *Odonthalia*, whereas they are borne on modified branchlets (trichoblasts) in *Neorhodomela*. Those of *Beringiella* are unknown. The fertile trichoblasts of *Neorhodomela* are formed in a manner corresponding to that of vegetative trichoblasts. According to HOMMERSAND (1963), the former type of spermatangial branches is found in the most primitive genera of the Rhodomelaceae such as the subfamilies Bostrychioideae and Rhodomeloideae,

whereas the latter type is found in the subfamily Polysiphonioideae. In the course of evolution, the spermatangial branches may tend to become restricted to one kind of modified special branch. The spermatangial branches of *Neorhodomela* are considered to be the most advanced type shared with the Polysiphonioideae. *Rhodomela confervoides* also has the spermatangial branchlets borne on trichoblasts in addition to those on unmodified branches and shows an affinity with *Neorhodomela.*

Procarps are formed on fertile trichoblasts in *Rhodomela, Beringiella* and *Neorhodomela,* whereas they are formed on reduced polysiphonous branchlets in *Odonthalia* except in some species. There is a general tendency in the course of evolution for the procarps to become restricted to one kind of modified special branch, or even to be localized on a particular segment or a particular pericentral cell, as pointed out by HOMMERSAND (1963). Furthermore, the procarp-bearing trichoblasts tend to become branched and well developed. This tendency is found in the tribe Rhodomeleae. The reduced polysiphonous procarp-bearing branchlet of *Odonthalia* is the most primitive in the tribe. The reduced monosiphonous unbranched procarp-bearing branchlet of *Odonthalia lyallii* (MASUDA, 1981 a), *O. setacea* (MASUDA, 1981 a), *O. annae* and *O. yamadae* can be recognized as a prototype of female trichoblasts. These trichoblasts are transitional from reduced procarp-bearing polysiphonous branchlets to reduced unbranched female trichoblasts of *Beringiella labiosa* (WYNNE, 1980), *Rhodomela confervoides* and *Neorhodomela oregona.* Frequent occurence of coupled procarps on a single branchlets in *Neorhodomela oregona* and *Odonthalia corymbifera* is a more primitive condition.

Tetrasporangia are borne in pairs per segment in *Rhodomela, Neorhodomela* and *Odonthalia,* whereas they are borne solitarily per segment in *Beringiella* (WYNNE, 1980). In the evolution of the Rohodomelaceae there has been a tendency toward reduction in the number of tetrasporangia per segment (HOMMERSAND, 1963). In this connection the production of a single tetrasporangium per segment in *Beringiella* is the most advanced condition.

Dorsiventrality is present only in *Neorhodomela* and characterizes the genus from *Rhodomela, Odonthalia* and *Beringiella.* The dorsiventrality is expressed by curved sporelings and by the arrangement of vegetative and fertile trichoblasts.

Thus, these four genera are distinctly defined at the generic level. They are related to each other in several features mentioned above and form an assemblage among the family Rhodomelaceae. I think that this assemblage should be treated as the tribe Rhodomeleae. Judging from the general tendency of the evolutionary lines of the Rhodomelaceae for basic characters

such as branching manner, trichoblasts, spermatangial branches, procarp-bearing branches, production number of tetrasporangia per segment and dorsiventrality, the genus *Odonthalia* may be the most primitive and the genus *Neorhodomela* may be the most advanced in the Rhodomeleae.

HOMMERSAND (1963) revised the taxonomic system of the Rhodomelaceae, which was established by SCHMITZ and FALKENBERG (1897) and FALKENBERG (1901) and had been accepted by later phycologists for more than half a century. He refered to SCHMITZ and FALKENBERG's subdivisions, which had been treated as subfamilies, as tribal ranks and newly established three subfamilies as follows.

(1) Bostrychioideae including a single tribe Bostrychieae.
(2) Rhodomeloideae comprising 4 tribes, Rhodomeleae, Lophothalieae, Heterocladieae, and Polyzonieae.
(3) Polysiphonioideae composed of 8 tribes, Pterosiphonieae, Streblocladieae, Polysiphonieae, Lophosiphoniae, Pleurostichidieae, Amansieae, Chondrieae, and Laurencieae.

In addition, the tribe Rhodolachneae was established by WOMERSELY (in WOMERSELY and BAILEY, 1970). The tribe shows some similarities with the Rhodomeleae and Bostrichieae, but its subfamilial status has not been proposed. The taxonomic relationships among the tribes are discussed in detail by HOMMERSAND (1963). According to him, the Rhodomeleae is the most primitive among the Rhodomeloideae. However, the discovery of several new characters of the genus *Neorhodomela* suggests that the position of the Rhodomeleae should be reconsidered.

The Rhodomeloideae is circumscribed as follows: (1) the procarps are borne on determinate polysiphonous lateral branches, which generally lack trichoblasts, and the procarps may be formed on any segment except the basal one and are frequently borne in rows on successive segments; (2) the spermatangia are not usually associated with trichoblasts, and in genera in which they are, such as *Lophocladia* and *Wrightiella*, the spermatangia are formed on a regenerated polysiphonous branch that is borne laterally on a trichoblast; (3) the vegetative trichoblasts, when present, are persistent and conspicuously pigmented; (4) the tetrasporangia are produced near the tips of branches, which become swollen, or on special stichidioid branches of limited growth, but not ordinarily along the axis of unspecialized indeterminate branches (HOMMERSAND, 1963). In contrast, the Polysiphonioideae is circumscribed as follows: (1) the fertile determinate branches terminate in a trichoblast, and a single procarp is produced on the suprabasal segment;

(2) the spermatangial branch is initiated as a trichoblast, and the polysihonous axis is pedicellate on a short, monosiphonous stalk ; (3) vegetative trichoblasts, when present, are deciduous and usually colorless ; and (4) the tetrasporangia are distributed along the axes of ordinary indeterminate branches, or on relatively unspecialized determinate branches (HOMMERSAND, 1963).

In *Rhodomela* and *Neorhodomela* the procarp is borne on the suprabasal segment of the trichoblasts as in the Polysiphonioideae. In *Neorhodomela* the spermatangia are exclusively produced on the trichoblast. Although the vegetative trichoblasts of *Rhodomela* and *Neorhodomela* are pigmented, they are not persistent but are deciduous. These important characters, especially those of *Neorhodomela*, ally the tribe Rhodomeleae more with the Polysiphonioideae than with any other tribes of the Rhodomeloideae.

The dorsiventrality which is expressed by the curved sporelings and by the arrangement of the vegetative and fertile trichoblasts in *Neorhodomela* bears resemblance to the so-called dorsiventral species belonging to the tribe Amansieae and Lophosiphonieae, both of which are placed in the Polysiphonioideae. *Halopithys pinastroides* and *Rytipholoea tinctoria* (the Amansieae), and *Ctenosiphonia hypnoides* and *Lophosiphonia cristata* (the Lophosiphonieae) have dorsal trichoblasts arranged in a single row along the median line of the convex side (FALKENBERG, 1901 ; BØRGESEN, 1915-20, 1930). The trichoblast arrangement of *Neorhodomela* does not coincide with that of these dorsiventral species. The trichoblasts of *Neorhodomela* are arranged in two rows on the dorsal convex side. This suggests that there is an affinity among the Rhodomeleae, Amansieae and Lophosiphonieae. On the other hand, this may indicate an evidence of parallel evolution between the Rhodomeloideae and the Polysiphonioideae.

On the other hand, the genus *Odonthalia* resembles the tribe Pterosiphonieae in having alternate-distichous branching and showing congenital fusion between the segments of the lateral branches and the main axis. The reduced female trichoblasts of some species of *Odonthalia* resemble those of *Pterosiphonia bipinnata* (MASUDA, unpublished). In other basic characters such as the nature of pericentral cells and the spermatangial branches, *Odonthalia* differs from the Pterosiphonieae. This may also indicate an evidence of parallel evolution between the two subfamilies.

The Rhodomeleae differs from the tribes of the Polysiphonioideae as well as the other tribes of the Rhodomeloideae in thallus structure as is well known. In the Rhodomeleae the pericentral cells are divided transversely into tiers and a pit-connection is retained between the central cell and the upper pericentral cell. In this respect, the Rhodomeleae resembles the Bostrychioideae and Rhodolachneae both in which the pericentral cells are

also divided transversely into tiers. However, in the latter two tribes, the pit-connection is retained between the central cell and the lower pericentral cell. The occurrence of the spermatangia on unspecialized polysiphonous branches in *Rhodomela* and *Odonthalia* allies the Rhodomeleae with the Bostrychioideae and the Lophothalieae of the Rhodomeloideae. Furthermore, the alternate-distichous branching of *Odonthalia* allies the Rhodomeleae with the Bostrychioideae. Thus, the status of the Rhodomeleae among the Rhodomelaceae is unique. The Rhodomeleae shows a great diversity as if it linked the three subfamilies to each other.

The following synoptical key is given for the taxa examined.

1. Thalli terete, with spirally arranged branches and trichoblasts . . . . . 2. *Rhodomela*
1. Thalli terete, with spirally arranged branches and dorsal trichoblasts . . . . . 5. *Neorhodomela*
1. Thalli compressed to flat, with alternate-distichously arranged branches . . . . . 8. *Odonthalia*
   2. Thalli arising from an expanded basal disc 3
   2. Thalli arising from a small basal disc and stolons 4
3. Main axes stout, becoming gradually more slender upward . . . . . *R. confervoides*
3. Main axes thick only at lower portion, tapering abruptly upward . . . . . *R. lycopodioides* f. *tenuissima*
   4. Simple determinate branchlets short, less than 2 mm in length, thorn-like . . . . . *R. sachalinensis*
   4. Simple determinate branchlets long, more than 1 cm in length, subulate . . . . . *R. teres*
5. Main axes covered with indeterminate branches 6
5. Main axes covered with simple or bifurcate determinate branchlets 7
   6. Adventitious branches with indeterminate growth; vegetative trichoblasts numerous throughout the life history . . . . . *N. munita*
   6. Adventitious branches with limited growth; vegetative trichoblasts formed just prior to reproductive maturity . . . . . *N. oregona*
7. Axillary adventitious branches with indeterminate growth; simple determinate branchlets slender, up to 500 μm in diameter . . . . . *N. aculeata*

7. Axillary adventitious branches with limited growth; simple determinate branchlets thick, up to 800–1000 μm in diameter . . . . . *N. larix*
   8. Thalli with conspicuous midribs . . . . . *O. yamadae*
   8. Thalli without conspicuous midribs 9
9. Branches narrow, less than 2 mm in breadth . . . . . *O. annae*
9. Branches broad, more than 4 mm in breadth 10
   10. Thalli with evanescent midribs; cystocarps and tetrasporangial branchlets borne on narrow and short modified branches; cystocarps small, less than 500 μm in diameter . . . . . *O. corymbifera*
   10. Thalli without evanescent midribs; cystocarps and tetrasporangial branchlets borne on narrowly tapering branches or on unmodified branches; cystocarps large, more than 1300 μm in diameter . . . . . *O. macrocarpa*

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Summary

The taxonomy of the tribe Rhodomeleae (Rhodomelaceae, Rhodophyta) has been a persistent unresolved problem because of the extremely complicated morphology. The present study was undertaken based on field-collected and cultured plants to evaluate the vegetative and reproductive features used for the taxonomic criteria by comparing these plants. In this work the Japanese species were chiefly investigated. The type species of *Rhodomela*, *R. confervoides* from France, and *Neorhodomela larix* from the North America were added for comparison with the Japanese species.

The following new taxa and new combinations were reported: *Rhodomela sachalinensis* MASUDA, sp. nov., *R. teres* (PERESTENKO) MASUDA, comb. nov., *Neorhodomela* MASUDA, gen. nov., *N. munita* (PERESTENKO) MASUDA, comb. nov., *N. aculeata* (PERESTENKO) MASUDA, stat. et comb. nov., *N. larix* (TURNER) MASUDA, comb. nov., *N. oregona* (DOTY) MASUDA, comb. nov., *Odonthalia macrocarpa* MASUDA, sp. nov., and *O. yamadae* MASUDA, sp. nov.

The taxonomic relationships between the species of each genus have been discussed on the basis of comparative morphology.

The genus *Odonthalia* was shown to be the most primitive and the *Neorhodomela* to be the most advanced in the Rhodomeleae as judged from the general tendency of the evolutionary lines of the Rhodomelaceae.

In laboratory culture experiments, the four species of *Odonthalia* showed a narrow range of seawater temperatures and day lengths for sporogenesis or gametogenesis and the four species of *Neorhodomela* showed a wide range of these corresponding to the observed reproductive phenology, respectively.

The geographic distribution of the ten Japanese species was shown to

be related to the ocean currents.

The results of interspecific hybridization among isolates of the four species of *Neorhodomela* were negative. Only intraspecific crosses were positive. The Japanese isolate of *N. oregona* hybridized with the North American isolate.

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Plate 1

Rhodomela confervoides (HUDSON) SILVA

A, field-collected plant; B–D, cultured plants grown at 14°C, 14:10 LD.

A. Tetrasporangial plant collected at Ile Verte, Roscoff, on March 21, 1973 (parent plant for culture study, *Masuda* 13766 leg. T. YOSHIDA).

B. Spermatangial plant (2 and a half months old, *Masuda* 13768).

C. Procarpic plant (2 and a half months old, *Masuda* 13769).

D. Cystocarpic plant (4 and a half months old, *Masuda* 13777).

Scale in D applies also to B & C.

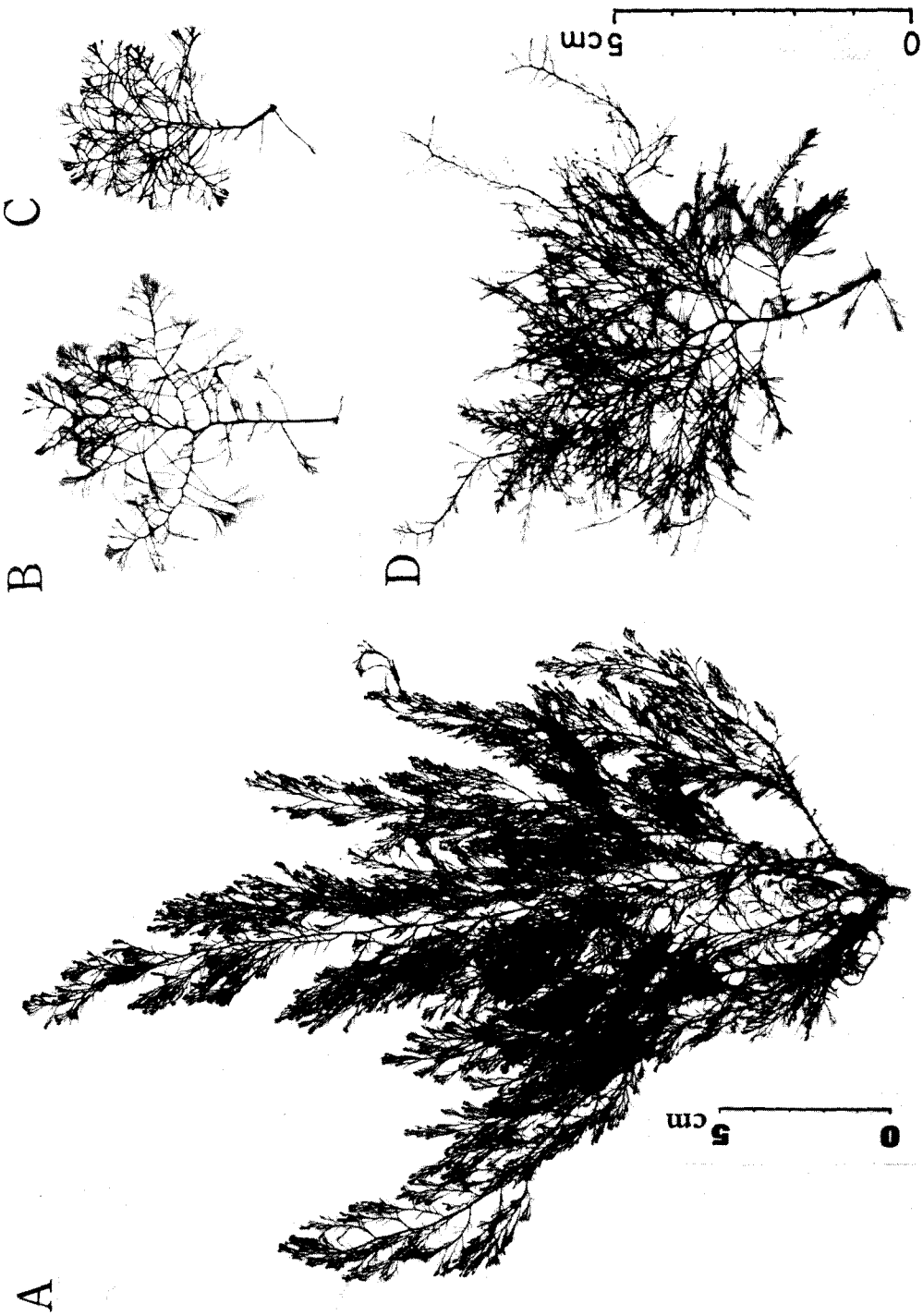
A
B
C
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Plate 2

Rhodomela confervoides (HUDSON) SILVA

A–O, cultured plants grown at 10°C, 14 : 10 LD ; P, field-collected plant.

A. Portion of a tetrasporangial branch.

B. Tetraspore.

C–H. Development of tetrasporelings : C, one day old ; D, three days old ; E, five days old ; F, seven days old ; G, fourteen days old ; H, apical portion of a 21-day-old sporeling.

I–J. Spermatangial branches borne on a 2 and half months old plant.

K. Procarps borne on a 2 and half months old plant.

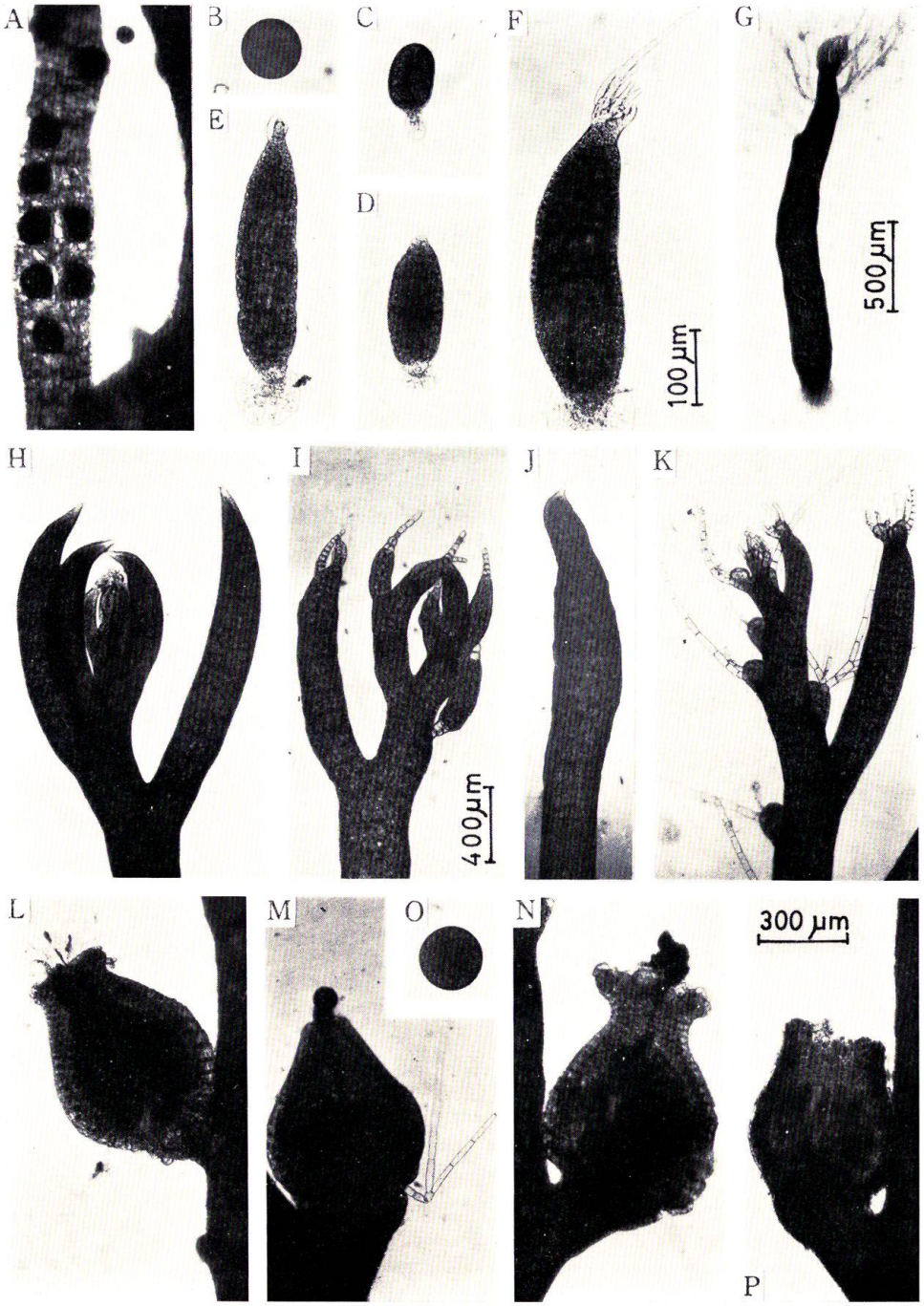
L–N. Mature cystcarps with trichoblasts formed on a 4 and half months old plant.

O. Carpospore.

P. Mature cystocarp.

(Photographed from living material except P.)

Scale in F applies also B–E & O ; scale in I applies also to J ; scale in P applies also to A, H, K, & L–N.


A
B
C
D
E
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G
100 µm
500 µm
H
I
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300 µm
P

Plate 3

Rhodomela sachalinensis MASUDA

A. Tetrasporangial plant (Holotype, SAP 031874=*Masuda* 6590).

B. Tetrasporangial plants collected at Higashisoya, Sakhalin on August 29, 1929 (*Tokida* 899).

C. Spermatangial plant (epiphytized by *Ceramium kondoi*) collected at Yoman, Sakhalin on July 30, 1935 (TOKIDA herbarium).

D. Tetrasporangial plants collected at Hanasaki on September 27, 1970 (*Masuda* 9504).

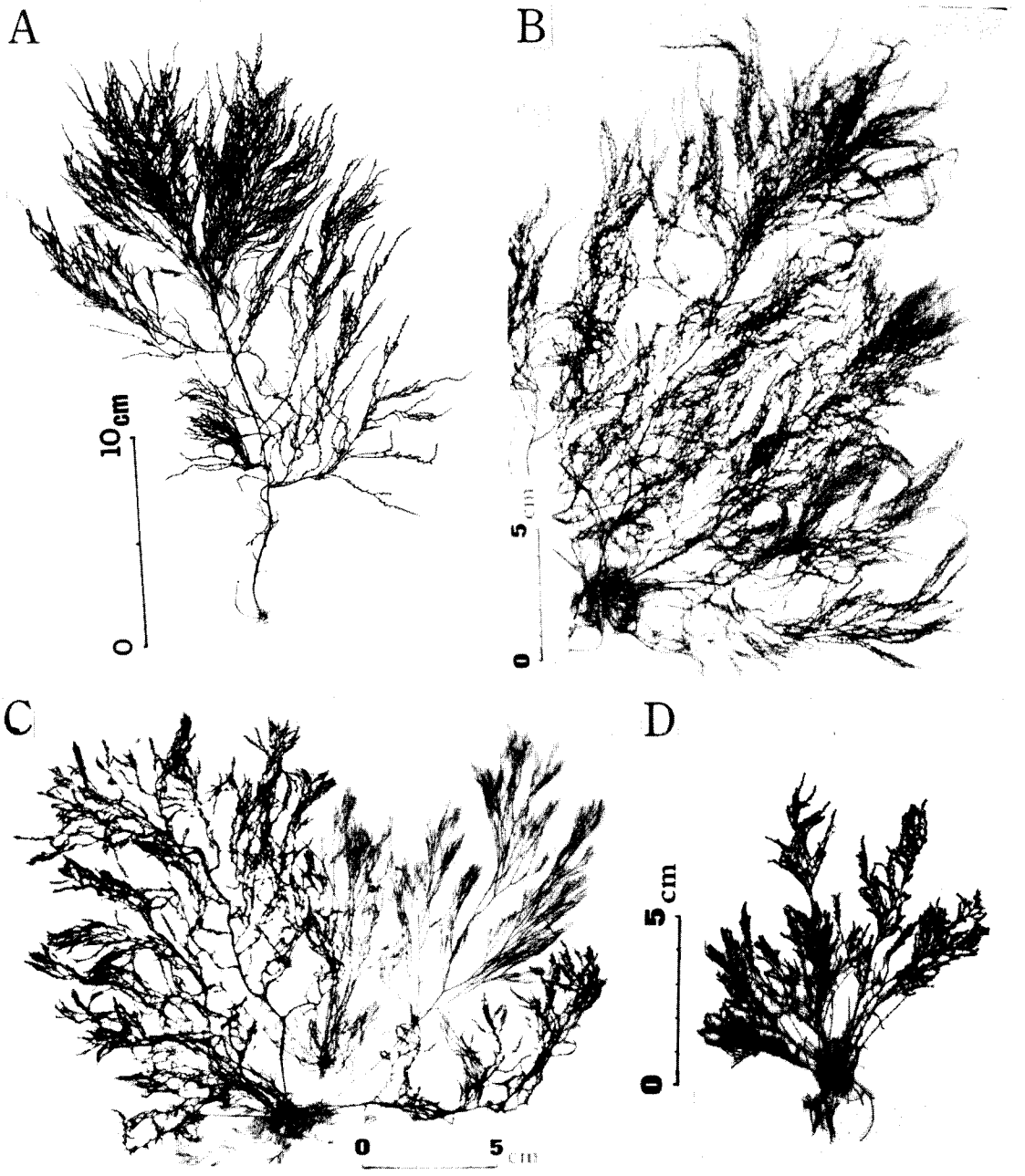

A
10cm
0
B
5 cm
0
C
0
5 cm
D
5 cm
0

Plate 4

Rhodomela sachalinensis MASUDA

A, B, field-collected plants; C–O, cultured plants grown at 14°C, 14 : 10 LD.

A. Carpospore.

B. Tetraspore.

C–K. Development of tetrasporelings: C, one day old; D, E, three days old; F, five days old; G, seven days old; H, I, ten days old, issuing trichoblasts; J, seventeen days old; K, one month old.

L. Trichoblasts borne on a 2-month-old plant.

M. Stolon developed on a 3-month-old plant.

N, O. Spermatangial branches borne on a 3-month-old plant.

(Photographed from living material except J & K.)

Scale in B applies also to A; scale in G applies also to C–F, H, I & L; scale in N applies also to O.

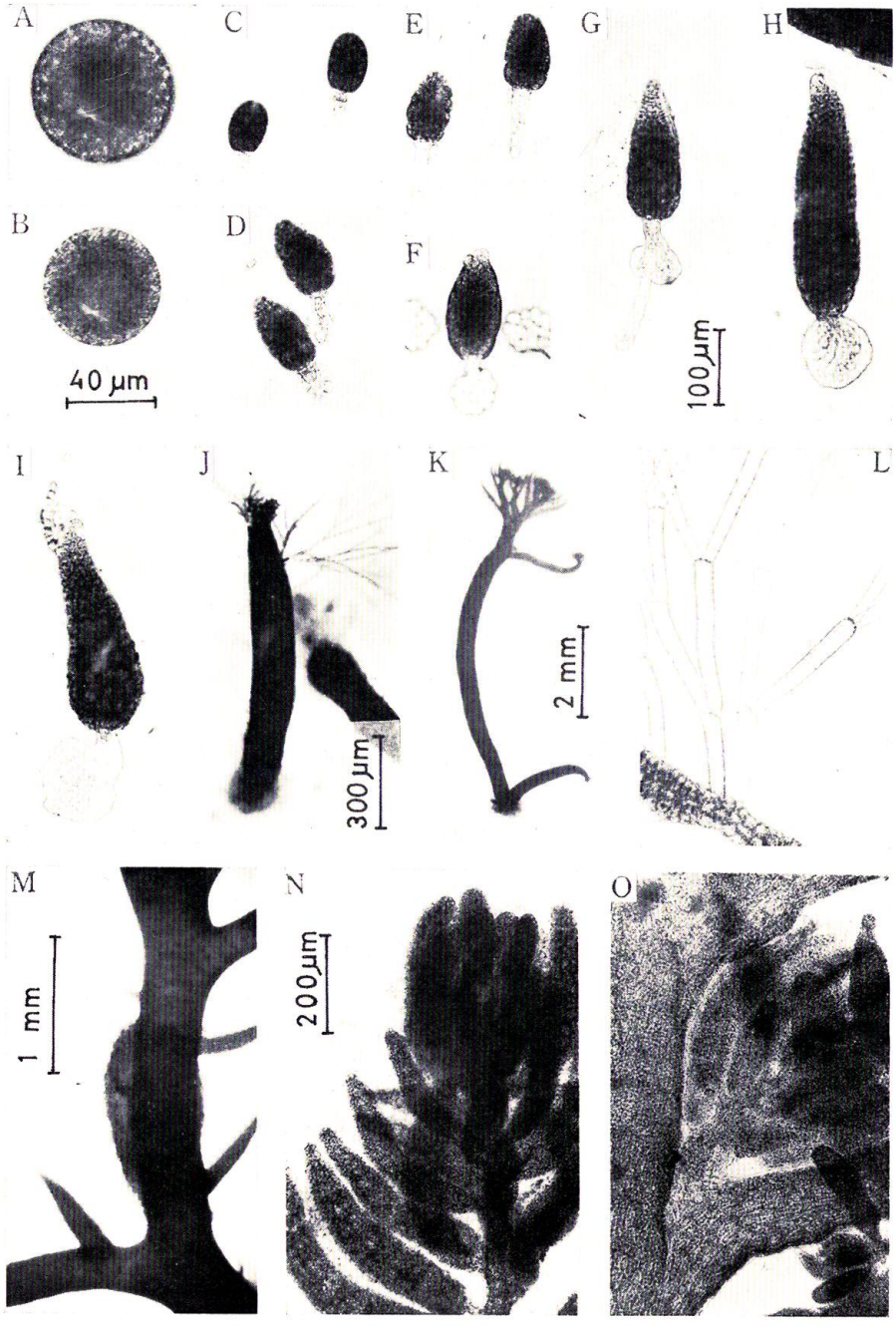

A
B
C
D
E
F
G
H
40 μm
100 μm
I
J
K
L
300 μm
2 mm
M
N
O
1 mm
200 μm

Plate 5

Rhodomela teres (PERESTENKO) MASUDA

A–D, field-collected plants; E–H, cultured plants.

A. Holotype specimen of *Rhodomela gracilis* YAMADA et NAKAMURA collected at Muroran on July 2, 1935 (cystocarpic, SAP 23366 leg. Y. NAKAMURA).

B. Tetrasporangial plant collected at Shakotan, Shikotan Island on July 28, 1934 (NAGAI herbarium in SAPA, as *Odonthalia floccosa*).

C. Spermatangial plant collected at Notoro, Sakhalin on April 26, 1937 (TOKIDA herbarium, as *Odonthalia floccosa*).

D. Sterile plant with proliferous branches (arrows) collected at Muroran on November 16, 1970 (*Masuda* 7851).

E–G. Two-month-old plants derived from carpospores: E, grown at 10°C, 10: 14 LD; F, grown at 10°C, 14: 10 LD; G, grown at 14°C, 14: 10 LD.

H. Six-month-old spermatangial plant grown at 14°C, 14: 10 LD for 2 month and then transferred to 10°C, 14: 10 LD.

Scale in E applies also to D & F–H.

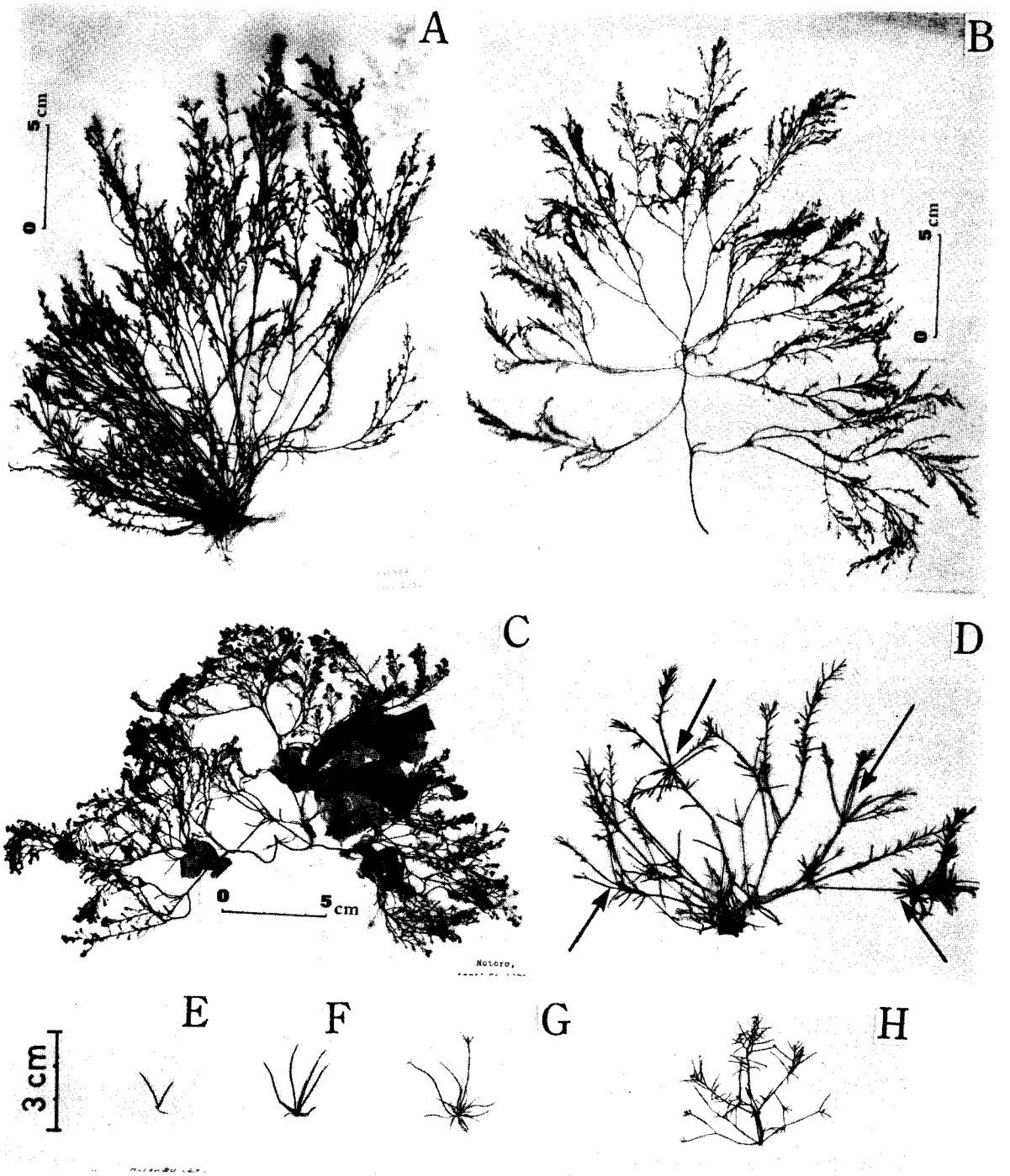

A
0
5cm
B
0
5cm
C
0
5cm
D
E
F
G
H
3cm

Plate 6

Rhodomela teres (PERESTENKO) MASUDA

A, B, field-collected plants; C–O, cultured plants.

A. Carpospore.

B. Tetraspore.

C–L. Development of tetrasporelings grown at 14°C, 14 : 10 LD: C, attached tetraspore; D, one day old; E, three days old; F, seven days old; G, fourteen days old; H, the same plant as G, showing a basal portion; I, one month old; J, apical portion of a one-month-old plant; K, apical portion of a 2-month-old plant, issuing a discoid rhizoid (arrow); L, stolon produced on a 2-month-old plant.

M. Spermatangial branches borne on a 6-month-old plant grown at 14°C, 14 : 10 LD for 2 months and then shifted to 10°C, 14 : 10 LD.

N. Procarps borne on a 6-month-old plant grown at 14°C, 14 : 10 LD for 2 months and then shifted to 10°C, 14 : 10 LD.

O. Tetrasporangial branches formed on a 10-month-old plant grown at 10°C, 14 : 10 LD.

(Photographed from living material except I & N.)

Scale in H applies also to A–F; scale in K applies also to G, J & L–O.

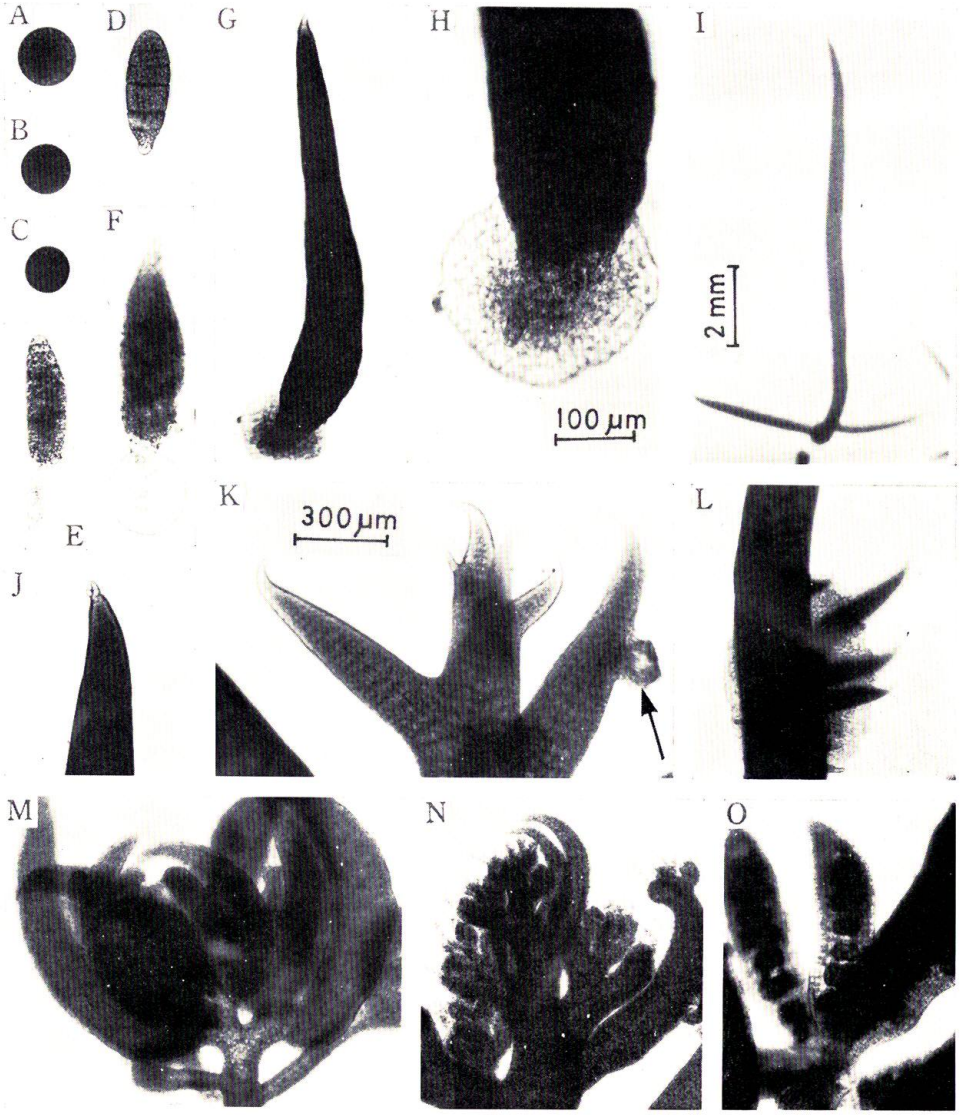

A
B
C
D
F
G
H
I
2 mm
100 µm
E
J
K
300 µm
L
M
N
O

Plate 7

Rhodomela confervoides (HUDSON) SILVA

A. Upper portion of an indeterminate branch of a tetrasporangial plant, showing trichoblasts.

Rhodomela sachalinensis MASUDA

B. Lower portion of an indeterminate branch of a tetrasporangial plant.

C. Spermatangial branchlets formed on an axillary adventitious branch.

D. Spermatangial branchlets formed on the upper portion of an ordinary branch.

E. Tetrasporangial branchlets borne on an ordinary branch.

F. Tufted tetrasporangial branchlets borne adventitiously in the axil.

Rhodomela teres (PERESTENKO) MASUDA

G. Spermatangial branches formed on the uppermost portion of indeterminate branches.

H. Spermatangial branchlet borne on a determinate branchlet.

I. Tetrasporangial branchlets formed at the uppermost portion of an ordinary branch.

J. Tufted tetrasporangial branchlets formed adventitiously in the axil.

Scale in C applies also to D & H; scale in F applies also to E, I & J.

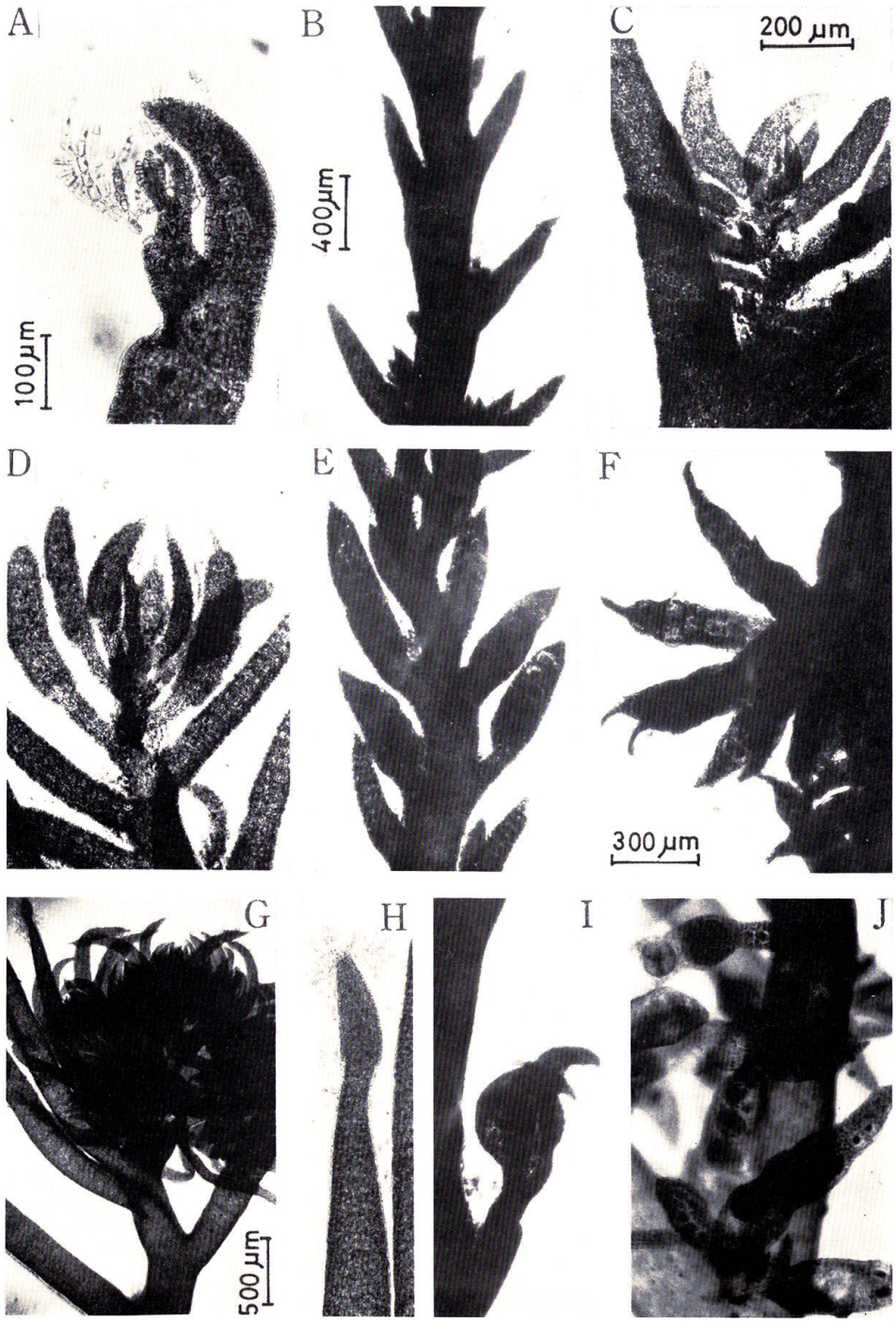

A
100 µm
B
400µm
C
200 µm
D
E
F
300 µm
G
500 µm
H
I
J

Plate 8

Cross-section (A, B, E–I & K–M) and longitudinal-section of thalli (C, D & J); A–C, F, G & I–L, field-collected plants; D, E, H & M, cultured plant.

Rhodomela confervoides (HUDSON) SILVA

A. Lower portion of an old main axis.

B. Middle portion of an axis of a proliferous branch.

C. Lower portion of an old main axis.

D, E. Lower portion of main axes of a 2-month-old plant grown at 14°C, 14 : 10 LD.

Rhodomela sachalinensis MASUDA

F. Lower portion of a main axis.

G. Stolon.

H. Lower portion of a main axis of a 4-month-old plant grown at 14°C, 14 : 10 LD.

Rhodomela teres (PERESTENKO) MASUDA

I, J. Lower portion of old main axes.

K. Stolon.

L. Determinate branchlet.

M. Lower portion of a main axis of a 14-month-old plant grown at 10°C, 14 : 10 LD.

Scale in A applies also to B, E–I & K–M; scale in C applies also to D & J.

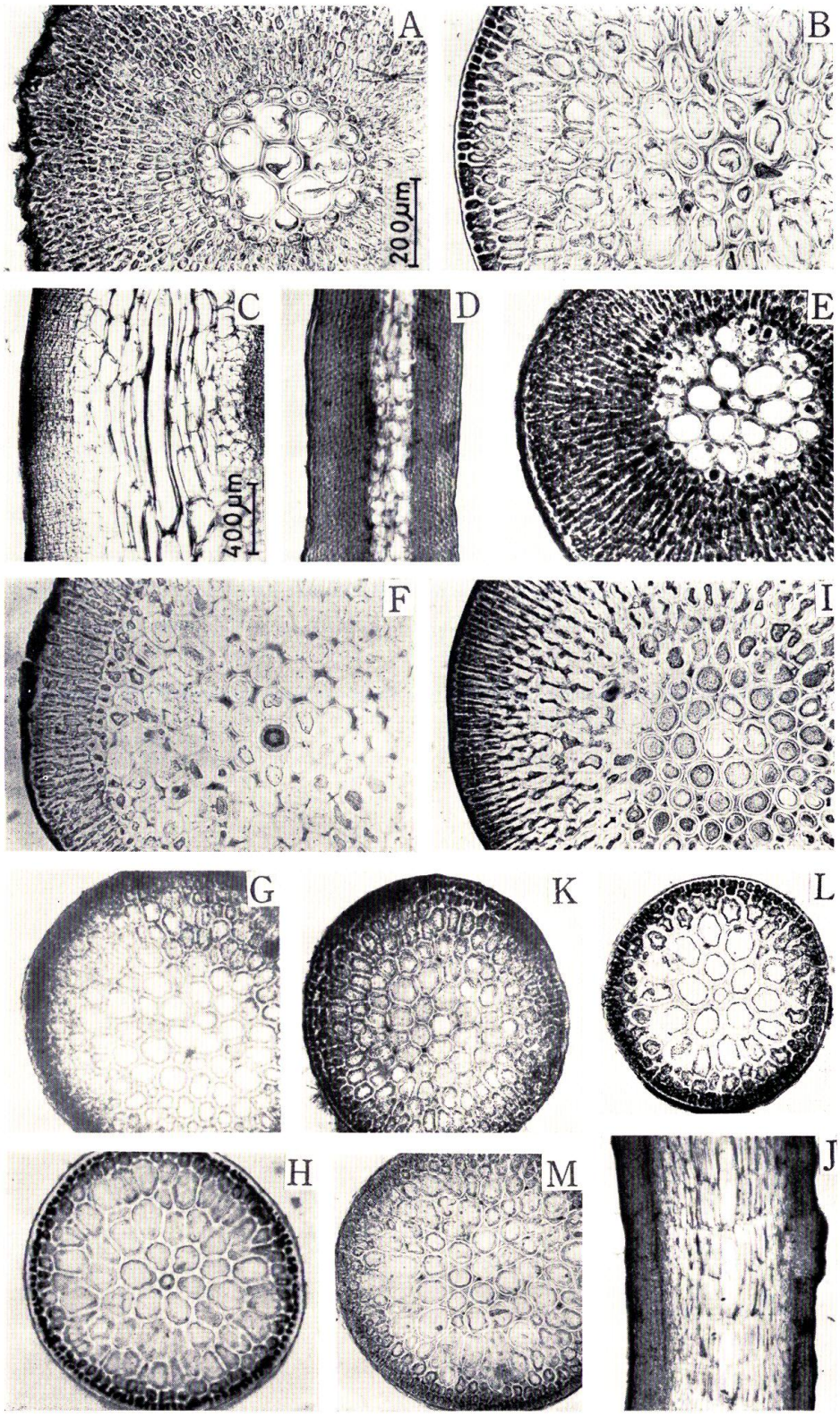

A
200μm
B
C
400μm
D
E
F
I
G
K
L
H
M
J

Plate 9

Neorhodomela munita (PERESTENKO) MASUDA

A, B, F & G, field-collected plants; C–E, cultured plants grown at 14°C, 14 : 10 LD.

A. Cystocarpic plant collected at Muroran on May 30, 1971 (*Masuda* 12575).

B. Spermatangial plant collected at Muroran on May 30, 1971 (*Masuda* 12469).

C. Spermatangial plant (2 months old, *Masuda* 12873).

D. Caytocarpic plant (3 months old, *Masuda* 12874).

E. Tetrasporangial plant (3 months old, *Masuda* 12875).

F. Sterile plants collected from Echigo Province in July 1908 (YENDO herbarium in TI).

G. Cystocarpic plant collected from Kaiba-to, Sakhalin on July 27, 1930 (TOKIDA herbarium).

Scale in C applies also to D & E; scale in F applies also to G.

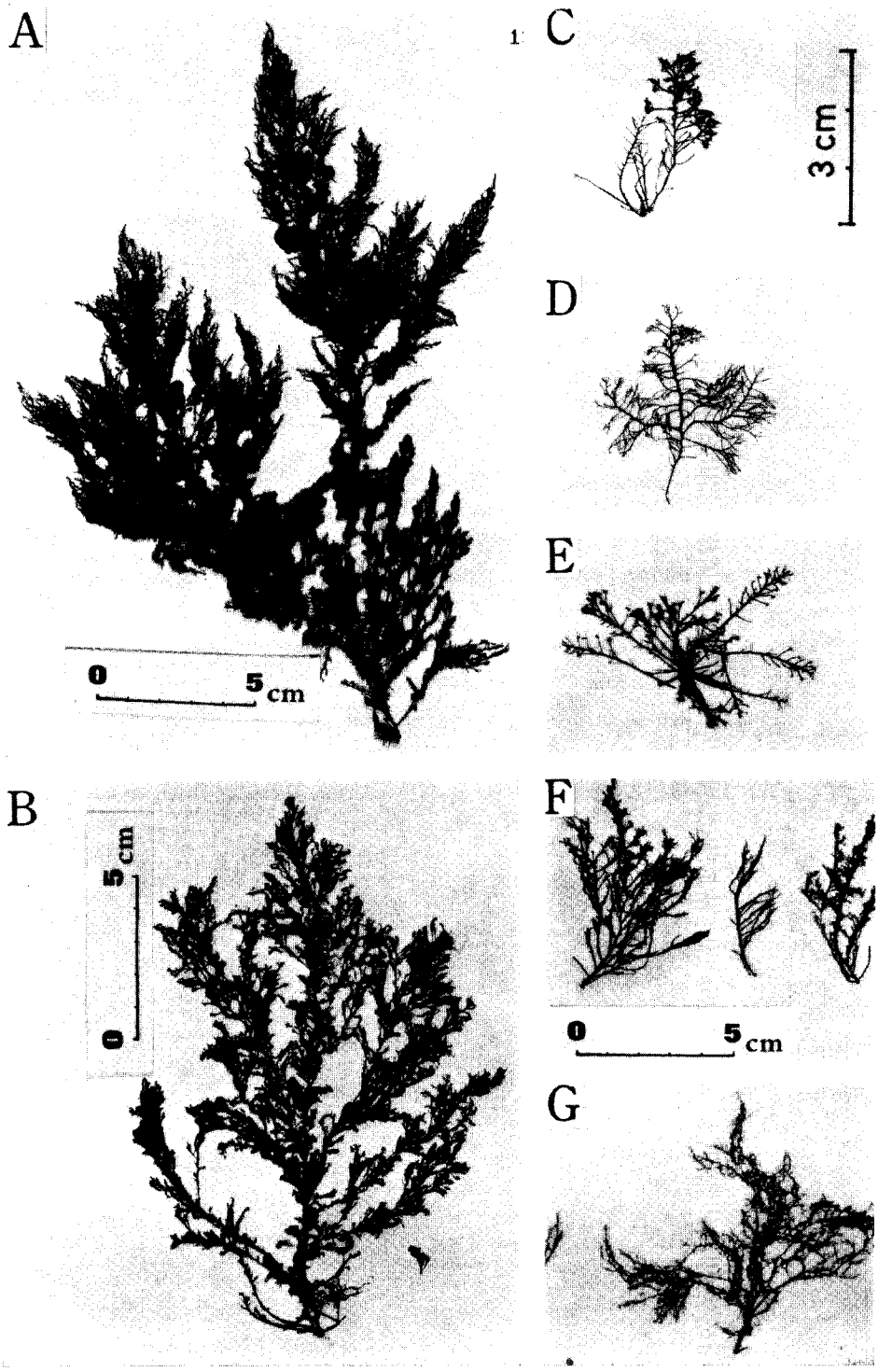

A
0
5 cm
C
3 cm
D
E
B
5 cm
0
F
0
5 cm
G

Plate 10

Neorhodomela munita (PERESTENKO) MASUDA

A, B, field-collected plants; C–Q, cultured plants grown at 14°C, 14 : 10 LD.

A. Carpospores.

B. Tetraspores.

C–L. Development of tetrasporelings: C, attached tetraspore; D, one day old; E, F, three days old; G, ten days old; H, I, fourteen days old; J, twenty-one days old; K, L, one month old.

M. Spermatangial branchlets borne on the abaxial side of branches (2 months old).

N, O. Procarps borne on the abaxial side of branchlets (2 months old).

P. Cystocarp borne on a 3-month-old plant.

Q. Tetrasporangial branches borne on a 2-month-old plant.

(Photographed from living material except K.)

Scale in B applies also to A, C–F, H & O; scale in G applies also to I, J, L–N, P & Q.

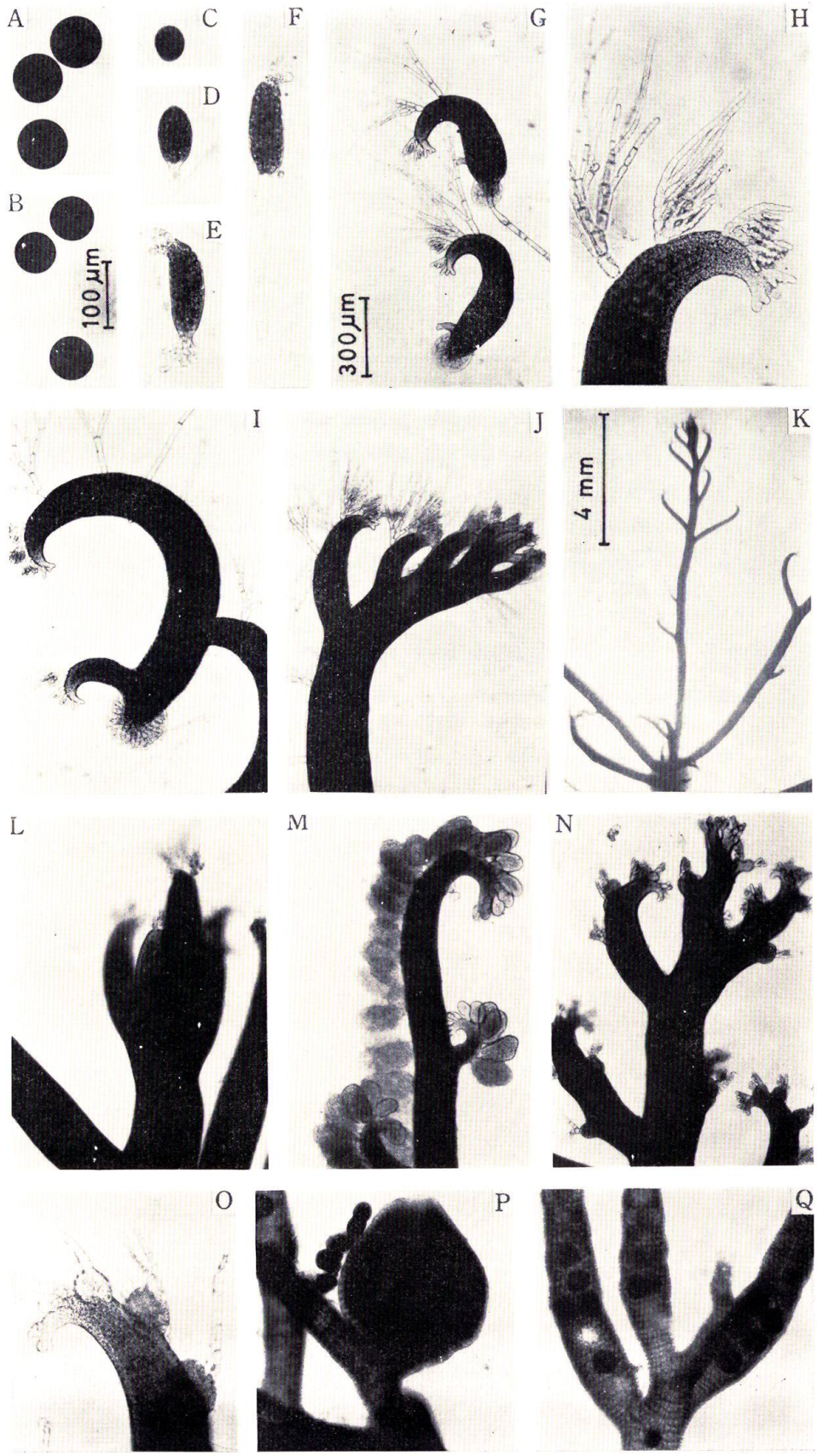

A
B
100 µm
C
D
E
F
G
300 µm
H
I
J
K
4 mm
L
M
N
O
P
Q

Plate 11

Neorhodomela aculeata (PERESTENKO) MASUDA

A, F, field-collected plants; B–E, cultured plants grown at 14°C, 14 : 10 LD.

A. Cystocarpic plant collected at Muroran on August 29, 1970 (parent for culture study, *Masuda* 13147).

B. Spermatangial plant (2 months old, *Masuda* 13211).

C. Procarpic plant (2 months old, *Masuda* 13212).

D. Cystocarpic plant (3 months old, *Masuda* 13229).

E. Tetrasporangial plant (2 months old, *Masuda* 13204).

F. Tetrasporangial plant collected at Utoro on October 27, 1968 (*Masuda* 6451).

Neorhodomela larix (TURNER) MASUDA

G. Tetrasporangial plant collected at Glacier Point, Vancouver Island on July 29, 1973 (*Masuda* 13779, leg. L. D. DRUEHL).

H. Tetrasporangial plant collected at Bodega Head, California on May 21, 1973 (*Masuda* 13778, leg. J. A. WEST).

I. Sterile plants collected at Lands End, California in January 1929 (YAMADA herbarium).

Scale in C applies also to B, D & E.

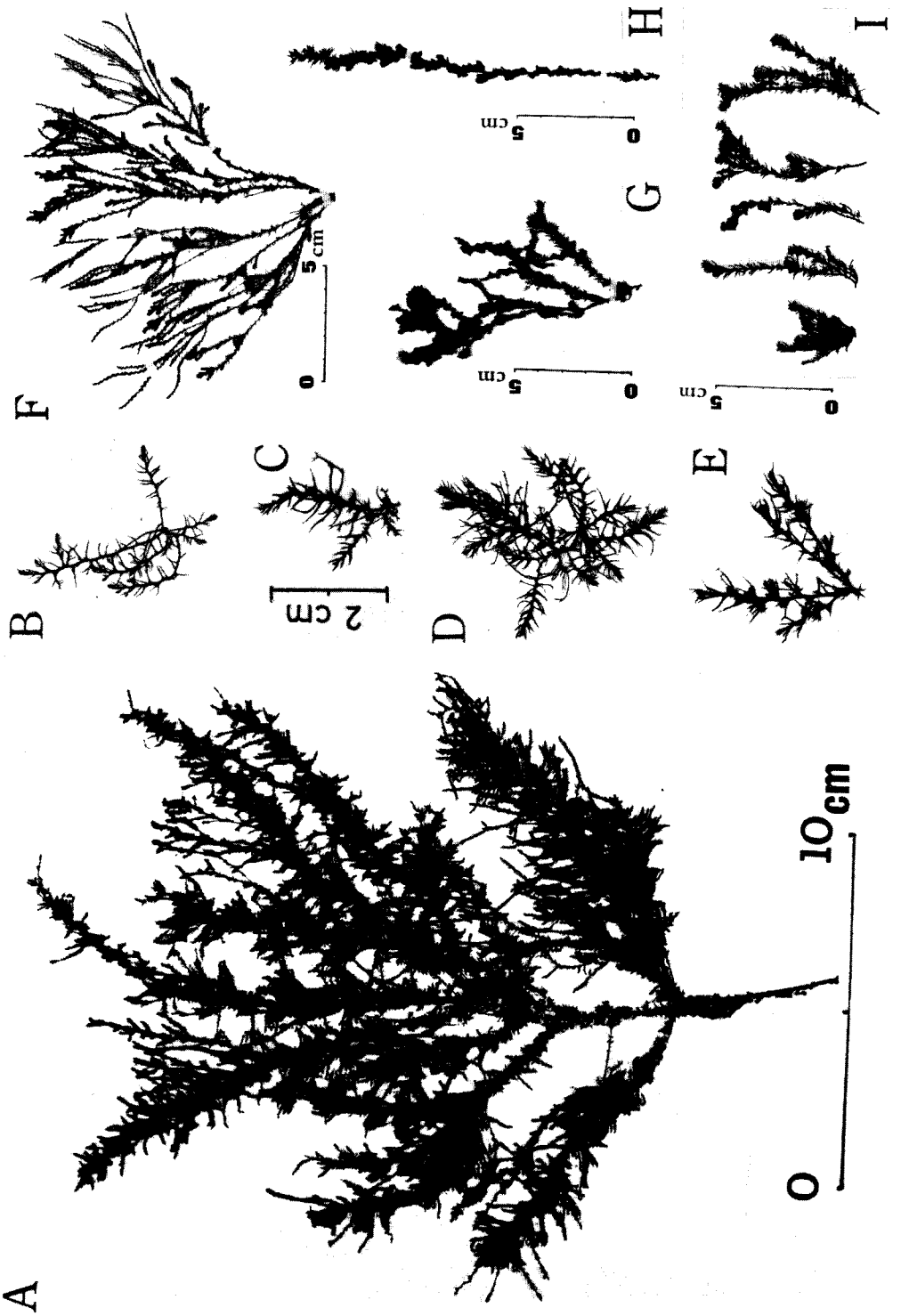

A
0
10cm
B
C
2 cm
D
E
0
5cm
F
0
5 cm
G
0
5cm
H
I

Plate 12

Neorhodomela aculeata (PERESTENKO) MASUDA

A, B, field-collected plants; C–Q, cultured plants grown at 14°C, 14:10 LD.

A. Carpospores.

B. Tetraspores.

C–K. Development of carposporelings: C, one day old; D, E, three days old; F, G, ten days old; H, fourteen days old; I, seventeen days old; J, K, one month old.

L. Young axillary adventitious branch borne on a one and half month old plant.

M. Tetrasporangial branchlets formed on a 2-month-old plant.

N. Spermatangial branchlets borne on the abaxial side of a determinate branchlet borne on a 2-month-old plant.

O, P. Procarps; on the abaxial side of a determinate branchlet (O), and on an axillary adventitious branch (P), both of which were formed on a 2-month-old plant.

Q. Cystocarp formed on a 3-month-old plant.

(Photographed from living material except K.)

Scale in B applies also to A & C–F; Scale in N applies also to G–J, L, M & O–Q.

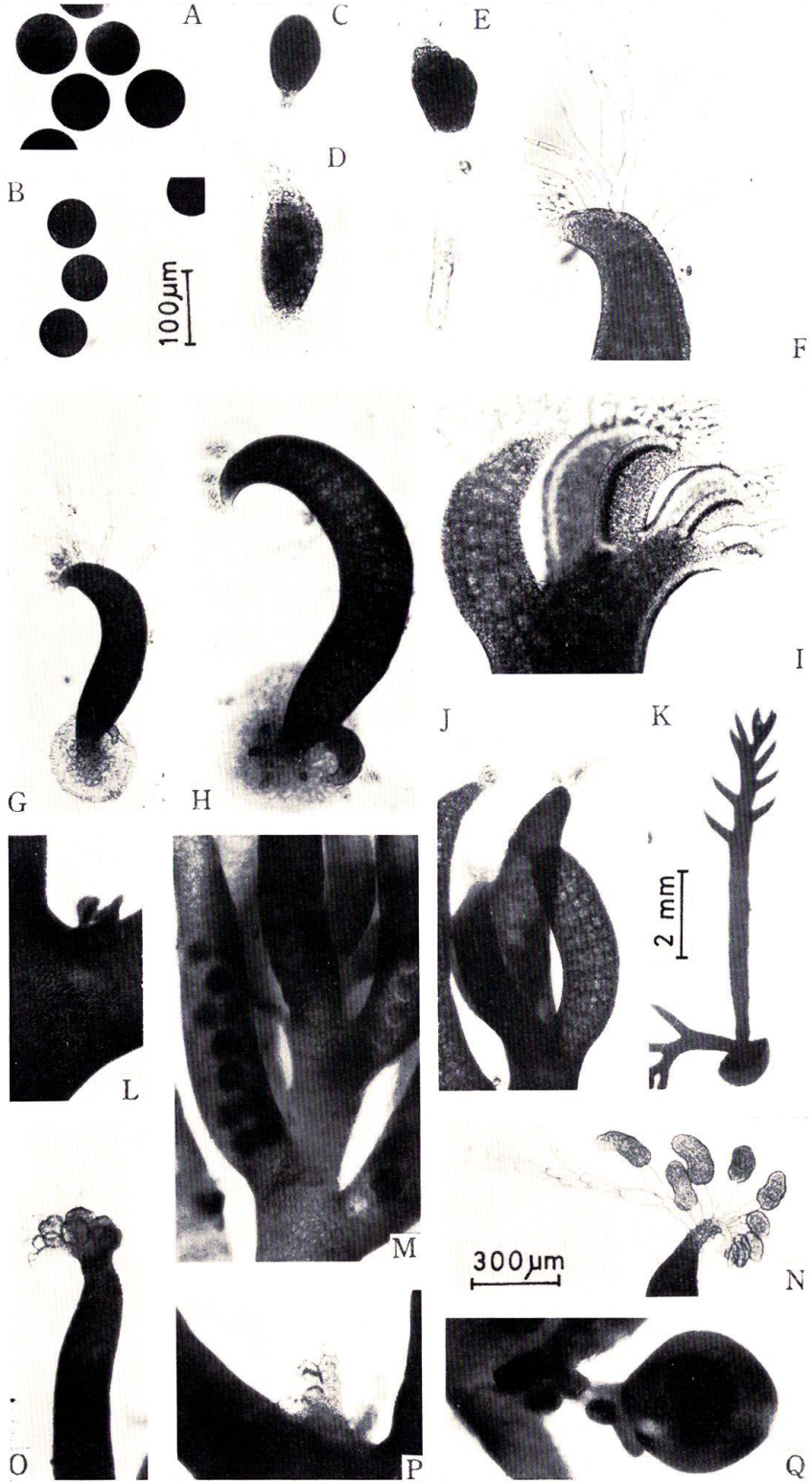

A
B
C
D
E
F
100μm
G
H
I
J
K
2 mm
L
M
N
300μm
O
P
Q

Plate 13

Neorhodomela oregona (DOTY) MASUDA

A, F, field-collected plants; B-E, cultured plants grown at 14°C, 14:10 LD.

A. Tetrasporangial plant collected at Akkeshi on June 24, 1971 (parent for culture study, *Masuda* 9304).

B. Spermatangial plant (2 months old, *Masuda* 9373).

C. Procapic plant (2 months old, *Masuda* 9374).

D. Cystocarpic plant (4 months old, *Masuda* 9379).

E. Tetrasporangial plant (3 months old, *Masuda* 9385).

F. Cystocarpic plant collected at Hamanaka on July 3, 1973 (*Masuda* 13011, leg. K. MIYAJI).

Scale in B applies also to A & C-F.

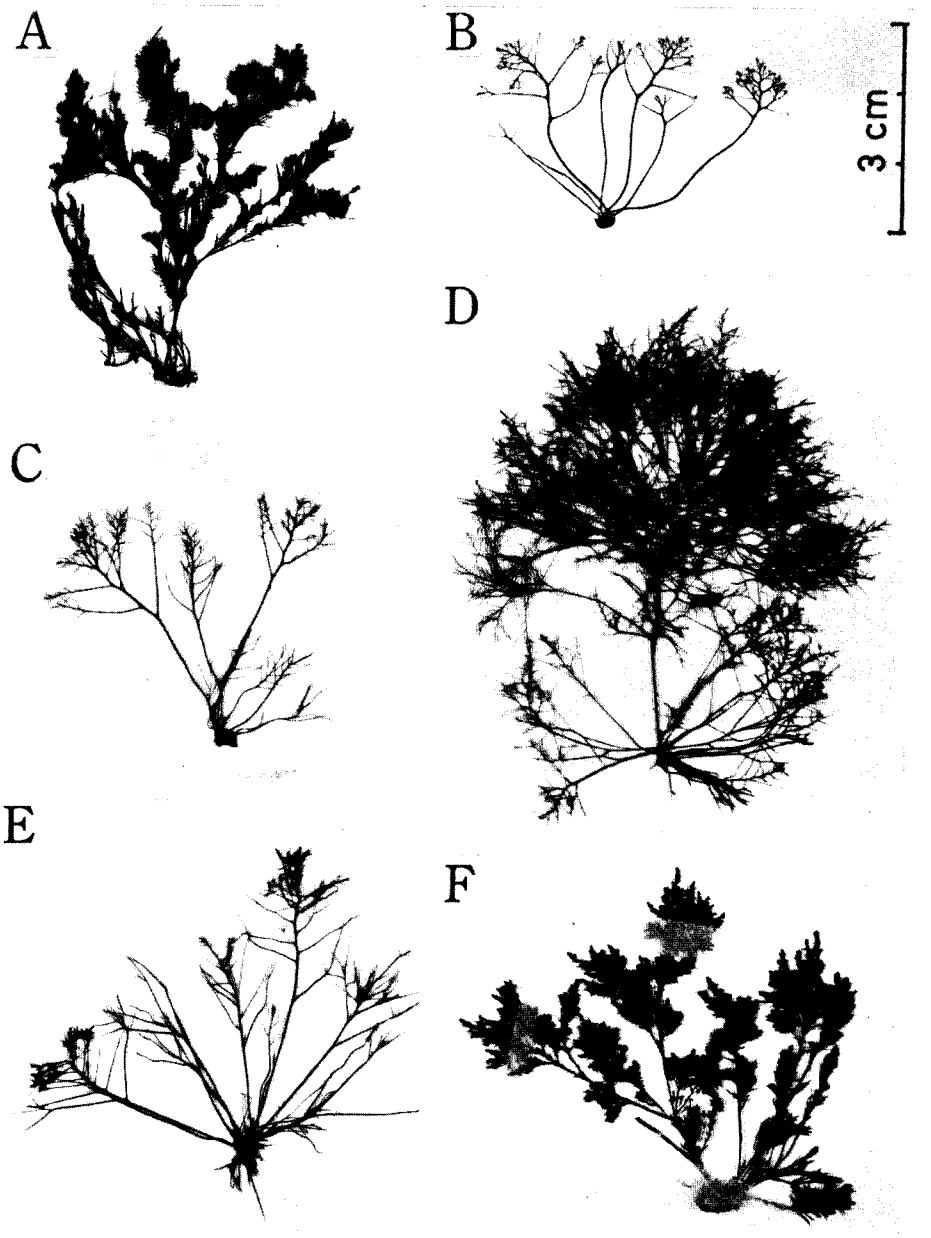

A
B
3 cm
D
C
E
F

Plate 14

Neorhodomela oregona (DOTY) MASUDA

A, field-collected plant; B–Q, cultured plants grown at 14°C, 14 : 10 LD.

A. Tetraspore.

B–K. Development of tetrasporelings: B, one day old; C, D, three days old; E, seven days old; F, G, ten days old; H, I, fourteen days old; J, fourty-five days old; K, fifty days old.

L. Spermatangial branches arranged in a spiral manner on the apical portion of an indeterminate branch borne on a 2-month-old plant.

M. Spermatangial branchlets and procarps borne on the same branch in 2-month-old culture.

N. Procarps arranged in a spiral manner on the apical portion of an indeterminate branch formed on a 2-month-old plant.

O. Cystocarp developed on a 3-month-old plant.

P. Carpospore.

Q. Tetrasporangial branches formed on a 3-month-old plant.

(Photographed from living material except L.)

Scale in G applies also A–E, L–N & P; scale in H applies also to F, I–K, O & Q.


A
B
C
D
E
F
100μm
G
300μm
H
I
J
K
L
M
N
O
P
Q

Plate 15

Neorhodomela munita (PERESTENKO) MASUDA

Field-collected plants.

A. Trichoblasts on the abaxial side of a determinate branchlet.

B. Spermatangial branchlets on the abaxial side of a determinate branchlet.

C. Procarps on the abaxial side of a determinate branchlet.

D, E. Cystocarps.

F. Tetrasporangial branches.

Neorhodomela oregona (DOTY) MASUDA

Field-collected plants.

G. Spermatangial branchlets on an axillary adventitious branch.

H. Cystocarps.

I. Tetrasporangial branches.

Use scale in B for A–C & G; scale in H for D–F, H & I.

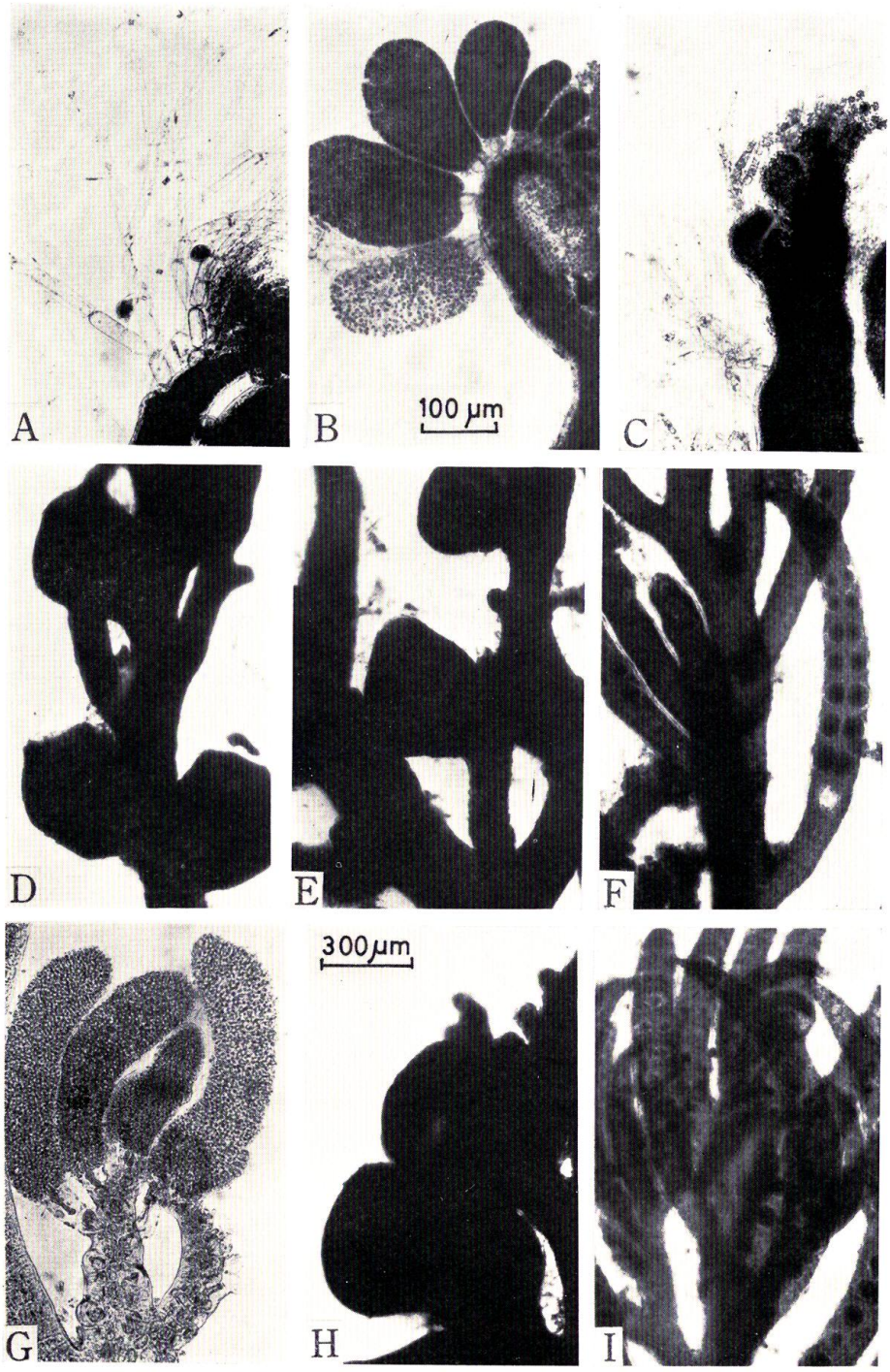

A
B
100 µm
C
D
E
F
300µm
G
H
I

Plate 16

Neorhodomela aculeata (PERESTENKO) MASUDA

Field-collected plants.

A. Trichoblasts borne on the abaxial side of a determinate branchlet.

B. Spermatangial branchlets on axillary adventitious branches.

C. Procarps borne on the abaxial side of a determinate branchlet.

D. Cystocarp.

E. Tetrasporangial branchlets.

Neorhodomela larix (TURNER) MASUDA

Field-collected plants.

F. Spermatangial branchlets on axillary adventitious branches.

G, H. Cystocarps.

I. Tetrasporangial branchlets.

Use scale in A for A–C & F; scale in H for D, E & G–I.

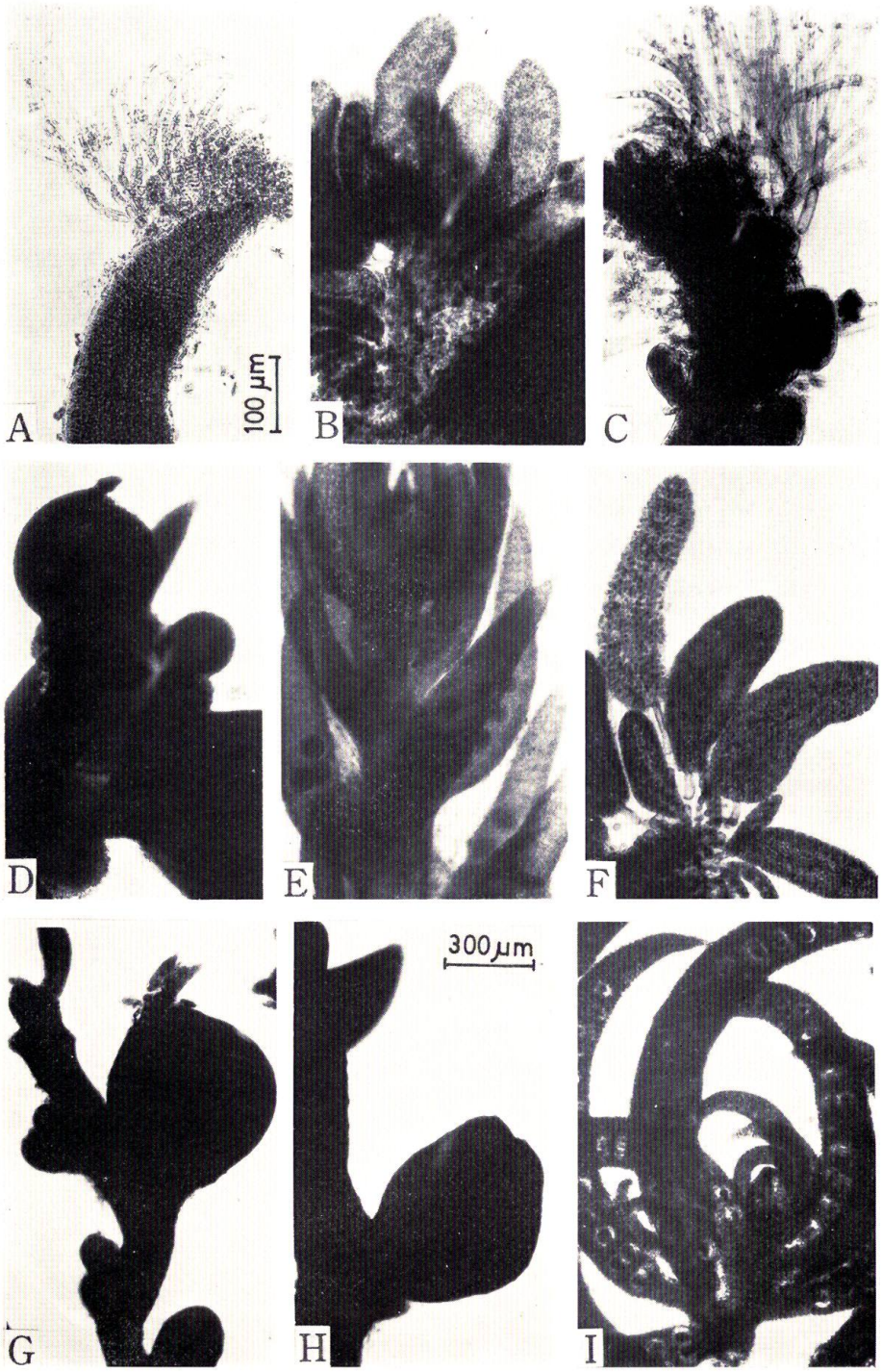

A
100 µm
B
C
D
E
F
G
300µm
H
I

Plate 17

Cross section (A, C–H, J, L & M) and longitudinal section (B & K) of main axes and of a determinate branchlet (I). A–D, F & H–L, field-collected plants; E, G & M, cultured plants grown at 14°C, 14 : 10 LD.

Neorhodomela munita (PERESTENKO) MASUDA

A, B. Lower portion of second year plants.

C. Lower portion of a first year plant.

D. Middle portion of a first year plant.

E. Lower portion of a 2-month-old plant.

Neorhodomela aculeata (PERESTENKO) MASUDA

F. Lower portion of an old plant.

G. Lower portion of a 2-month-old plant.

Neorhodomela larix (TURNER) MASUDA

H. Lower portion of an old plant.

I. Determinate branchlet.

Neorhodomela oregona (DOTY) MASUDA

J, K. Lower portion ot old plants.

L. Middle portion of a proliferous branch.

M. Lower portion of a 2-month-old plant.

Use scale in F for B–F; scale in L for A, C–E & G–M.

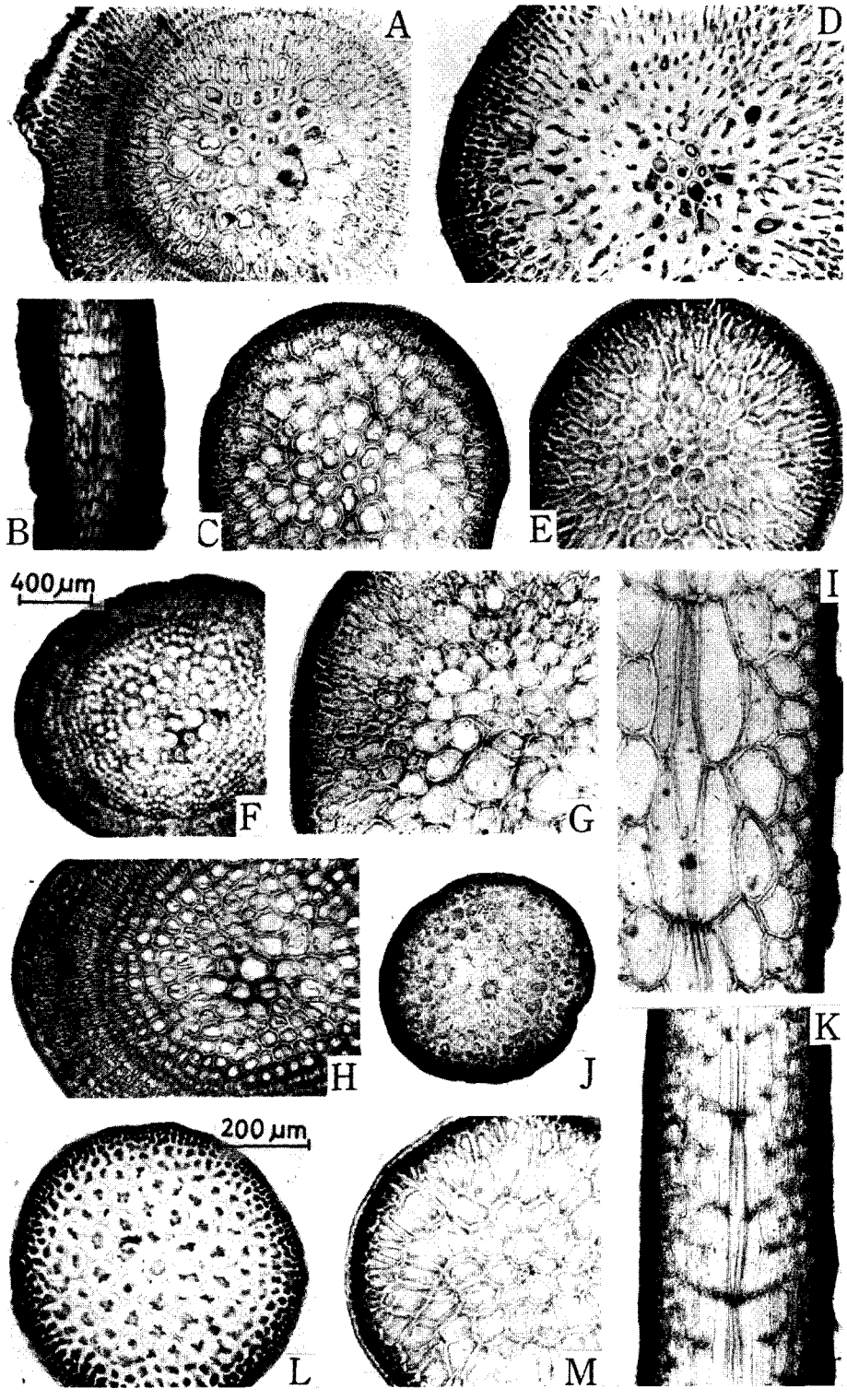

A
D
B
C
E
400μm
F
G
I
H
J
K
200 μm
L
M

Plate 18

Odonthalia annae PERESTENKO

A. Cystocarpic plant collected at Rausu, Hokkaido on May 13, 1968 (*Masuda* 6927).

B. Tetrasporangial plant with proliferous branches (arrow) collected at Rausu on May 13, 1968 (*Masuda* 6883 a).

C. Spermatangial plant grown at 10°C, 14 : 10 LD for 2 months and then, transferred to 5°C, 10 : 14 LD (6 months old, *Masuda* 9707).

D. Sterile plant collected at Atoiya-misaki, Kunashiri Island on August 1, 1929 (NAGAI herbarium in SAPA, as *Odonthalia ochotensis*, No. 404).

Scale in C applies also to D.

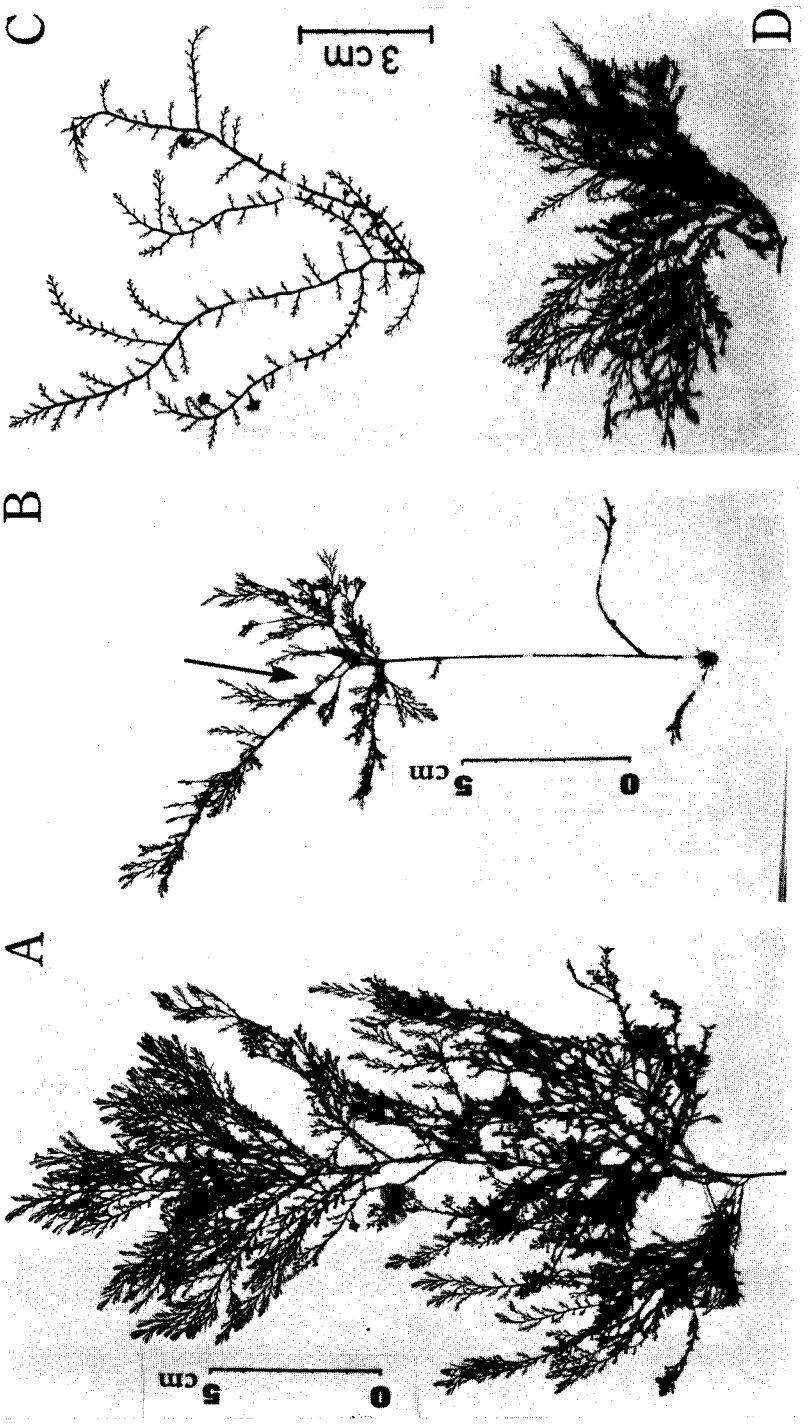

C
3 cm
D
B
0
5 cm
A
0
5 cm

Plate 19

Odonthalia annae PERESTENKO

A. Carpospore from a field-collected plant.

B. Tetraspore from a field-collected plant.

C–L. Development of tetrasporelings grown at 10°C, 14 : 10 LD : C, one day old ; D, E, three days old ; F, five days old ; G, H, seven days old ; I, fourteen days old, issuing an adventitious branch (arrow); J, K, twenty-one days old ; L, one month old.

M. Spermatangial branches borne on a 6-month-old plant grown at 10°C, 14 : 10 LD for 2 months and then, shifted to 5°C, 10 : 14 LD.

N. Procarps with simple trichoblasts formed on a 6-month-old plant grown at 10°C, 14 : 10 LD for 2 months and then, shifted to 5°C, 10 : 14 LD.

(Photographed from living material except L.)

Scale in F applies also to A–E, G, H & N; scale in K applies also to I, J & M.

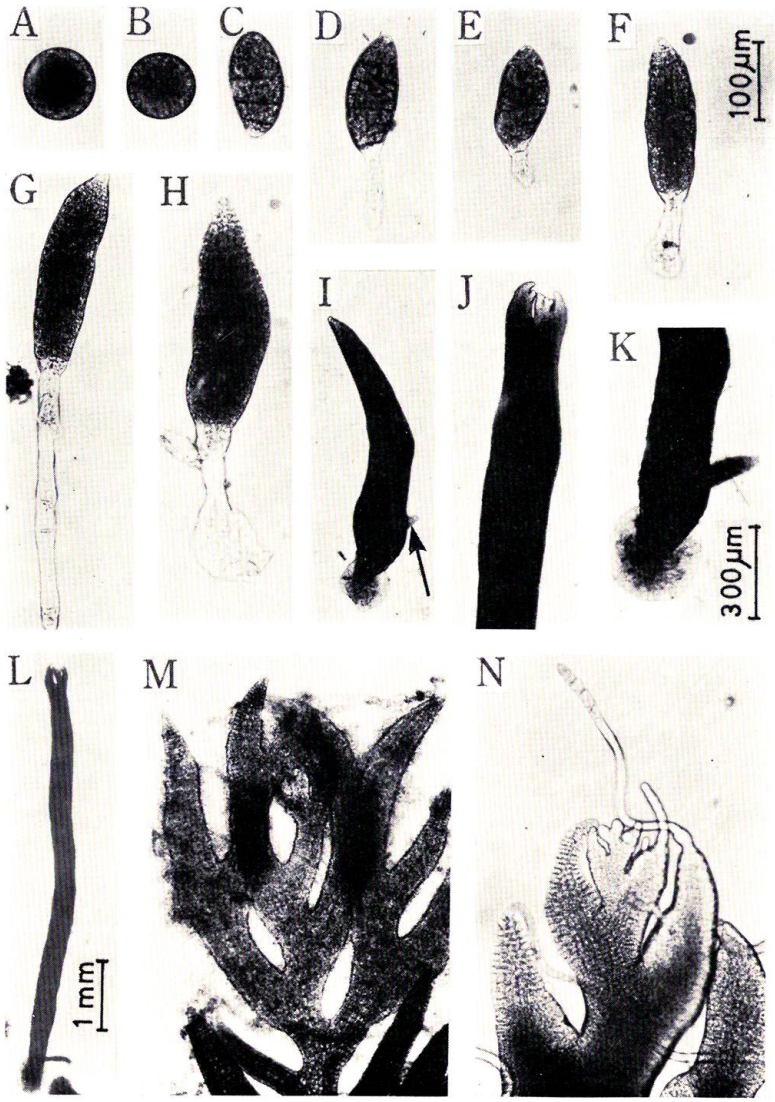
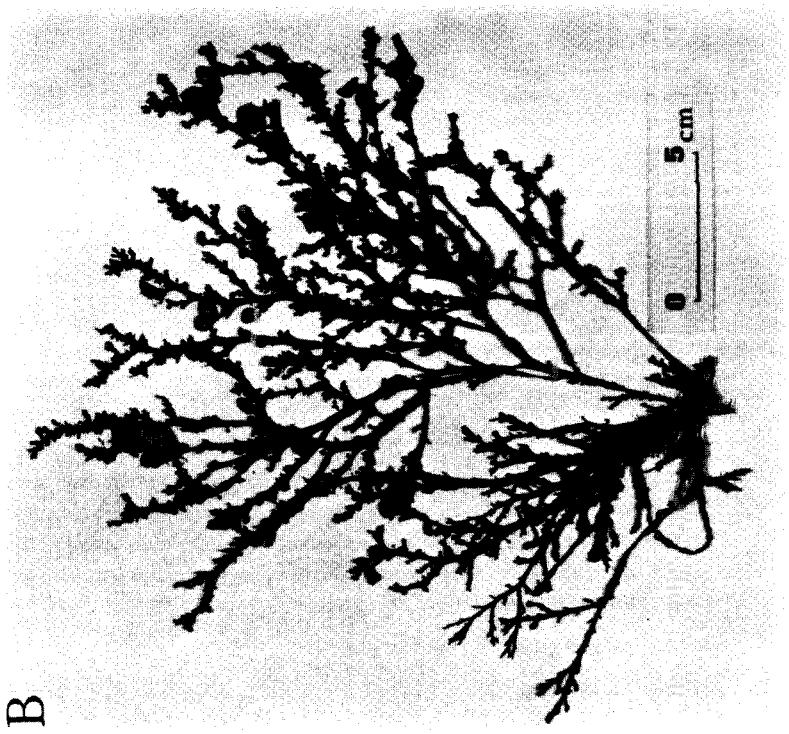

A
B
C
D
E
F
100μm
G
H
I
J
K
300μm
L
1mm
M
N

Plate 20

Odonthalia corymbifera (GMELIN) GREVILLE

A. Spermatangial plant collected at Muroran, Hokkaido on July 30, 1972 (*Masuda* 10245).

B. Cystocarpic plant collected at Muroran on November 16, 1970 (*Masuda* 10187).


B
0
5 cm

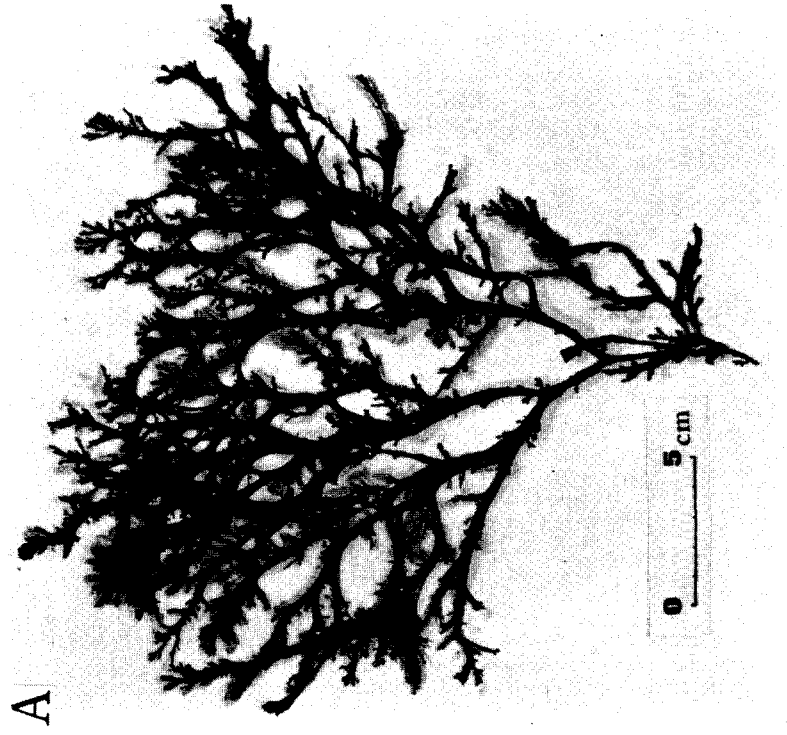

A
0
5 cm

Plate 21

Odonthalia corymbifera (GMELIN) GREVILLE

C–L, cultured plants grown at 14°C, 14 : 10 LD.

A. Carpospores from a field-collected plant.

B. Tetraspores from a field-collected plant.

C–J. Development of carposporelings: C, attached spore; D, one day old; E three days old; F, seven days old; G, fourteen days old; H, twenty-one days old, issuing an adventitious branch (arrow); I, apical portion of a one-month-old sporeling; J, two-month-old plant issuing secondary upright shoots.

K. Tetrasporangial plant (9 months old).

L. Tetrasporangial branchlets borne on the plant shown in K.

(Photographed from living material except K.)

Scale in B applies also to A, C–F & I; scale in H applies also to G & L.

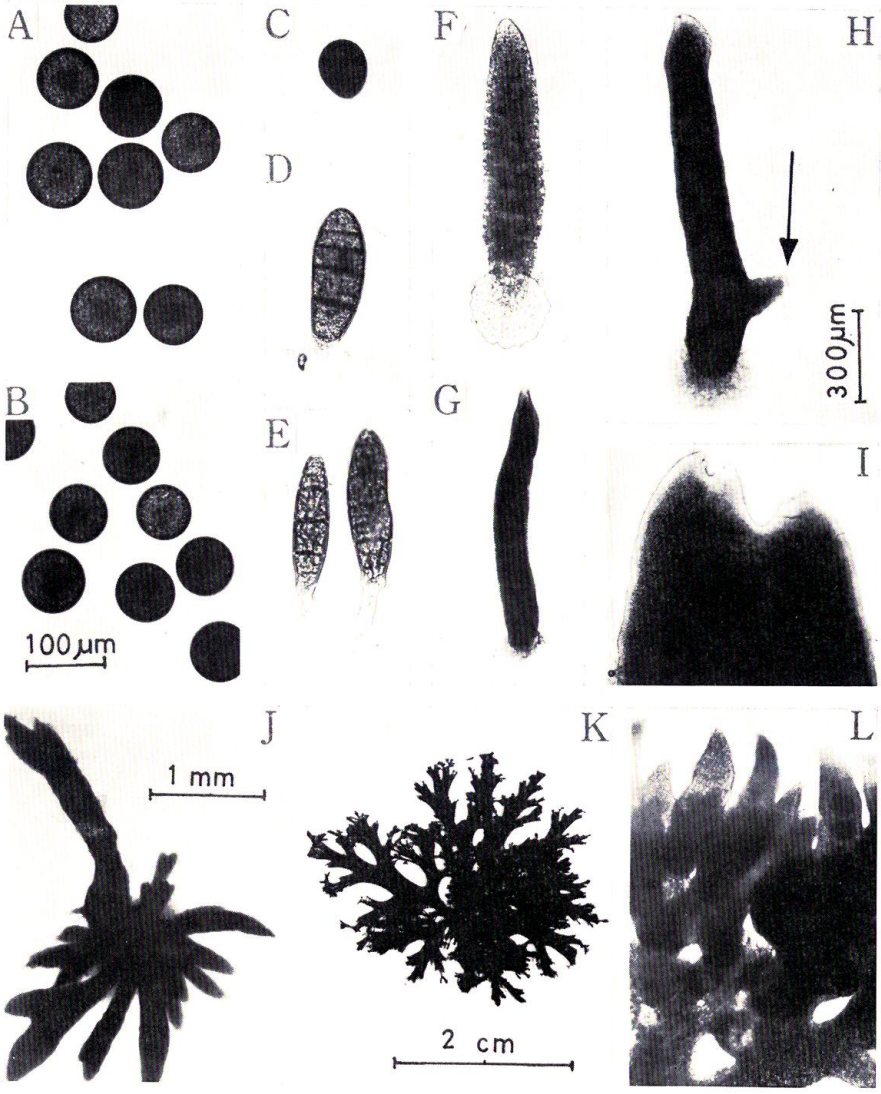

A
B
C
D
E
F
G
H
I
J
K
L
100 µm
300 µm
1 mm
2 cm

Plate 22

Odonthalia macrocarpa MASUDA

A. Cystocarpic plant (Holotype, SAP 032079=*Masuda* 13326).

B. Tetrasporangial plant collected at Muroran on March 20, 1971 *Masuda* 13356).

C. Tetrasporangial plant grown at 10°C, 14 : 10 LD for 3 months and then, transferred to 10°C, 10 : 14 LD (11 months old, *Masuda* 13735).

D. Spermatangial plant grown at 10°C, 10 : 14 LD (8 months old, *Masuda* 13761).

E. Procarpic plant grown at 10°C, 10 : 14 LD (8 months old, *Masuda* 13760).

Use scale in C for C–E.

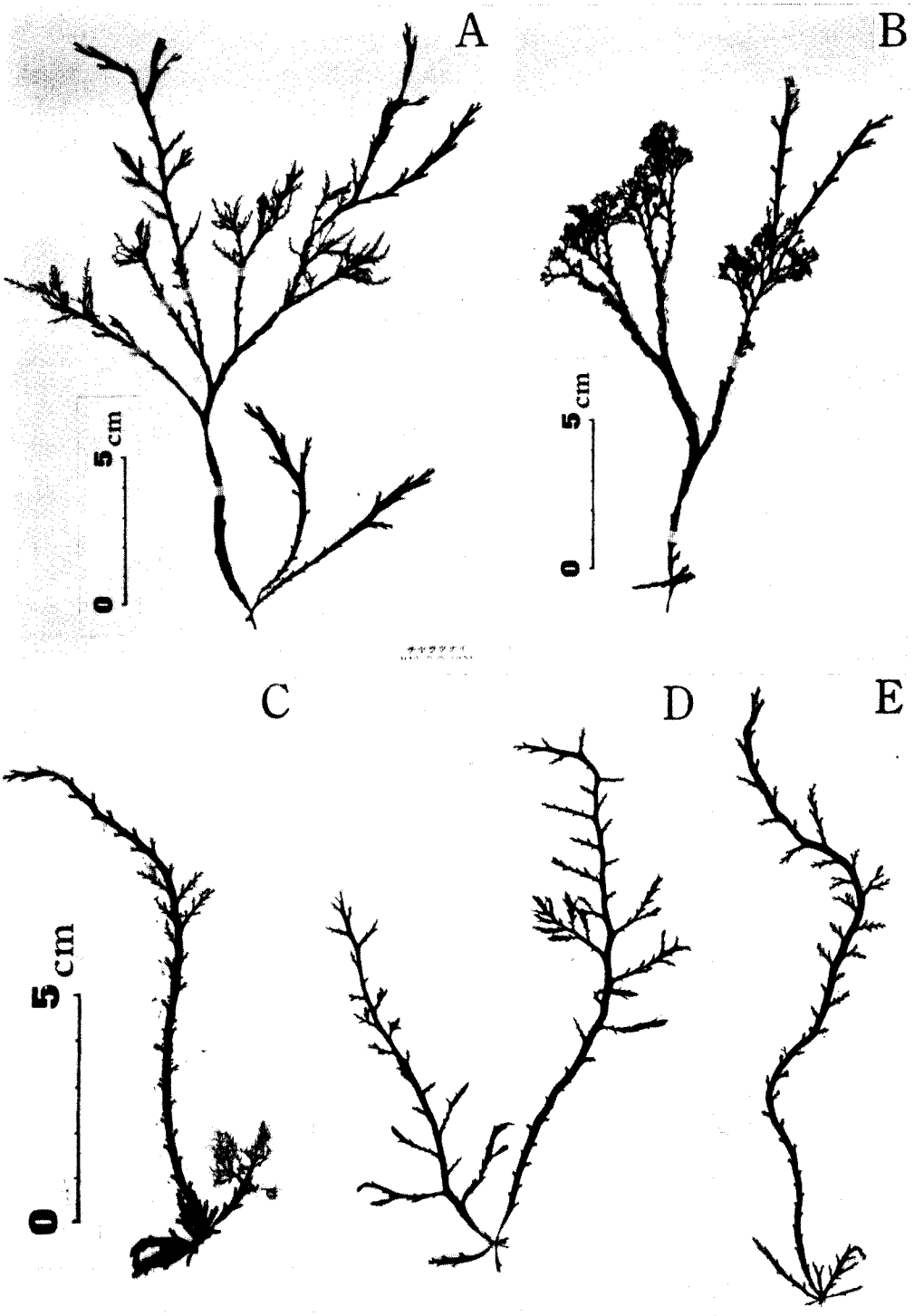

A
5 cm
0
B
5 cm
0
C
5 cm
0
D
E

Plate 23

Odonthalia macrocarpa MASUDA

A. Carpospore from a field-collected plant.

B. Tetraspore from a field-collected plant.

C. Attached tetraspore.

D-Q. Development of carposporelings grown at 10°C, 14 : 10 LD : D, one day old ; E, three days old ; F, G, five days old ; H, J, seven days old ; K, L, ten days old ; M, fourteen days old ; N, seventeen days old ; O, P, two months old, showing apical portion (O) and basal portion (P); Q, four-month-old plant.

R. Apical portion of a spermatangial branch borne on a 8-month-old plant grown at 10°C, 10 : 14 LD.

S. Procarps formed on a 8-month-old plant grown at 10°C, 10 : 14 LD.

T. Portion of a tetrasporangial branchlet borne on the plant shown in Plate 22, C.

(Photographed from living material except Q.)

Scale in K applies also to A–J, L, M, S & T ; scale in N applies also to O & R.

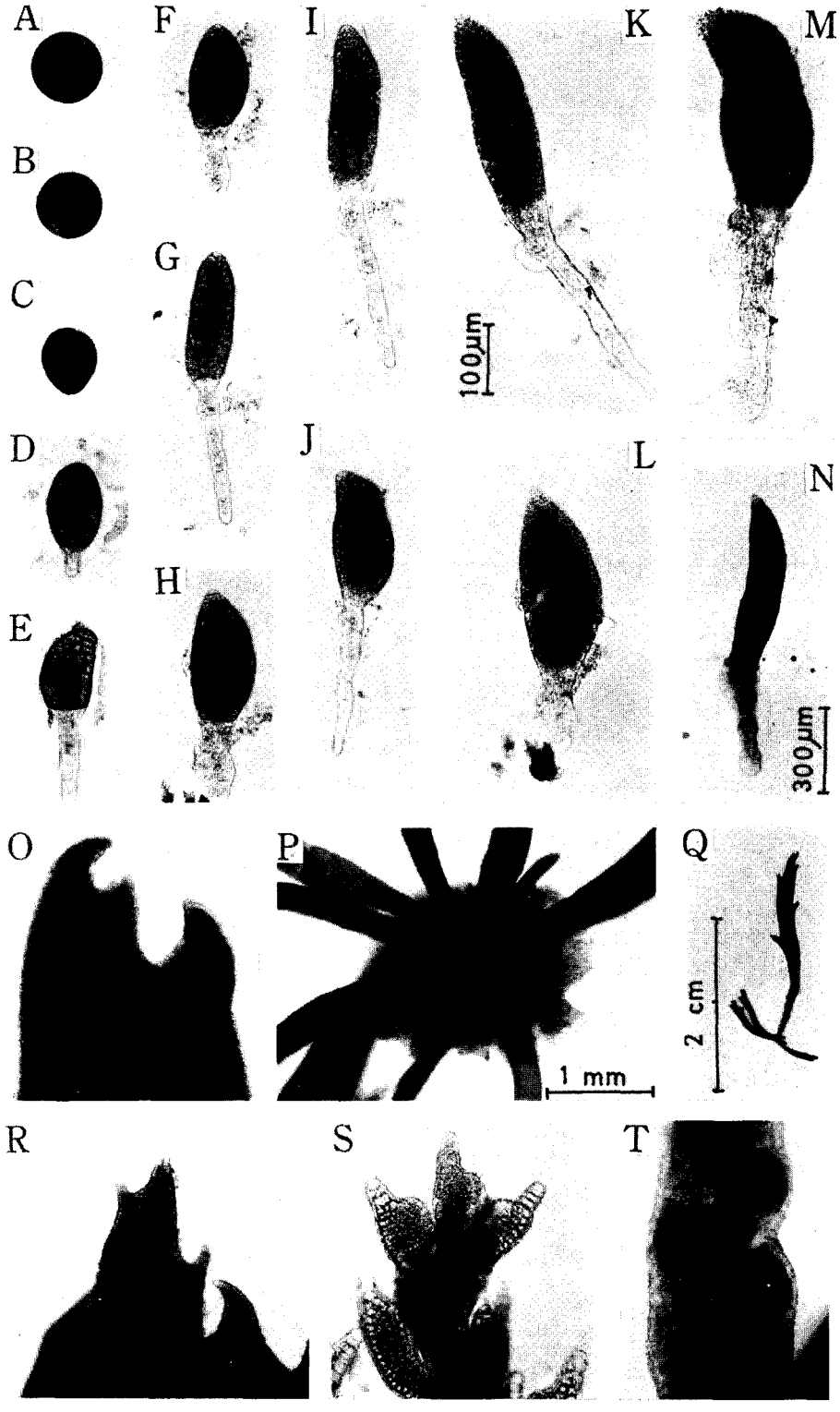

A
B
C
D
E
F
G
H
I
J
K
L
M
N
100μm
300μm
O
P
Q
1 mm
2 cm
R
S
T

Plate 24

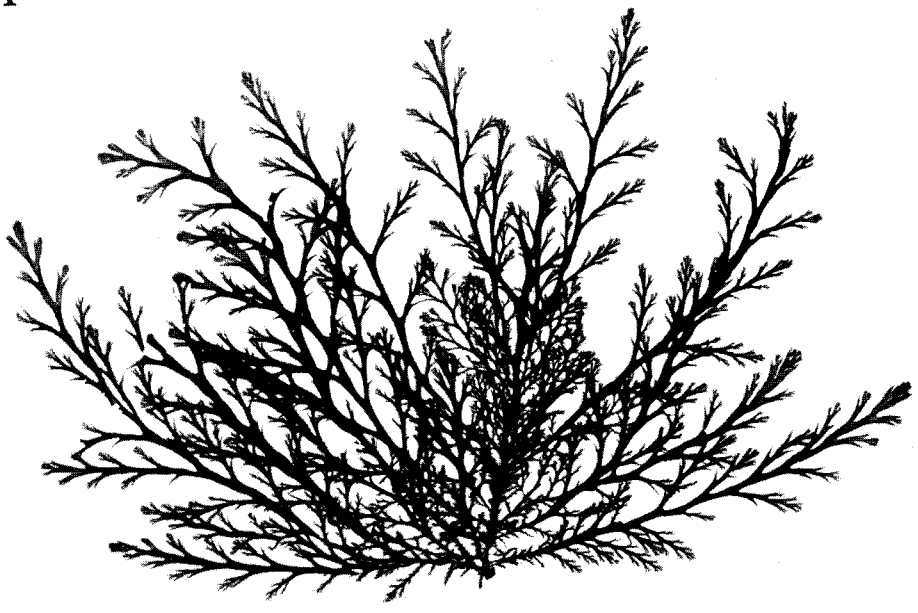
Odonthalia yamadae MASUDA

A. Tetrasporangial plant collected at Akkeshi, Hokkaido on April 8, 1974 (*Masuda* 13780).

B. Cystocarpic plant (Holotype, SAP 032116=*Masuda* 13781).

Scale in B applies also to A.

A



B

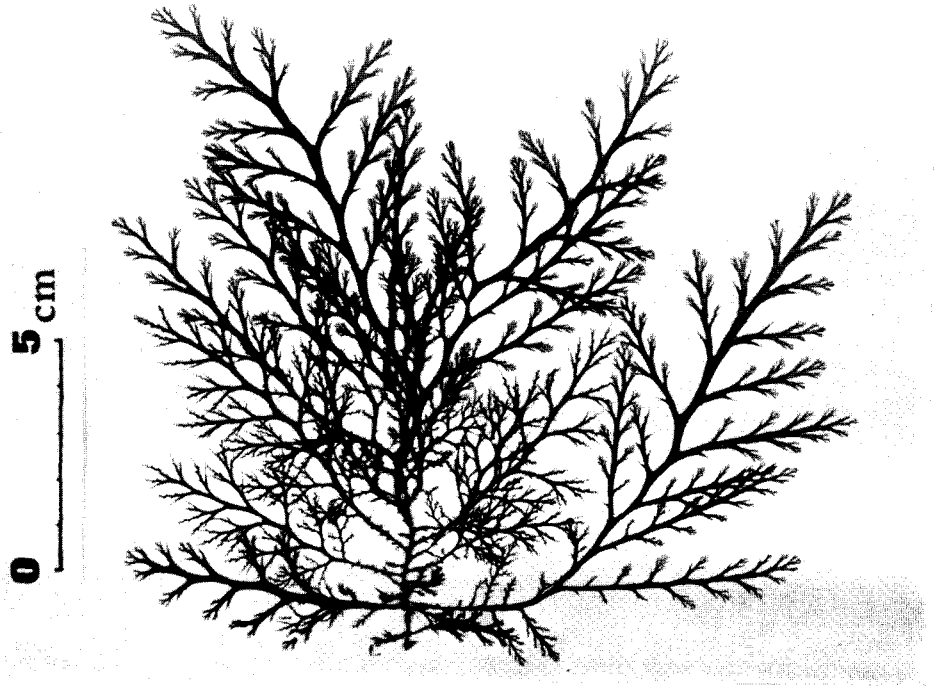


Plate 25

Odonthalia yamadae MASUDA

A. Carpospore from a field-collected plant.

B. Tetraspore from a field-collected plant.

C–K. Development of tetrasporelings grown at 5°C, 14 : 10 LD (C, D & G–J) and 10°C, 14 : 10 LD (E, F, K & L): C, one day old; D, E, three days old; F, G, seven days old; H, fourteen days old; I, J, twenty-one days old; K, L, one month old.

M. Adventitious branches issuing from the marginal portion of a second order branch of a 6-month-old plant derived from an excised apical tip of branch and grown at 5°C, 14 : 10 LD.

N. Apical portion of a spermatangial branch formed at the uppermost portion of an ordinary branch (8-month-old plant derived from an excised apical tip of branch and grown at 5°C, 10 : 14 LD).

O. Procarps with simple trichoblasts formed at the uppermost portion of a narrowly tapering branch (8-month-old plant derived from an excised apical tip of branch and grown at 5°C, 14 : 10 LD).

(Photographed from living materials.)

Scale in M apilies also to I, K & L; scale in O applies also to A–H & J.

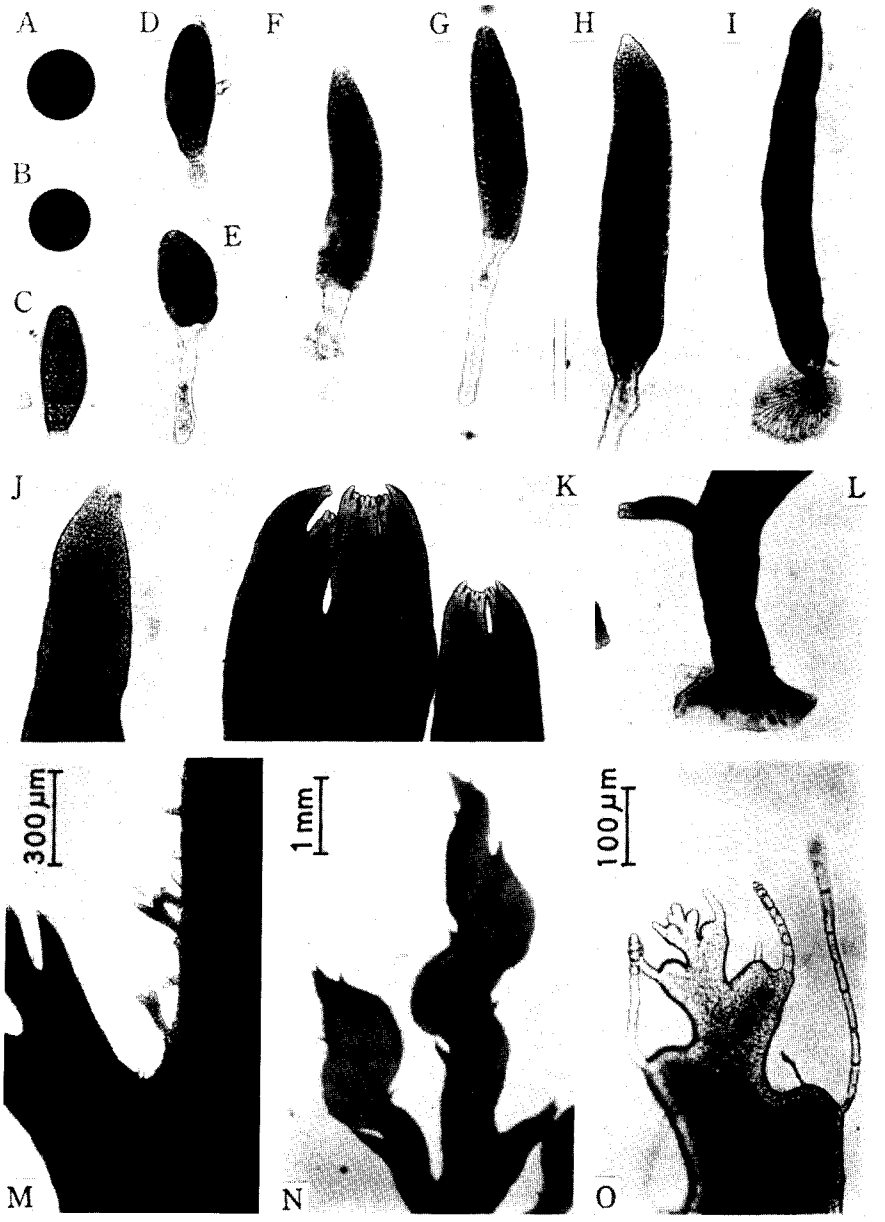

A
B
C
D
E
F
G
H
I
J
K
L
300 µm
M
1 mm
N
100 µm
O

Plate 26

Cystocarps of *Odonthalia*

A. *Odonthalia annae* PERESTENKO.

B. *O. corymbifera* (GMELIN) GREVILLE.

C. *O. macrocarpa* MASUDA.

D. *O. yamadae* MASUDA.

Use scale in A for A–D.

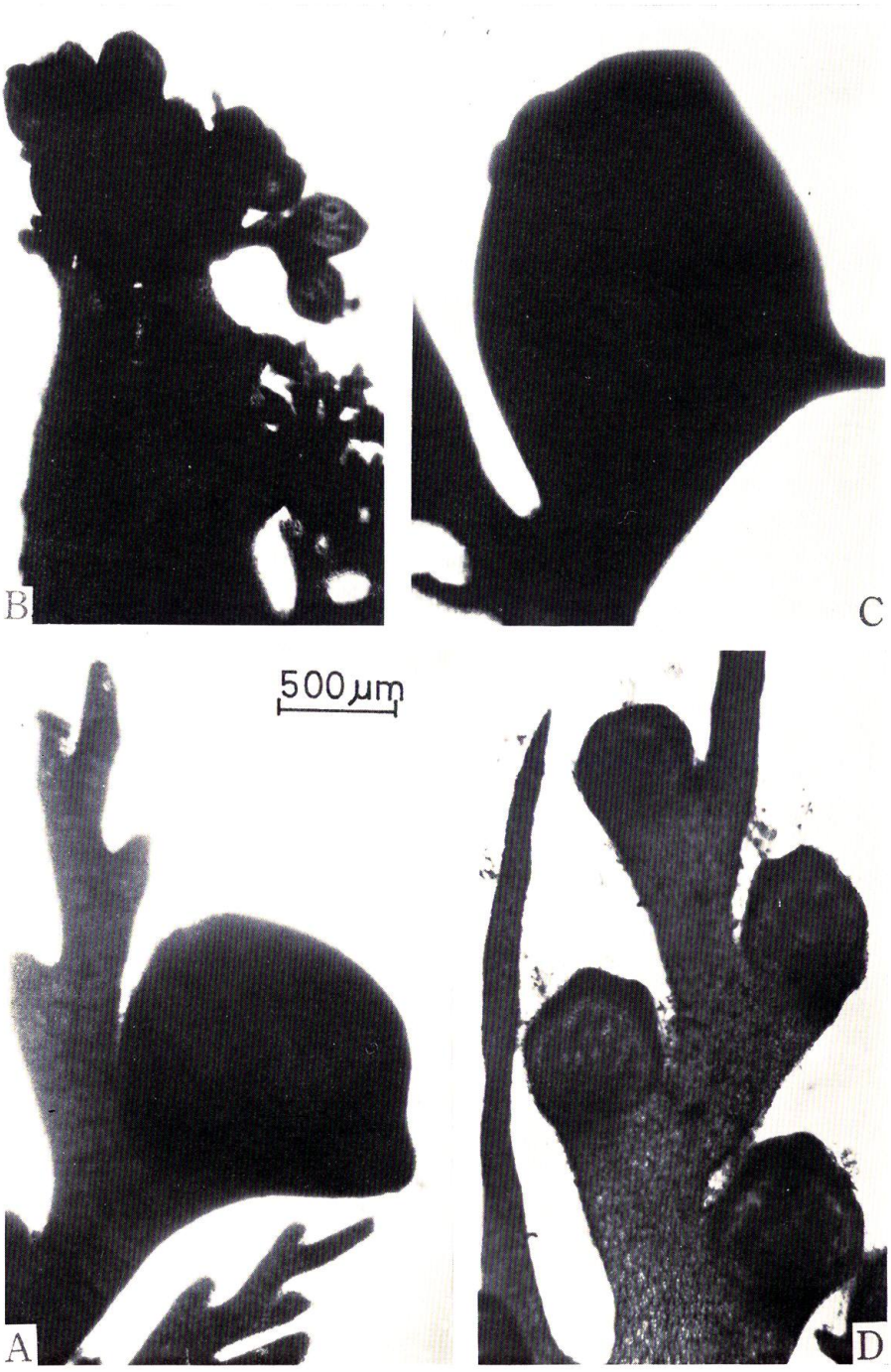

B
C
500 µm
A
D

Plate 27

Tetrasporangial branchlets of *Odonthalia*

A. *Odonthalia annae* PERESTENKO.

B. *O. corymbifera* (GMELIN) GREVILLE.

C. *O. macrocarpa* MASUDA.

D. *O. yamadae* MASUDA.

Use scale in C for A–D.

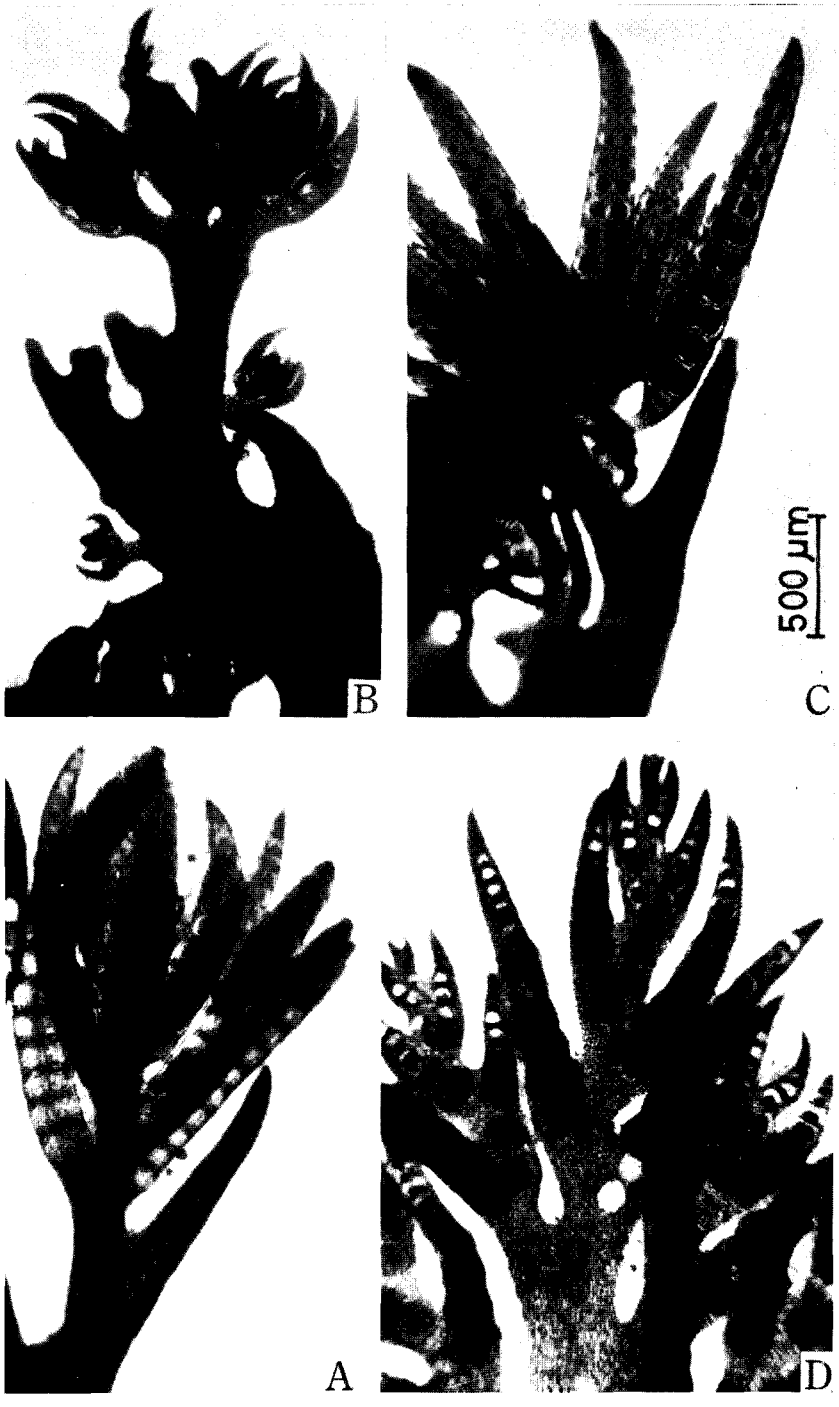

B
C
500 µm
A
D

Plate 28

Cross-section (B, D, E & G–K) and longitudinal section (A, C & F) of the main axes.

Odonthalia yamadae MASUDA

A. Lower portion of a mature plant.

B. Middle portion of a mature plant, showing a midrib.

Odonthalia annae PERESTENKO

C, D. Lower portion of a mature plant.

Odonthalia corymbifera (GMELIN) GREVILLE

E, F. Lower portion of a mature plant.

G. Lower portion of a young plant.

H. Middle portion of a mature plant.

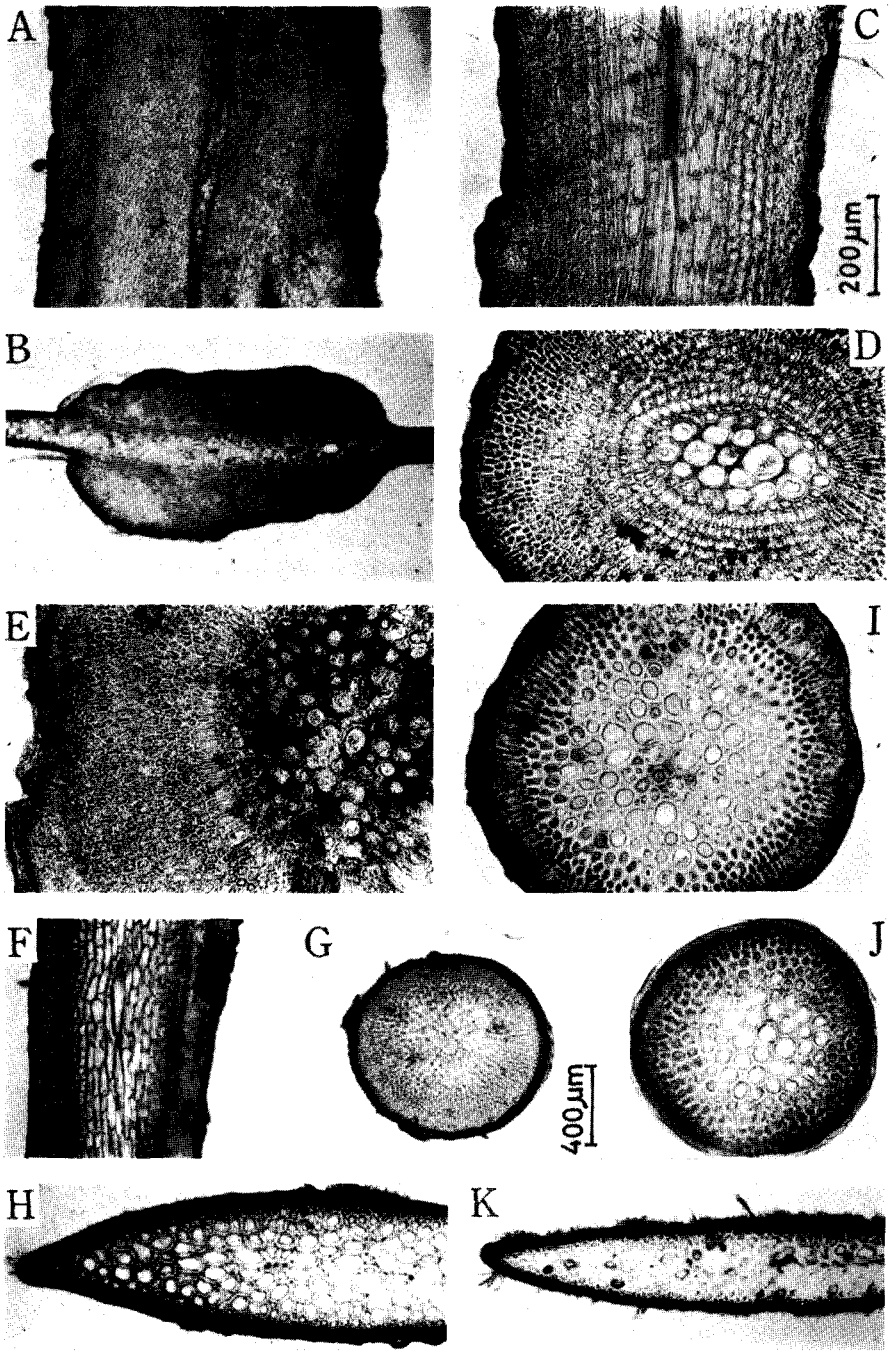
Odonthalia macrocarpa MASUDA

I. Lower portion of a mature plant.

J. Lower portion of a young plant.

K. Middle portion of a mature plant.

Scale in C applies also to D, E, I & J; scale in G applies also to A, B, F, H & K.


A
C
200μm
B
D
E
I
F
G
400μm
J
H
K