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Karyology and effects of temperature and photoperiod on the life-cycle of *Porphyra leucosticta* Thuret in Le Jolis (Bangiales, Rhodophyta) from the Mediterranean Sea

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Gargiulo, G. M., De Masi, F., Genovese, G. and Tripodi, G. 1994. Karyology and effects of temperature and photoperiod on the life-cycle of *Porphyra leucosticta* Thuret in Le Jolis (Bangiales, Rhodophyta) from the Mediterranean Sea. Jpn. J. Phycol. 42: 271–280.

Porphyra from the Strait of Messina (Italy), previously referred to *P. leucosticta* Thuret in Le Jolis, was the subject of field and laboratory studies. Cross-gradient light-temperature culture indicate that conchospore formation requires short daylength (9L : 16D) and a temperature of 15–18°C. Conchospore release requires short daylength and a temperature of 18°C. Results of culture investigations are used to explain the seasonal periodicity of growth and reproduction of this species in the study site. The life history in culture involves an alternation between a macroscopic blade and microscopic filamentous conchocelis phase. Typically, blades develop from conchospores with bipolar development while conchocelis develops from carpospores with unipolar development. In addition, both blade and filamentous phases exhibit direct development. Three chromosomes (n=3) were observed in vegetative blade cells, spermatia and vegetative conchocelis cells.

Key Index Words: Conchocelis—*karyology*—*life-cycle*—*photoperiod*—Porphyra leucosticta—*Mediterranean*—*taxonomy*.

The red algal genus *Porphyra* (Bangiales, Rhodophyta) is represented by more than 75 species (Mumford and Cole 1977). Several of these species, which are particularly abundant on cold-temperate and boreal shores of the Pacific and Atlantic Oceans, are of considerable economic significance (Tseng and Sun 1989). Consequently, it is not surprising that the biology, ecology and karyology of *Porphyra* species have been extensively investigated (for rewiews, see Cole 1990, Hawkes 1990, Tseng and Sun 1989).

For many of these species, the life history typically includes a conspicuous blade phase which alternates with a microscopic filamentous conchocelis phase (Cole and Conway 1980). In sexual species, the conchocelis phase is diploid, with meiosis occurring in the germinating conchospore (Burzycki and Waaland 1987, Ohme and Miura 1988), resulting in a mosaic of genetically distinct cellular lines in the haploid blade (Tseng and Sun 1989). Numerous derived asexual life history variations have been reported for *Porphyra* species as well (Kapraun and Lemus 1987, Hawkes 1990).

Considerable information is now available correlating environmental factors, including water temperature, light intensity and photoperiod with conchospore production and release and seasonal occurrence of the blade phase (Conway and Cole 1977, Kapraun and Lemus 1987, Waaland *et al.* 1990).

Karyological studies indicate a basic haploid chromosome number of n=3-4 for most *Porphyra* species (Cole 1990, Kapraun *et al.* 1991). As in the closely related genus *Bangia* (Cole *et al.* 1983, Gargiulo *et al.* 1991), some species of *Porphyra* are reported to include populations with different chromosome

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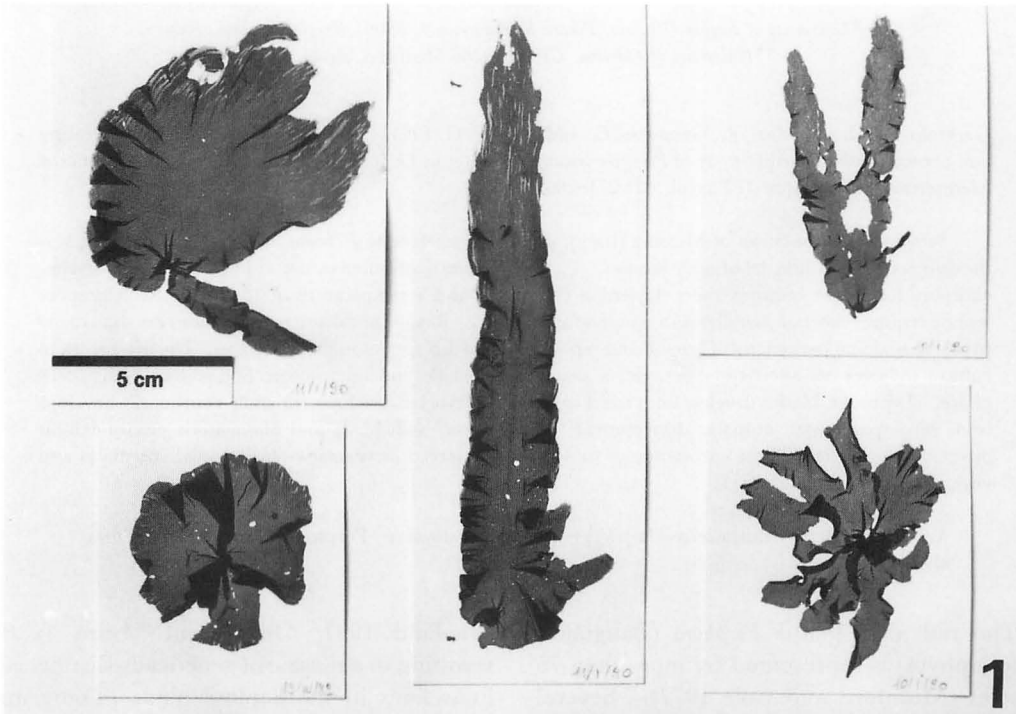
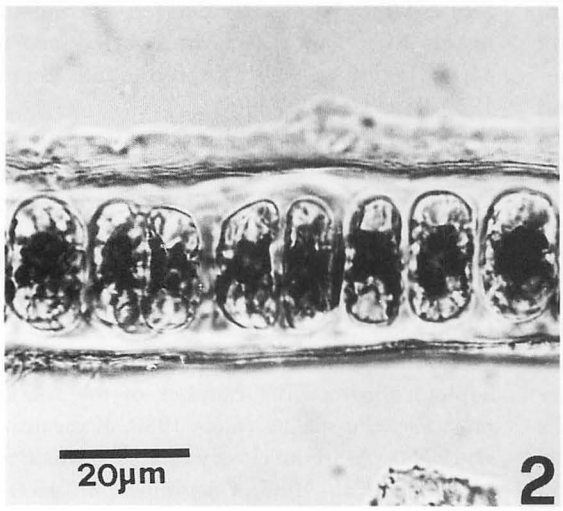
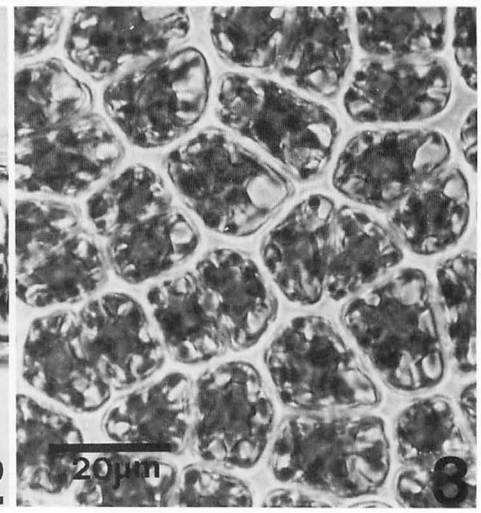
numbers (Kapraun *et al.* 1991).

Four species of *Porphyra* have been reported from the Mediterranean: *P. leucosticta* Thuret in Le Jolis, *P. linearis* Greville, *P. perforata* J. Agardh and *P. umbilicalis* (L.) J. Agardh (Hamel 1924, Lanfranco 1969). No published information is available for the life histories in controlled conditions, or on conchospore formation and release for Mediterranean isolates of any of these species. Karyological data for Mediterranean specimens are limited to chromosome numbers for the blade phase of three of these species (Kapraun and Freshwater 1987, Gargiulo *et al.* 1989).

This comunication presents the results of culture and karyological studies conducted to





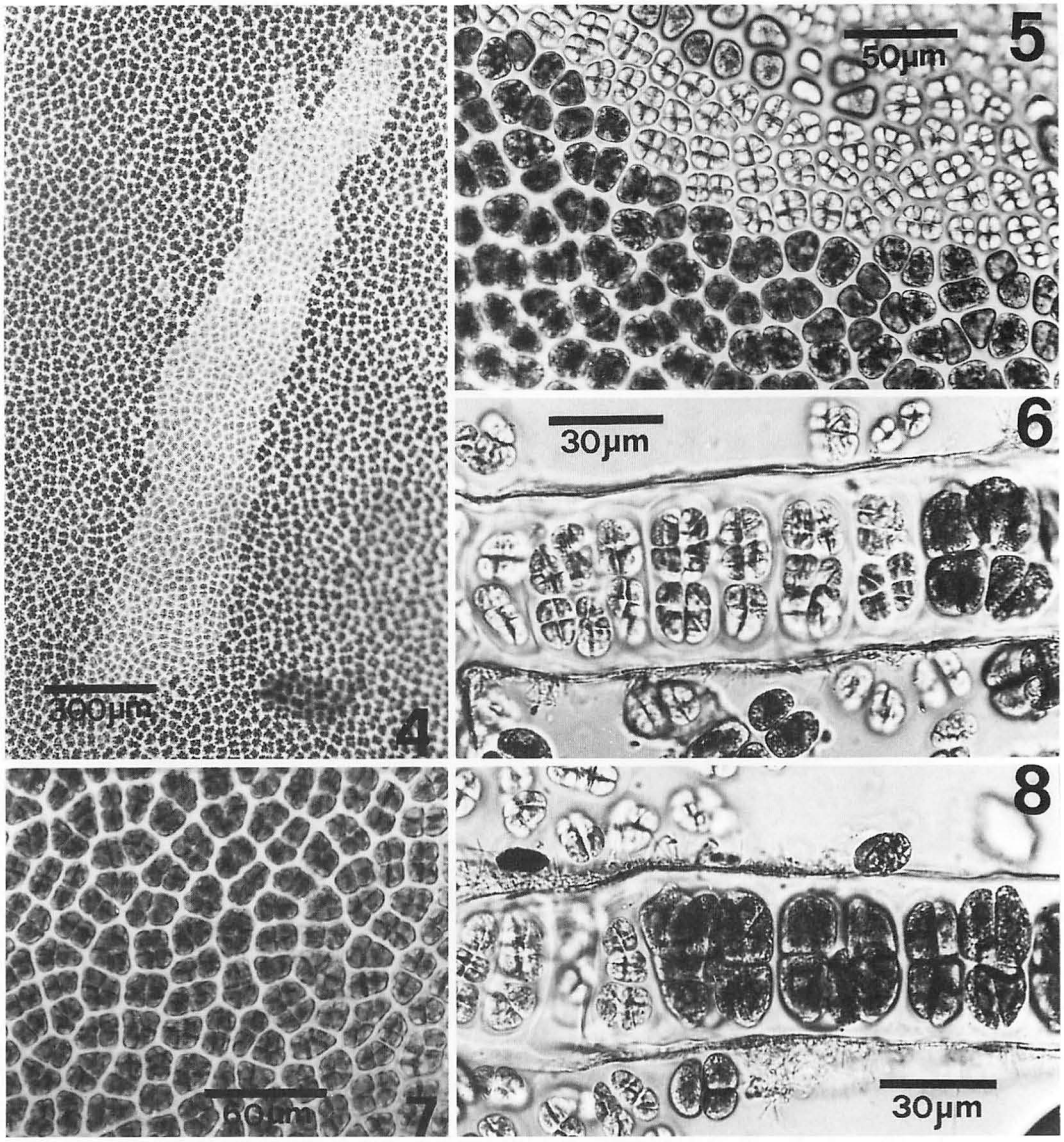


Figs. 1–3. *Porphyra leucosticta*. Fig. 1. Lanceolate, orbiculate or multilobed gametophytic thalli from the studied population. Fig. 2. Cross section of the monostromatic lamina. Fig. 3. Surface view of the lamina.

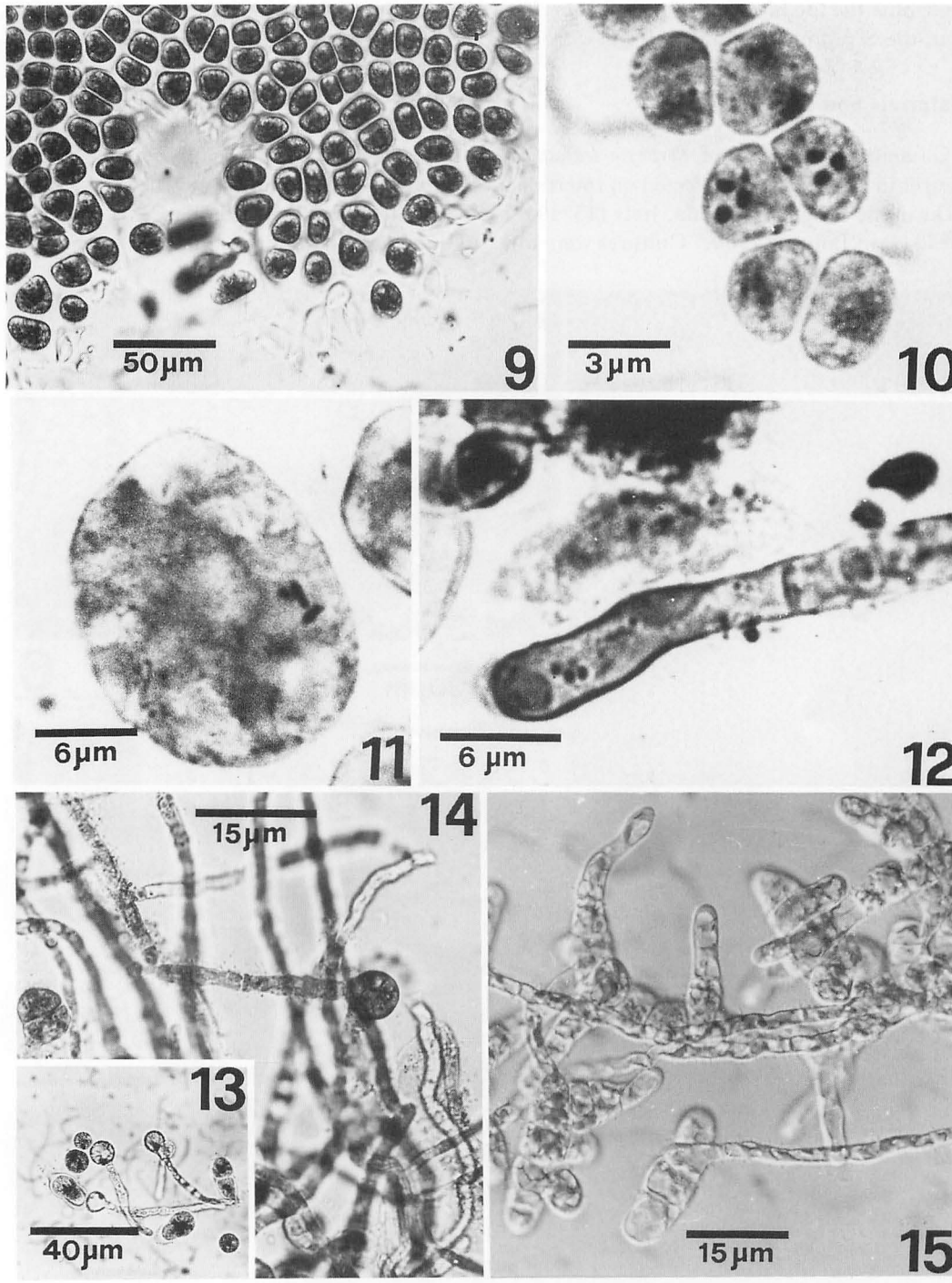
determine the life history of *Porphyra leucosticta* from the Strait of Messina, Italy.

Materials and Methods

Gametophytic plants of *Porphyra leucosticta* Thuret in Le Jolis were collected on intertidal rocks in the Strait of Messina, Italy (15°40′E, 38°30′N) in January 1990. Cultures were initiated from carpospores released from excised fragments of fertile fronds, gently brushed and washed with sterile seawater to reduce contaminants. Fragments were placed in Petri dishes (50 mm diam.) with sterile seawater. After spore release, excised fragments were removed and the spores incubated in a modified von Stosch's Medium (Guiry and Cunningham 1984), changed



Figs. 4–8. *Porphyra leucosticta*. Fig. 4. An elongate area of gametophytic thalli where spermatangia are differentiated; the other cells are carposporangia. Fig. 5. Surface view of the lamina with spermatangia. Fig. 6. Cross section of a fertile thallus, where spermatangia are visible. Fig. 7. Surface view of carposporangia. Fig. 8. Cross section of a fertile thallus with carposporangia.



Figs. 9–15. *Porphyra leucosticta*. Fig. 9. Surface view of marginal monosporangia. Figs. 10–12. Haploid mitotic nuclei with n=3. Fig. 10. Two spermatangia in late prophase. Fig. 11. Vegetative thallus cell. Fig. 12. Vegetative conchocelis cell. Fig. 13. Early stages of unipolar germination of carpospore. Fig. 14. Conchocelis thallus originated from unipolar germination of carpospores. Fig. 15. Conchosporangia differentiated on conchocelis filaments.

Table 1. Effect of photoperiod and temperature on the carpospore germination of *Porphyra leucosticta* at 50 $\mu E \cdot m^{-2} \cdot s^{-1}$

Photoperiod (h light : h dark)	Temperature (°C)	Carpospore germination
8 : 16	10	+
	15	+
	18	+
	22	+
	25	−
12 : 12	10	+
	15	+
	18	+
	22	+
	25	−
16 : 8	10	+
	15	+
	18	+
	22	+
	25	−

weekly. About twenty globose tufts of *conchocelis* filaments were allowed to grow in each dish, and three dishes where used in each experiment.

A cross-gradient incubator was used to test growth and reproduction of conchocelis filaments in different combinations of light and temperature. Cool white OSRAM fluorescent lamps produced a photon flux density at the surface of cultures between 5 and 70 $\mu E \cdot m^{-2} \cdot sec^{-1}$, measured with a LICOR Quantum radiometer model LI 185 A. Light regimes were: 8L : 16D; 9L : 15D; 12L : 12D; 16L : 8D. Experimental temperatures ranged between 10 and 28°C.

Field observations on local marine environmental conditions and on phenology of *P. leucosticta* were carried out weekly during three years (1990-92).

Chromosome counts were obtained for cultured and field collected material after fixation in 3 : 1 ethanol : glacial acetic acid and aceto-orcein staining (Gargiulo *et al.* 1991).

Observations and photomicrographs were made on a Leitz Diaplan microscope equipped with a standard optical system and Nomarsky interferential contrast.

Observations

1. *Thallus morphology.* Gametophytic plants are monoecious; the blades are lanceolate to multilobed with ruffled margin, up to 15 cm, but umbilicate plants are also frequent (Fig. 1). The base of the blade is orbiculate with a tiny holdfast. Plants are reddish purple, with linear whitish patches where spermatangia are formed. The plants are saxicolous.

2. *Microscopic observations.* The blade is monostromatic (Fig. 2), in surface view cells appear roughly quadrangular 10–15 × 15–20 μm (Fig. 3). Spermatangia differentiate

Table 2. Effect of photoperiod and temperature on the formation of conchosporangia of *Porphyra leucosticta* at 50 $\mu E \cdot m^{-2} \cdot s^{-1}$

Photoperiod (h light : h dark)	Temperature (°C)	% of *Conchocelis* thalli producing sporangia
8 : 16	10	Filaments remain vegetative
	15	100% conchosporangia formed
	18	100% conchosporangia formed
	22	Filaments remain vegetative
12 : 12	10	Filaments remain vegetative
	15	15% conchosporangia formed
	18	15% conchosporangia formed
	22	Filaments remain vegetative
16 : 8	10	Filaments remain vegetative
	15	Filaments remain vegetative
	18	Filaments remain vegetative
	22	Filaments remain vegetative

Table 3. Effect of photoperiod and temperature on the conchospores release of *Porphyra leucosticta* at 50 $\mu E \cdot m^{-2} \cdot s^{-1}$

Photoperiod (h light : h dark)	Temperature (°C)	% of *Conchocelis* thalli releasing spores
8 : 16	10	No release
	15	No release
	18	70% spores released
	22	No release
9 : 15	10	No release
	15	No release
	18	100% spores released
	22	No release
12 : 12	10	No release
	15	No release
	18	No release
	22	No release
16 : 8	10	No release
	15	No release
	18	No release
	22	No release

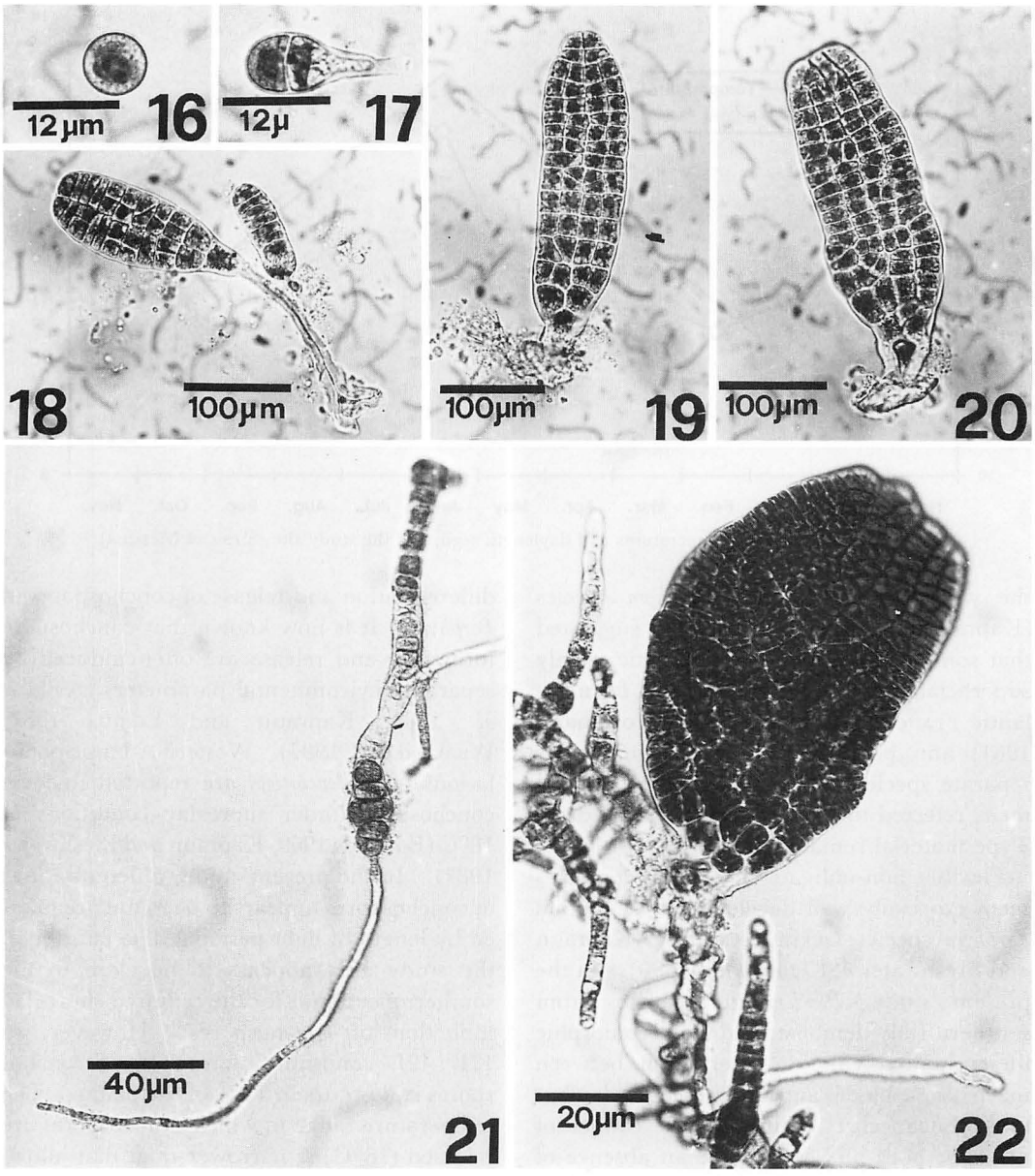
in the distal part of the blade in whitish stripes (Fig. 4) and marginal zones (Fig. 5). A single spermatangium (Figs. 5, 6, 8) is about 13×18 μm and forms 64 spermatia. Carpogonia are about 15×20 μm, formed adjacent to areas where spermatangia are differentiated. Developing carposporangia give rise to 8 carpospores (Figs. 5-8). Monospores are directly derived from vegetative cells on the margin of the blade (Fig. 9).

3. *Karyological observations.* Haploid chromosome numbers of $n=3$ were observed in spermatangia (Fig. 10), vegetative blade cells (Fig. 11) and conchocelis filaments (Fig. 12).

4. *Culture.* The fragments of leafy plants in culture released carpospores in all the tested conditions of light and temperature; the photoperiod had no influence on the release of carpospores. Germination of carpospores was observed 6 to 12 days from their release.

Unipolar germination of carpospores (Figs. 13, 14) results in the formation of branched filaments of the conchocelis stage which more or less adhere to the culture vessel or, more frequently, assume a free cushion shape. The effects of photoperiod and temperature on carpospore germination are shown in Table 1. Under optimal environmental conditions, the filaments differentiate conchosporangia (Fig. 15) that release conchospores. These germinate in a bipolar way forming new blades (Figs. 16-20). Under long-day conditions the *conchocelis* filaments never differentiated conchosporangia. The effects of photoperiod and temperature on the differentiation of cochosporangia on the filamentous plants are shown in Table 2. The release of conchospores was observed only under short-day regimes, and only at 18°C. The effects of photoperiod and temperature on the release of conchospores are shown in Table 3.

Formation of monospores on the conchocelis phase was not observed in these experiments. However, the unipolar germination of cells that are morphologically similar to conchospores resulted in conchocelis filaments (Fig. 21). In a few cases, the filaments formed irregular outgrowths lacking polarity (Fig. 22). These protothalli (*sensu* Cole and Conway 1980) soon disaggregate into single cells, which after bipolar germination, formed leafy gametophytic plants.



Figs. 16–22. *Porphyra leucosticta*. Figs. 16–20. Bipolar germination of carpospore and early formation of laminar gametophytic thallus. Fig. 21. *In situ* unipolar germination of a cell-like conchospore. Fig. 22. Formation of a protothallus from conchocelis filaments.

5. *Field observations.* The intertidal sea temperature where field observations were carried out ranged between 15°C in February and 25°C in August. The pattern of average temperatures as well as hours of light the year round are presented in Fig. 23.

Gametophytic blades appeared in November and were present until early June. Conchocelis filaments were not observed in nature.

Discussion

Porphyra leucosticta is reported to have one of

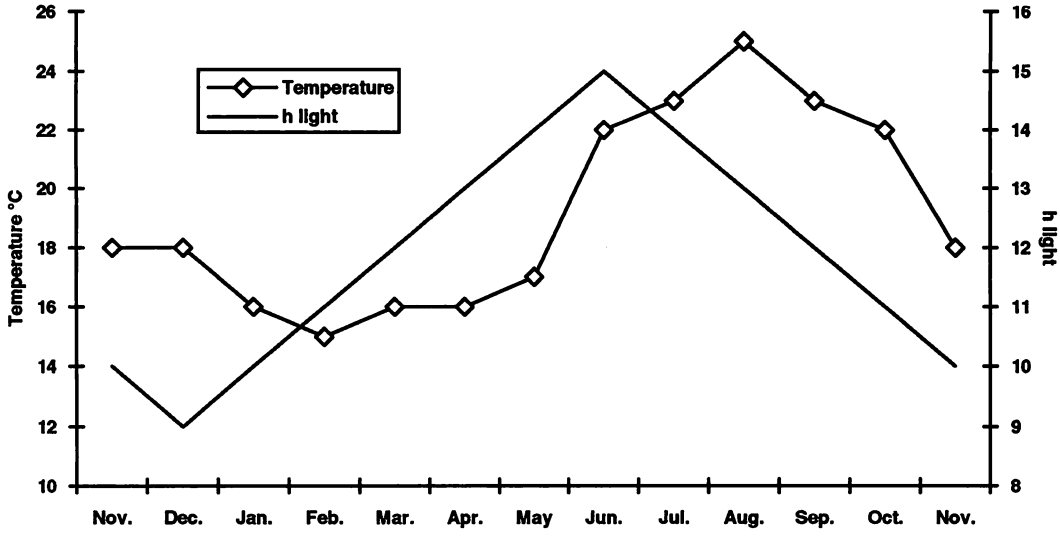


Fig. 23. Annual temperatures and daylength regime of the study site (Strait of Messina).

the widest ranges of any *Porphyra* species (Kapraun *et al.* 1991). It has been suggested that some of these regional populations only superficially resemble Type material from Atlantic France (Rosenvinge 1909, Kornmann 1961) and perhaps deserve recognition as separate species. The relationship of specimens referred to *P. leucosticta* in this study to Type material remains unknown.

Flexible non-obligate life history patterns seem especially well developed in temperate *Porphyra* species lacking sexuality (Kapraun and Freshwater 1987, Hawkes 1990). In the present study, *P. leucosticta* isolates from southern Italy demonstrated a heteromorphic life-cycle involving an alternation between macroscopic blades and a microscopic filamentous conchocelis. Chromosome counts of n=3 for both phases indicate an absence of sexuality and meiosis in these isolates. *Porphyra leucosticta* populations in North Carolina and Texas (Kapraun and Freshwater 1987, Kapraun *et al.* 1991), Uruguay (Coll and de Oliveira 1977a, b) and Helgoland (Kornmann 1961) are reported to have similar asexual life histories. In contrast, populations from Nova Scotia are reported to be sexual (Yabu 1978, Lindstrom and Cole 1992).

Kurogi (1959) first demonstrated the effects of temperature and photoperiod on the differentiation and release of conchospores in *Porphyra*. It is now known that conchospore formation and release are often induced by separate environmental parameters (Avila *et al.* 1986, Kapraun and Lemus 1987, Waaland *et al.* 1987). Western Atlantic populations of *P. leucosticta* are reported to form conchospore under short-day conditions at 18°C (Edwards 1969, Kapraun and Freshwater 1987). In the present study, differentiations of conchospores appears to be mainly regulated by length of light period. The latitude of the study area appears to be close to the southernmost limit for the required short-day induction of conchospores. However, in 12L : 12D conditions, formation of conchospores still occurs in 15% of the plants. The temperature range in which conchospores are released (18°C) is narrower than that allowing their formation (15-18°C). Water temperature in the intertidal in latitudes to the south of the study area becomes critical, often exceeding the temperature which permits differentiation of conchosporangia.

It is noteworthy that in culture, *P. leucosticta* demonstrated direct development of blades from the filamentous phase by differentiation of prothallus cells (Cole and Conway 1980). Germination of conchospore-like monospores resulted in the formation of new filamentous

thalli. The importance of these accessory reproductive modes to the persistence of *P. leucosticta* in the study area remains unknown.

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G. M. Gargiulo・F. De Masi*・G. Genovese*・G. Tripodi*：地中海産 *Porphyra leucosticta* Thuret in Le Jolis（紅藻，ウシケノリ目）の核学と生活環における温度と日長条件の効果について

イタリア，メッシナ海峡のアマノリ属のうち，これまで *Porphyra leucosticta* Thuret in Le Jolis として扱われてきた種につき野外及び室内での研究を行った。本種は照度・温度勾配装置による培養の結果，殻胞子の形成には短日条件 (9L : 16D) と 15–18°C の温度条件を必要とすることが明らかになった。また，殻胞子の放出には 18°C と短日条件が必要である。培養結果により調査地点での季節変化の説明を試みた。培養下では大型の葉状体と顕微鏡的な大きさのコンコセリスの間での交代がみられた。ふつう殻胞子から葉状体が発達する際には双極的な発芽をするのに対し，コンコセリスが発達する際には単極的な発芽をする。また，葉状体，糸状体のいずれも直接型の発芽をする。栄養的な葉状体，造精器，コンコセリスの栄養細胞では染色体数は n＝3 であった。(University of Reggio Calabria, Piazza S. Francesco 4, 89061 Reggio Calabria, Italy,* University of Messina, CP 58 98166 Messina S. Agata, Italy)

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The ultrastructure of tetrasporogenesis in *Dictyota dichotoma* (Hudson) Lamouroux (Dictyotales, Phaeophyceae)

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Katsaros, C. I. and Pentaris, K. 1994. The ultrastructure of tetrasporogenesis in *Dictyota dichotoma* (Hudson) Lamouroux (Dictyotales, Phaeophyceae). Jpn. J. Phycol. 42: 281–290.

The first sign of tetrasporogenesis in *Dictyota dichotoma* (Hudson) Lamouroux is the outgrowth of certain epidermal cells that follow a characteristic differentiation process. These cells soon become polarized and constitute the tetrasporangium mother cells (TMCs). Three distinct zones are established along their growth axis: one apical, full of small vesicles, one central, in which most of the organelles are aggregated, and a basal one with large vacuoles and peripheral chloroplasts. The nucleus is displaced towards the basal zone and, as the cell grows outwards, the thick multilayered external wall breaks while new layers are deposited on its internal surface. An asymmetrical division of the TMC results in the formation of the tetrasporangium, which is obviously larger than the stalk cell(s), with more dense cytoplasm and numerous organelles distributed along its anticlinal axis. This cell undergoes a characteristic differentiation proccess, the polarity pattern changing from axial to radial. Finally, it becomes almost spherical. After meiosis, four haploid nuclei are formed and the organelles are arranged in groups around them. During these stages many active dictyosomes are observed, secreting an amorphous material, that is deposited between the membranous septa separating the tetraspores, as well as in the inner side of the external wall. This material is probably mucilagenous and may help, by absorbing water, in the breaking of the external wall, thus facilitating the release of the spores.

Key Index Words: asymmetrical division—Dictyota—*Phaeophyceae—polarity—tetrasporogenesis—ultrastructure.*

The study of the reproductive processes of algae has been proved a significant tool for the understanding of many cytological, taxonomical and physiological problems. Moreover, these studies, combined with the fine structural investigation of thallus development and differentiation, give answers to some important morphogenetic problems.

Within the brown algal order Dictyotales the study of the reproduction has started very early, with the pioneer work of Williams (1897, 1904a, b, 1905). More than fifty years later a number of light microscope studies appeared, dealing with tetraspore formation in some members of Dictyotales, like *Dictyota dichotoma* (Hudson) Lamouroux, *Dictyopteris divaricata* (Okamura) Okamura, *Padina japonica* Yamada and *P. crassa* Yamada (Ishii *et al.* 1959, Kumagae *et al.* 1960). On an ultrastructural level, there are detailed studies on thallus structure and development of *D. dichotoma* and *Dictyopteris membranacea* (Stackh.) Batt. (Katsaros 1980, Katsaros and Galatis 1985, 1988, Gaillard *et al.* 1986). However, only a few ultrastructural studies have been published, dealing with reproductive stages. These describe the structure of sperms of *D. dichotoma* (Manton *et al.* 1953, Manton 1959) and eggs of *Dictyota binghamiae* J. Agardh (Neushul and Liddle 1968), as well as oogonia and eggs of *Zonaria farlowii* S. & G. (Neushul and Liddle 1968, Liddle and Neushul 1969). In addition, the sexual reproduction of *Dictyota diemensis* Kützing was recently studied in detail by means of both, light and electron microscopy (Philips *et al.* 1990). As far as we know, there is no ultrastructural information on tetrasporogenesis of any member of this class.

The aim of the present study is to inves-

tigate the ultrastructural changes accompanying the tetrasporogenesis in *D. dichotoma*, with particular attention to those preceding, accompanying and/or following the establishment of a new polarity axis and the shift in the differentiation process.

Materials and Methods

Thalli of *Dictyota dichotoma* were collected between April and June at a depth of 1-3 m at "Rafina", about 30 km from Athens, Greece. Small pieces of mature thallus portions bearing tetrasporangia and unreleased tetraspores were fixed and processed for EM according to Katsaros and Galatis (1986), with a more prolonged (up to three days) infiltration time (see also Hallam and Luff 1988). Thin sections were examined and photographed with a Philips 300 electron microscope.

Results

Tetrasporangium mother cell (TMC)

Tetrasporogenesis in *D. dichotoma* is not synchronous. Therefore, all the developmental stages can be traced on a limited thallus area. Tetrasporangia occur alone or in small groups along the central part of the thallus, at some distance from the apex.

The first sign of TMC formation is the outgrowth of certain epidermal cells (Fig. 1). Sometimes two or more adjacent cells are observed swelling in parallel. These cells are devoid of large vacuoles and have a more dense cytoplasm compared to their neighbouring cells. The swelling grows outwards resulting in a pear-like form (Fig. 3). The structural polarization of this cell is further expressed by the deposition of additional layers of wall material in the external periclinal wall (Figs. 1, 2) and the gradual distribution of the cell elements in three distinct zones along the cell axis: 1) an apical zone with numerous dictyosomes, vesicles and small vacuoles, 2) a subapical zone in which the nucleus and most of the organelles around it are localized, and 3) a basal one with well developed vacuoles and peripherally distributed chloroplasts (Figs. 2, 3).

As the cell grows outwards, the thick multilayered external wall breaks and new, less dense layers are deposited on its internal surface. A large number of vesicles and small vacuoles are observed in the apical region (Fig. 2). The nucleus is larger than that of typical epidermal cells and is usually lobed. A centriole is usually displaced in a depression of the nuclear envelope (Fig. 6). The chloroplasts are smaller than those of typical epidermal cells, with poor internal membrane organization (cf. Figs. 4 and 5). Small vacuoles, dictyosomes, physodes and endoplasmic reticulum (ER) membranes are observed among them (Fig. 5).

TMC-surrounding epidermal and stalk cells

The epidermal cells surrounding the TMC follow a characteristic differentiation process parallel to TMC formation. This process results in a polar organization of these cells which is expressed by: 1) Cell outgrowth that is parallel to that of the TMC, but not so extensive (Figs. 1, 3). 2) Zonation of the organelles in a way similar to that of the

Fig. 1. Light micrograph showing two TMCs and the surrounding epidermal cells, as appear in transverse thallus section. TMC: tetrasporangium mother cell. Scale bar=30 μm.

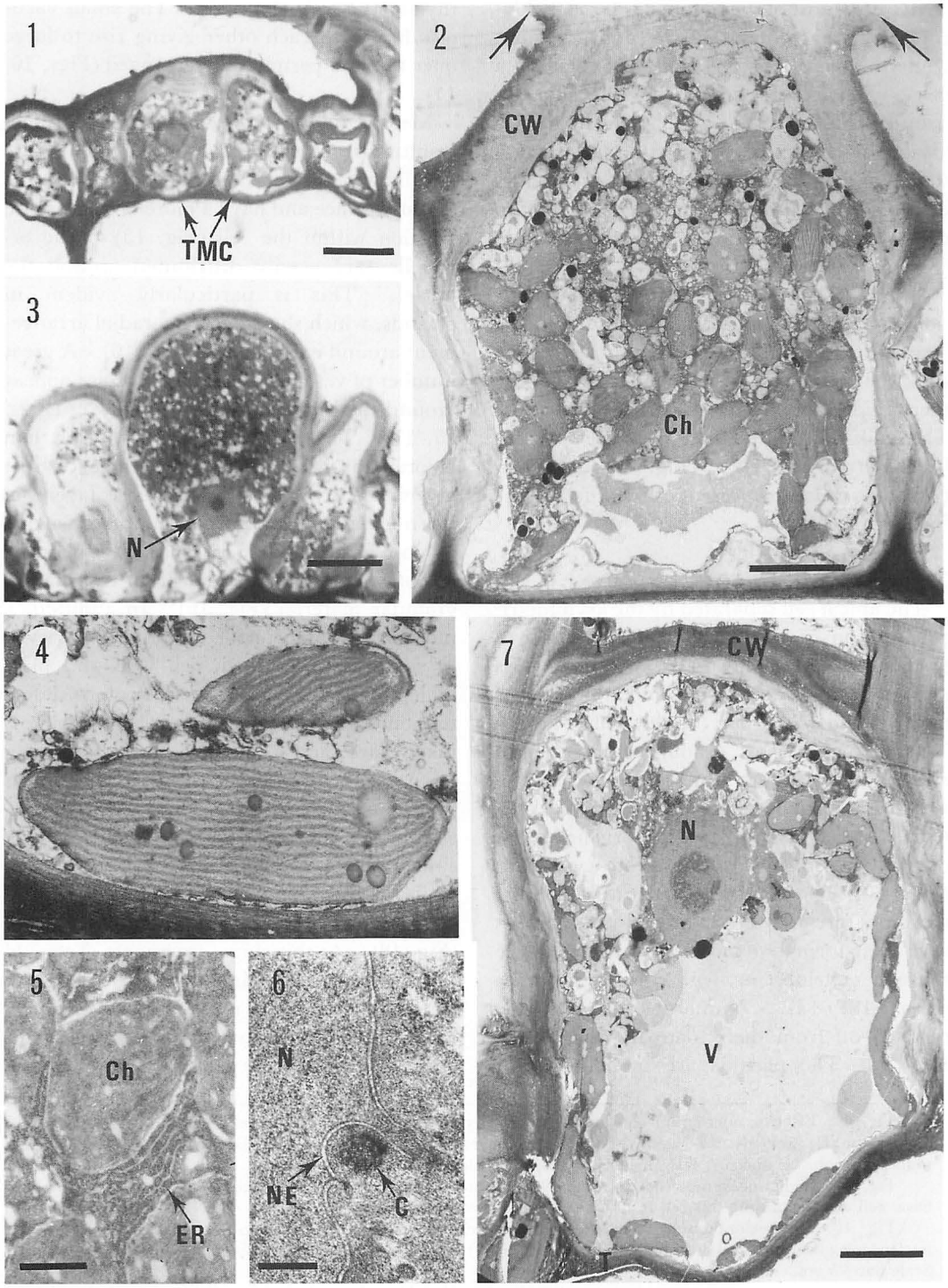
Fig. 2. Transverse thallus section passing through the cortical cytoplasm of a TMC at an early developmental stage. The distribution of cell elements varies gradually along its anticlinal axis. Note the break of the external layers of the cell wall at the apical dome area (arrows). Ch: chloroplast, CW: cell wall. Scale bar=5 μm.

Fig. 3. Light micrograph of a TMC at a more advanced developmental stage. The polarization is further expressed by the position of the nucleus towards the basal part of the cell. N: nucleus. Scale bar=25 μm.

Figs. 4, 5. Plastids of a typical epidermal cell (Fig. 4) and of a TMC (Fig. 5). Ch: chloroplast, ER: endoplasmic reticulum. Scale bar=1 μm.

Fig. 6. Part of the nucleus and the perinuclear cytoplasm of a TMC. The nuclear envelope shows invaginations and the centriole is located in a deep depression of it. C: centriole, N: nucleus, NE: nuclear envelope. Scale bar=0.5 μm.

Fig. 7. Epidermal cell surrounding a TMC. CW: cell wall, N: nucleus, V: vacuole. Scale bar=5 μm.


1
TMC
2
CW
Ch
3
N
4
5
Ch
ER
6
N
NE
C
7
CW
N
V

TMC, i.e. most of the organelles (except chloroplasts) are gathered in the apical region, while the basal part is usually occupied by a large vacuole and typical peripherally distributed chloroplasts (Fig. 7). The nucleus is located in the central region with many dictyosomes and mitochondria around it (Figs. 7, 8). 3) The cell wall structure is similar to that of the TMC with thick multiple layers (Fig. 7).

After the completion of TMC differentiation, an asymmetrical division results in the formation of the tetrasporangium and one stalk cell (Figs. 9, 10). The latter can be further divided, giving rise to a two-celled stalk. The stalk cell is similar in structure with the basal part of the TMC (Fig. 10) and when two stalk cells are present, this difference is further amplified.

Tetrasporangium and tetraspore formation

The apical cell separated by the asymmetrical division of the TMC continues growth further, symmetrically in all directions. Its nucleus is large and lobed, and is positioned towards the basal part of the cell (Fig. 9). This cell undergoes gradual differentiation and finally becomes almost spherical (Fig. 11). The nucleus migrates towards the centre of the cell and most of the organelles are distributed in the perinuclear cytoplasm (Figs. 10, 11). A large number of active dictyosomes are observed around the nucleus with their formative faces associated with the nuclear envelope or with ER membranes (Figs. 12, 13). Numerous vesicles are pinched off from their maturing face (Figs. 12, 13). The plastids are small with few thylakoid bands (Fig. 14). The small vacuoles fuse with each other giving rise to large ones that are peripherally arranged (Figs. 10, 11).

Meiotic division takes place at this stage, resulting in four haploid nuclei. They are usually arranged in one plane parallel to the thallus surface and have a more or less central position within the cell (Fig. 15). The organelles are evenly distributed around the nuclei. This is particularly evident in plastids, which show a strictly radial arrangement around each nucleus (Fig. 16). A great number of vesicles and small vacuoles appear around the nuclei-organelle complexes (Figs. 15, 17). The cell wall appears thicker than before, consisting of at least three distinct layers: an external electron dense layer, an intermediate more transparent one consisting of loose fibrils, and an internal one consisting of both dense fibrillar and more transparent granular material (Fig. 16). In addition, a more or less amorphous material is observed in some areas between cell wall and plasmalemma (Fig. 16). After the complete formation of the four haploid nuclei, cytokinesis takes place, and a thin membranous septum separates the tetraspores (Figs. 17, 18). This septum at the first stages of its formation consists of two more or less parallel membranes similar to those of the surrounding vesicles, while in more advanced stages an electron dense material is deposited between them (Fig. 18). At this stage, fragments of the old external excised wall layers are observed (Fig. 17). The amorphous material along the internal face of the external cell wall appears increased, while similar material occurs on both

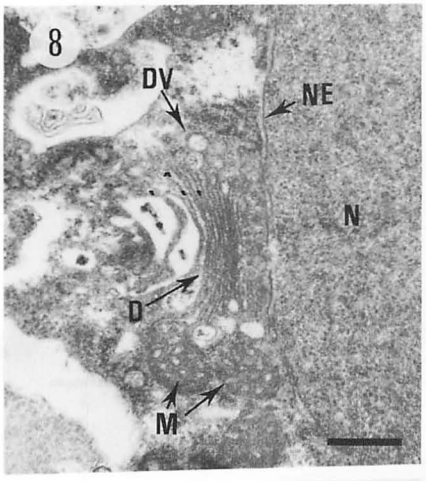
Fig. 8. Electron micrograph showing a part of the perinuclear cytoplasm of a cell surrounding a TMC. A dictyosome (D) is closely associated with the nuclear envelope by its formative face. DV: dictyosome vesicle, M: mitochondrion, N: nucleus, NE: nuclear envelope. Scale bar=0.5 μm.

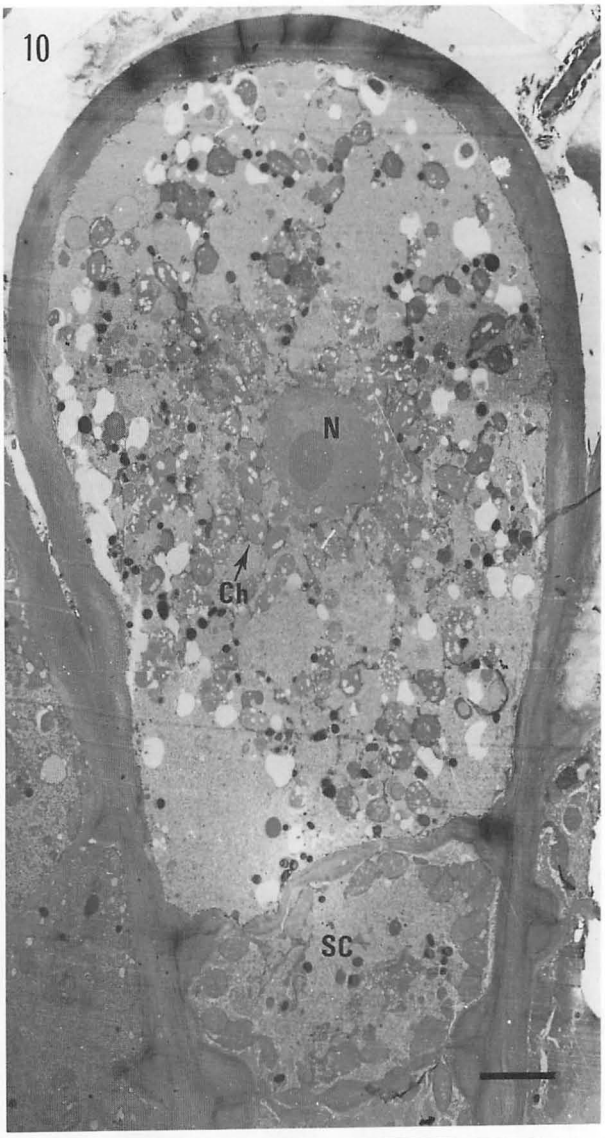
Fig. 9. Light micrograph showing a newly-formed tetrasporangium. The nucleus (N) is located close to the basal cell wall separating this cell from the stalk cell. Scale bar=25 μm.

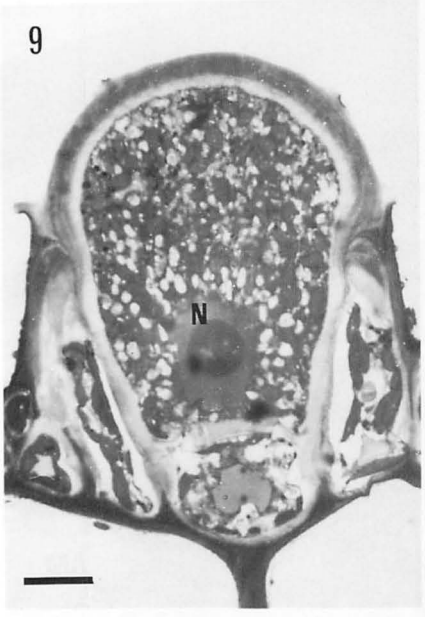
Fig. 10. Tetrasporangium at a more advanced developmental stage compared to that shown in Fig. 9. The nucleus has taken a central position and the stalk cell (SC) has been further divided. Ch: chloroplast, N: nucleus. Scale bar=5 μm.

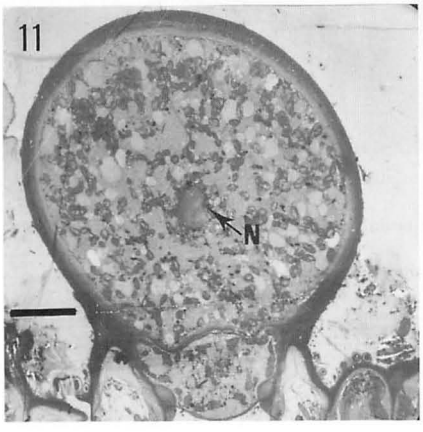
Fig. 11. Tetrasporangium before meiosis. Its shape is spherical and the nucleus (N) is centrally positioned. Scale bar=10 μm.

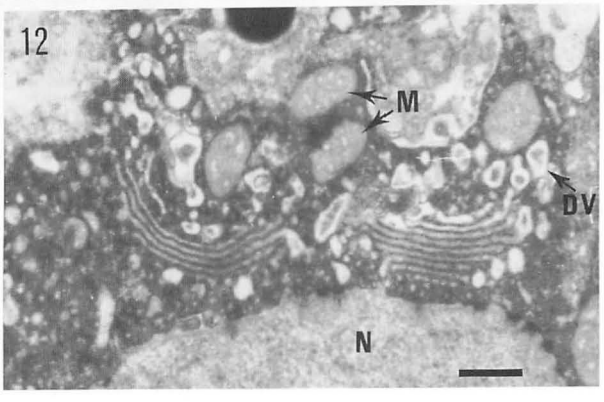
Fig. 12. Part of the nucleus and the perinuclear cytoplasm of a tetrasporangium. Two dictyosomes are closely associated with the nuclear envelope. DV: dictyosome vesicles, M: mitochondrion, N: nucleus. Scale bar=0.4 μm.


8
DV
NE
N
D
M


10
N
Ch
SC


9
N


11
N


12
M
DV
N

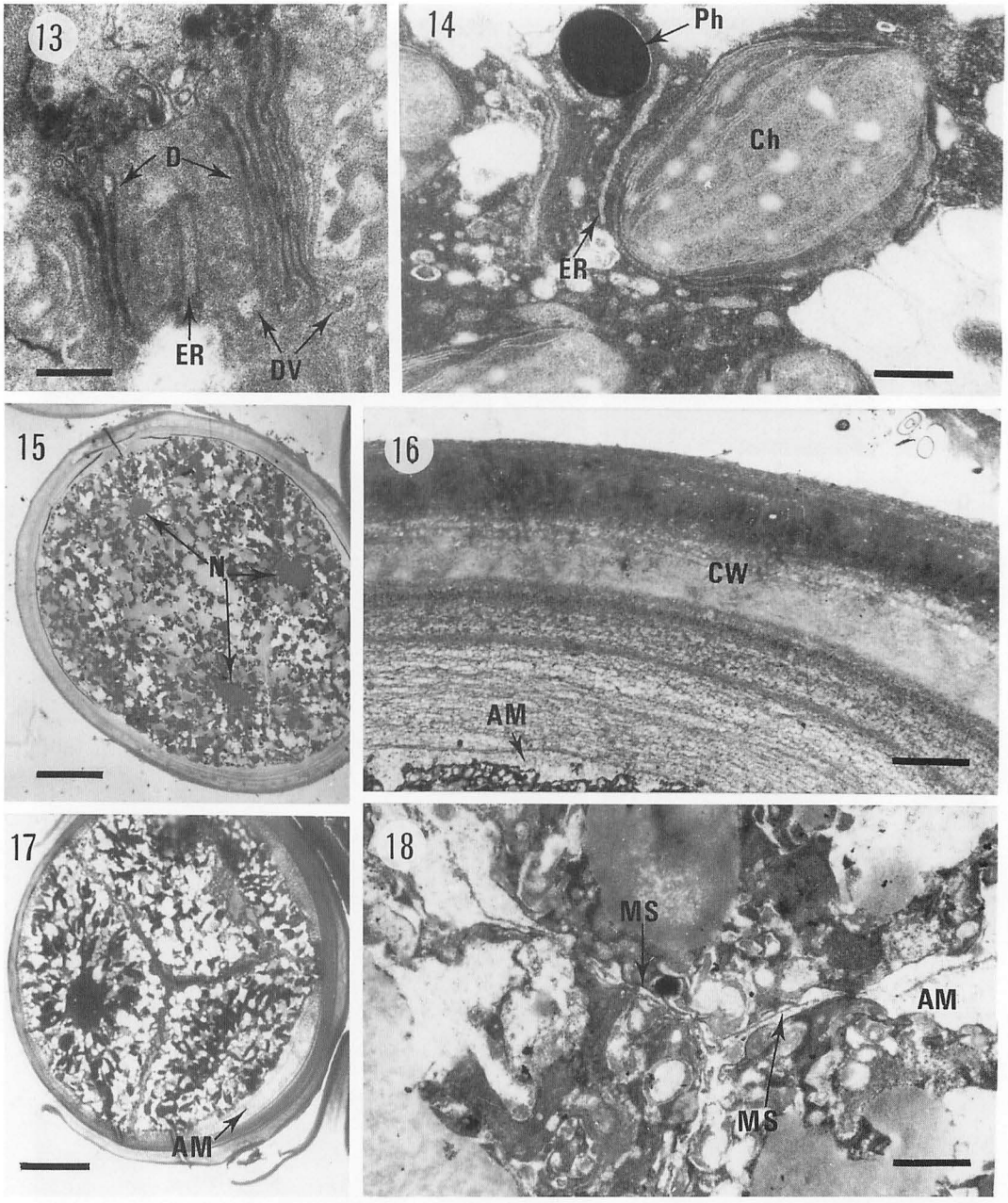


Fig. 13. Two active dictyosomes (D) of a young tetrasporangium. DV: dictyosome vesicle, ER: endoplasmic reticulum. Scale bar=0.3 μm.

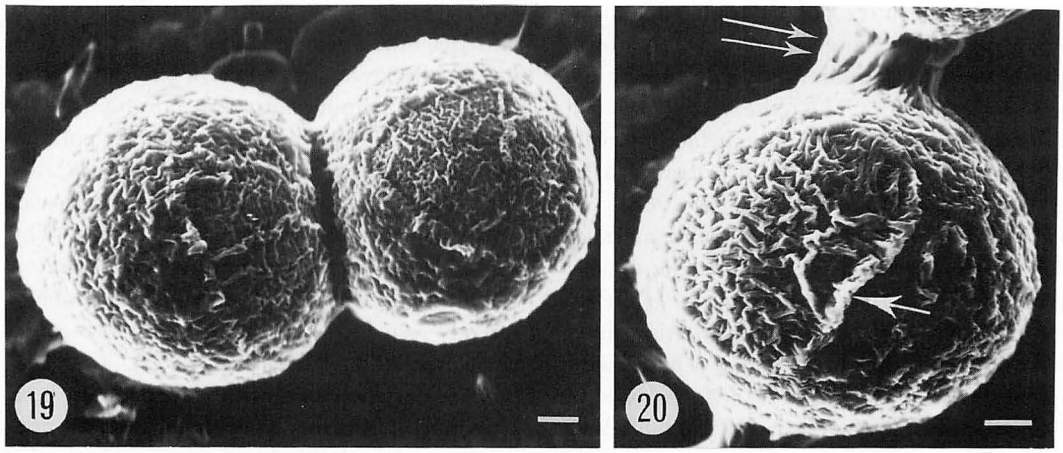
Fig. 14. Plastids of a tetrasporangium. Ch: chloroplast, ER: endoplasmic reticulum, Ph: physode. Scale bar=0.4 μm.

Fig. 15. Pre-cytokinetic tetrasporangium. Meiosis has already taken place. Three of the four haploid nuclei (N) are visible. Scale bar=10 μm.

Fig. 16. Part of the wall of a tetrasporangium at the stage of the meiotic division. AM: amorphous material, CW: cell wall. Scale bar=3 μm.

Fig. 17. Light micrograph showing a post-cytokinetic tetrasporangium. Three tetraspores are observed. AM: amorphous material. Scale bar=10 μm.

Fig. 18. Detail of the membranous septum (MS) separating the young tetraspores. AM: amorphous material. Scale bar=1 μm.



Figs. 19, 20. Scanning electron micrographs of young tetrasporangia. Their surface exhibits a shrink-like appearance. Arrow in 20 indicates the possible trace of the wall separating the tetraspores. Double arrows show amorphous material connecting two neighbouring tetrasporangia. Scale bar=10 μm.

sides of the partition membranes (Figs. 17, 18). Examination of material under the scanning electron microscope, reveals that the tetrasporangia at the stage before tetraspore release, appear spherical, with an irregular and shrinked external surface (Figs. 19, 20). Sometimes neighbouring tetrasporangia appear sticked together by an amorphous material (Fig. 20). In the tetrasporangium of Fig. 20 the cytokinesis of the meiotic division is probably finished, and the wall separating the tetraspores can be seen as an intense shrinkage on the external surface of the tetrasporangium.

Discussion

The present observations on the sequence of cell divisions that result in tetraspore formation, confirm those made with light microscope by Williams (1904a), Ishii *et al.* (1959) and Kumagae *et al.* (1960). The first ultrastructural change in the process of tetrasporogenesis is the de-differentiation of certain epidermal cells, the TMCs. The increased metabolic activity of these cells, compared to typical epidermal cells, is expressed by the dense cytoplasm and numerous small vacuoles. The chloroplasts, due to repeated divisions, become small and undifferentiated. This process is similar to that already described during branch or propagule mother cell formation in *Sphacelaria tribuloides* Meneghini (Katsaros 1980) and unilocular sporangium development in *Halopteris filicina* (Grateloup) Kützing (Katsaros and Galatis 1986). These changes are accompanied by outgrowth of the TMC, followed by the establishment of a new polar axis in it. Polarization is further expressed by the distribution of the organelles in particular zones. A similar organization occurs in apical cells of *Zonaria farlowii* (Neushul and Dahl 1972), *Dictyopteris membranacea* (Katsaros 1980, Katsaros and Galatis 1988), and *Sphacelaria tribuloides* (Katsaros 1980, Katsaros *et al.* 1983). It seems that at this stage the TMC behaves like an apical cell, showing a kind of tip growth. However, after the asymmetrical division of the TMC the polarity pattern changes from axial to radial. This results in the formation of the tetrasporangium, which gradually becomes almost spherical, with a radial distribution of the organelles around the centrally located nucleus. The cell organization at this stage is comparable to that of the sporangium of *H. filicina* before meiosis (Katsaros and Galatis 1986). However, ultimately the organelles in the tetrasporangium of *D. dichotoma* show a perinuclear distribution, whereas in *H. filicina* they are more or less evenly distributed throughout the sporangium volume.

The change in the polarity pattern is in accordance with a change in the growth pattern, which becomes apparent by the evenly expanding cell wall. The old external wall layers cannot accomodate the surface increase and break under the internal pressure, as in *H. filicina* (Katsaros and Galatis 1986). In parallel, the deposition of new wall material is carried out by numerous dictyosome vesicles released from active dictyosomes near the expanding cell wall. Similar observations have been made in other brown algal cells showing apical growth (Katsaros 1980, Katsaros *et al.* 1983, Katsaros and Galatis 1985, 1988, 1990, Gaillard *et al.* 1986).

The presence of specialized sterile cells surrounding the sporangial sori is not a general feature of Dictyotales, but it has also been observed in *D. diemensis* (Philips *et al.* 1990). Their fine structure is different from the typical epidermal cells, showing polar growth and increased metabolic activity. This activity is indicated by the shape and size of the nucleus, as well as the abundance of dictyosomes and dictyosome vesicles. Since the differentiation of the cells surrounding the TMCs in *D. dichotoma* is limited and stops before the completion of tetraspore formation, their particular activity can be attributed to a coordination with the TMCs.

After meiosis, the four haploid nuclei occupy a more or less central area of the cell and do not divide further, in contrast to *H. filicina* zoospore formation (Katsaros and Galatis 1986). The organelles are re-arranged, in order to give a full organelle complement to each nucleus. This is the "coenocytic tetranucleated stage", in which the organelles show radial arrangement around each of the nuclei. It is noteworthy that occasionally the four nuclei are arranged in one plane, usually parallel to that of the thallus. This protoplast reorganization is different from that observed in developing sporangia of Ectocarpales (Baker and Evans 1973a, b, Loiseaux 1973, Markey and Wilce 1976) and *H. filicina* (Katsaros and Galatis 1986), and was not observed in Laminariales (Toth 1974, Henry and Cole 1982). The differences in the pattern of protoplast reorganization between *D. dichotoma* and the other groups already mentioned, is due to the large difference in the number of the spores forming into the sporangia. Organelle movements and change in the polarity pattern are supposed to be based on interactions of cellular elements, like the cell wall and the cytoskeleton (Schnepf 1986). The organization of the microtubule cytoskeleton in polarized cell types of brown algae has been already studied by immunofluorescence (Katsaros 1992, Rusig *et al.* 1993).

The partition membrane separating the tetraspores, is formed after the protoplast reorganization, probably by the fusion of vesicles that have been aggregated around the nuclei-organelle complexes. A similar process has been described during zoosporogenesis in different brown algal orders (Loiseaux 1973, Toth 1974, Markey and Wilce 1976, Katsaros and Galatis 1986). The external cell wall of the post-cytokinetic tetrasporangium is usually thicker than that of the tetrasporangium mother cell. It appears similar to the three-layered cell wall of the *Fucus* zygote, which consists of an external rather amorphous layer, mainly of alginic acid and sulphated fucoidan, a median layer of cellulose and alginic acid, and an inner layer of sulphated fucoidan fibrils (Callow *et al.* 1978). Inside the external cell wall, and also on both sides of the membranous septa that separate the tetraspores, the amorphous deposits of granular material increase significantly. This material is possibly mucilagenous and may help, by absorbing water, in the breaking of the external cell wall and the release of the tetraspores. It has been reported that in various algal species a mucilagenous material secreted among zoospores generates pressure that forces the sporangial wall to break down locally (Loiseaux, 1973, Toth 1974, 1976a, b, Markey and Wilce 1976, Katsaros and Galatis 1986). However, a local digestion of the internal cell wall cannot be excluded (Markey and Wilce 1976, Toth 1976a, b), although Kumagae *et al.* (1960) have noticed that the four tetraspores are released together bounded by intact inner layers of cell wall.

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Christos I. Katsaros・Konstantinos Pentaris：褐藻アミジグサ *Dictyota dichotoma* (Hudson) Lamouroux（アミジグサ目）の四分胞子形成における微細構造

アミジグサの四分胞子形成は，ある表層細胞の外側への発達により始まり，それに引き続き特徴的な分化がみられる。これらの細胞はすぐに極性を持つにいたり，四分胞子嚢母細胞になる。これらの細胞の成長の軸において三つの顕著な領域が生じる。すなわち小さな小胞に満たされた頂端領域，ほとんどの細胞内小器官が集合した中心領域，大きな液胞と表面に集まった葉緑体がみられる基部領域である。核は細胞が外側に向けて成長するにつれ基部領域に移動し，厚い多層の外側の細胞壁は，新しい層が内側に向け形成されるにつれて崩壊する。四分胞子嚢母細胞の非相称分裂により四分胞子嚢が形成されるが，これは柄細胞よりはるかに大きく，またより密度の高い細胞質と背軸にそって分布する多くの細胞内小器官を有する。この細胞は特徴的な分化過程を経て極性が軸にそう方向から放射状に変化する。最終的にそれはほとんど球状になる。減数分裂の後，4つの単相の核が形成され細胞内小器官はそれらの回りに集まって配置する。この段階では多くの活動的なディクティオソームがみられ，不定形の物質を分泌している。これらは4分胞子を隔てている膜状の隔壁の間や外側の細胞壁の内側に蓄積する。この物質は多分粘質で，水分を吸収することで外側の細胞壁の崩壊を助け，それにより胞子の放出を引き起こしていると考えられる。(Institute of General Botany, University of Athens, Athens 157 84, Greece)

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Gamete surface and attachment during fertilization of *Palmaria* sp. (Palmariales, Rhodophyta)

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Mine, I. and Tatewaki, M. 1994. Gamete surface and attachment during fertilization of *Palmaria* sp. (Palmariales, Rhodophyta). Jpn. J. Phycol. 42: 291–299.

Attempts to characterize the gamete surface structures of *Palmaria* sp. (Palmariales, Rhodophyta) were made. The colorless covering of the living and chemically fixed spermatium was degraded by proteolytic enzymes added to the spermatial suspension without affecting cell structure and viability. The trichogyne cell wall was coated with a fibrous structure containing vicinal glycol residues which were destroyed by periodic acid oxidation followed by sodium borohydride reduction. A brief pretreatment of spermatia by proteolytic enzymes significantly inhibited the gamete attachment as well as the degradation of vicinal glycols of the trichogyne coat. These results suggest that the specific gamete attachment during fertilization of this alga is principally governed by these adhesive surface structures.

Key Index Words: cell surface—fertilization—gamete attachment—Palmaria—*proteolytic enzymes—Rhodophyta—spermatium—trichogyne—vicinal glycols.*

In the life history of red algae, syngamy is achieved by fusion between a non-flagellated spermatium liberated from a spermatangium and a trichogyne, a specialized process of a carpogonium formed on the thallus. Though amoeboid movement has frequently been noted in red algal spermatia (Dixon 1973), the initial attachment of the passively moving spermatia to the trichogyne is established immediately after spermatium inoculation to trichogynes (Mine and Tatewaki 1994). Therefore, adhesive gamete surfaces may play critical roles in the recognition and attachment between these, essentially non-motile gametes.

There have been a number of ultrastructural and cytochemical studies on the spermatial surface structure in red algae (e.g. Scott and Dixon 1973, Kugrens 1974, 1980, Peel and Duckett 1975, Fetter and Neushul 1981, Magruder 1984, Cole *et al.* 1985, Broadwater *et al.* 1991, Kim and Fritz 1993a, b, Mine and Tatewaki 1994). Some of these studies on bangiacean and ceramiacean algae have shown specialized spermatial appendages concerned with the attachment to trichogynes (Magruder 1984, Cole *et al.* 1985, Broadwater *et al.* 1991, Kim and Fritz 1993a, b). The ultrastructure (Broadwater and Scott 1982, Mine and Tatewaki 1994) and histochemical nature (Cole *et al.* 1985) of the receptive surface of female gametes have also been reported in some species.

Experimental studies on the attachment of spermatia to trichogynes have also existed in several red algae. Comparisons of gamete attachment between intraspecific and intergeneric fertilization have been made in ceramiacean (Magruder 1984) and palmariacean (Mine and Tatewaki 1993) algae. Kim and Fritz (1993a) developed an experimental system for quantitative assays of gamete attachment using a uniseriate ceramiacean alga. They demonstrated the inhibitory effect of a lectin and a specific sugar on the attachment.

The palmariacean algae have a unique life history (van der Meer and Todd 1980, van der Meer 1981, Mitman and Phinney 1985, Deshmukhe and Tatewaki 1990, Mine and Tatewaki 1993) providing a sufficient number

of naked, sessile carpogonia and good opportunities for observations and experiments of the fertilization processes (Mine and Tatewaki 1993, 1994). We have previously shown the morphology of the spermatial covering and trichogyne coat of *Palmaria* sp., both of which apparently mediate the gamete attachment during fertilization of this alga (Mine and Tatewaki 1994). In this paper, we report a part of the cytochemical feature of these gamete surface structures and the inhibition of gamete attachment by chemical and enzymatic pretreatment of the gamete surfaces.

Materials and Methods

Preparation of male and female gametes, and comparative spermatium inoculation

Mature sporophytes and male gametophytes of *Palmaria* sp. were collected from January to June of 1992 and 1993 at Charatsunai, Muroran, Hokkaido. Tetraspore germlings containing mature female gametophytes growing on coverslips, and spermatial suspensions from male gametophytes were prepared as described previously (Mine and Tatewaki 1994). Artificial seawater (ASW) was 450 mM NaCl, 30 mM $MgCl_2$, 16 mM $MgSO_4$, 10 mM KCl, 10 mM $CaCl_2$, and 8.25 mM Tris-HCl (pH 7.8).

To estimate the effect of gamete pretreatment on the gamete attachment, comparative spermatium inoculation experiments were conducted. Pretreatment procedures were as described below and spermatium inoculation was carried out as described previously (Mine and Tatewaki 1994) using pretreated and control gametes. After inoculation, coverslips with tetraspore germlings were then washed by pipetting 10 times with ca. 3 m*l* of calcium-depleting ASW (ASW without $CaCl_2$ added with 1 mM ethylene glycol-bis[beta-aminoethyl ether] N,N,N′,N′-tetraacetic acid) to remove indirectly co-aggregated spermatia (Figs. 1, 2). Samples were then fixed in 1% glutaraldehyde (GA) in ASW for 1-3 h at 4°C. After rinsing with ASW, samples were mounted in a 1 : 1 mixture of ASW and glycerol, and the numbers of trichogynes and attached spermatia were determined under light microscopy.

A gamete attachment was estimated by counting the number of attached spermatia divided by the number of trichogynes grown on the examined coverslip (designated 'spermatia/trichogynes'). In an experiment, tetraspore germlings derived from the same tetraspore suspension were used in both control and experimental duplicate coverslips and they were inoculated simultaneously with

Figs. 1–14. Light and transmission electron micrographs of *Palmaria* sp. Figs. 1, 2. Light micrographs of trichogynes inoculated with untreated spermatia. Living material. Scale bar=50 μm. Fig. 1. Washed in ASW. Numerous indirectly co-aggregated spermatia (arrowhead) remain around a trichogyne (arrow). Fig. 2. Washed in calcium-depleting ASW. Spermatia (arrowheads) attached directly to the trichogynes (arrows) remain. Figs. 3–7. Light micrographs of spermatia prepared in India ink/seawater. Scale bar=10 μm. Figs. 3–5. Living materials. Fig. 3. Untreated. Colorless, ca. 3 μm thick covering (arrowhead) excluding carbon particles of India ink is observed around the cell (arrow). Fig. 4. Treated with 1% Pronase E for 30 min. The spermatial covering (arrowhead) is thinner than that of untreated cells. Fig. 5. Treated with 1% Pronase E for 120 min. The spermatial covering cannot be detected. Figs. 6, 7. Spermatia fixed in 1% GA in seawater attached on coverslips coated with poly-L-lysin. Fig. 6. In 90% ethanol after gradual dehydration. Shrunken spermatial coverings (arrowheads) are outlined by sediment of carbon particles of India ink. Fig. 7. In water after dehydration followed by gradual rehydration. Spermatial coverings (arrowheads) have recovered in thickness. Figs. 8–10. Transmission electron micrographs. Median section of a spermatium. SC indicates a spermatial covering and an arrowhead indicates plasma membrane. Scale bar=0.5 μm. Fig. 8. Untreated spermatium. Fibrous reticulated spermatial covering is observed around plasma membrane. Fig. 9. Treated with 0.1% Pronase E for 90 min. The spermatial covering has thinned moderately. Fig. 10. Treated with 1% Pronase E for 90 min. The spermatial covering is no longer detected. Figs. 11–14. PATAg test on an oblique section of trichogyne. An arrowhead indicates a trichogyne coat. Scale bar=1 μm. Figs. 11, 12. Untreated trichogyne. Fig. 11. Section oxidized with periodic acid. The trichogyne coat is stained positively. Fig. 12. Section oxidized hydrogen peroxide as a control. The trichogyne coat is stained negatively. Figs. 13, 14. Trichogyne treated by oxidation and sodium borohydride reduction before preparation for PATAg test. Section was oxidized with periodic acid in PATAg test. Fig. 13. Trichogyne oxidized with periodic acid. The trichogyne coat is very slightly PATAg-positive. Fig. 14. Trichogyne oxidized with hydrogen peroxide. The trichogyne coat is significantly PATAg-positive.

spermatia of the same spermatial suspension.

Enzymatic treatment of spermatial covering

A spermatial suspension was diluted with ASW into 200 spermatia per μl suspension, mixed rapidly with an equal volume of ASW containing a proteolytic enzyme and kept at room temperature. Proteolytic enzymes used were Pronase E (Protease Type XIV; Sigma Chemical Co., St. Louis), trypsin (Type IX; Sigma), and papain (Wako Pure Chemicals, Tokyo). At the time of measurement, a small part of the mixture was mixed with 1/5-1/20 volume of India ink (Pellikan AG, Hanover) and the outer diameter of the transparent covering which excluded India ink was measured on 10 cells under light microscopy within 5 min. The thickness of the covering was calculated by subtracting the average cell diameter (5 μm) from the meas-

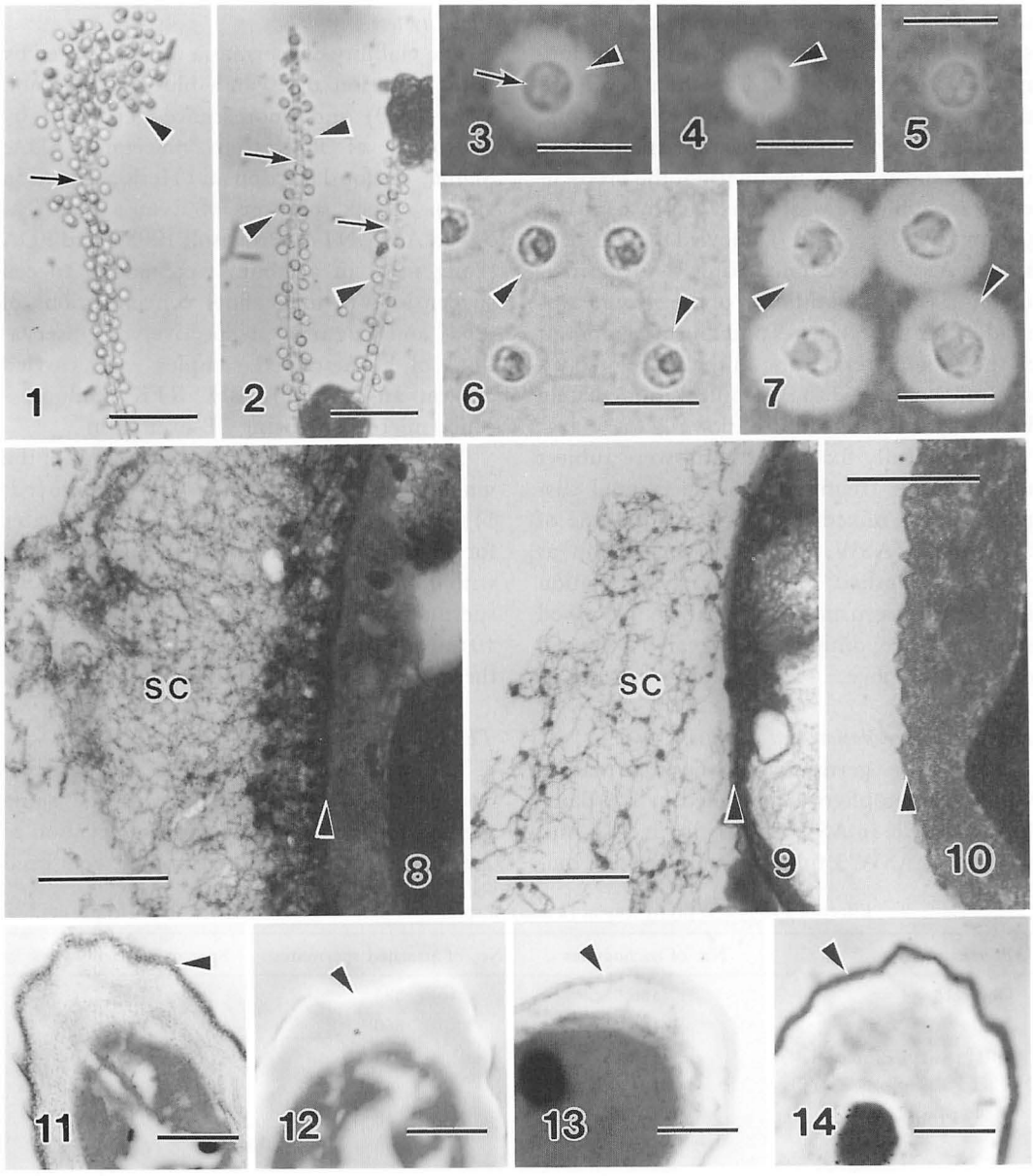


Table 1. Viability test of spermatia after complete degradation of covering.

Treatment	FDA	Evan's blue
None	+	−
1% Pronase E, 180 min	+	−
1% trypsin, 180 min	+	−
1% GA, 30 min	−	+
0.05% saponin, 30 min	−	+
70°C, 10 min	−	+

ured outer diameter and dividing by two. A stock solution of phenylmethylsulphonylfluoride (PMSF; Wako; 0.2 M in ethanol) was added along with trypsin in some experiments.

When enzyme-pretreated spermatia were used for spermatium inoculation, the pretreated spermatia were washed 3 times by centrifugation (1,500 × g, 5 min) followed by resuspension in ASW before inoculation. An approximately 3×10^5-fold dilution of the enzyme was made after these washes and an equal amount of the enzyme remaining in the pretreated inoculum was added to the control immediately before spermatium inoculation.

If chemically fixed spermatia were subject to enzymatic treatment, the spermatial suspension was mixed with an equal volume of 2% GA in ASW, incubated for 30 min at 4°C, and washed 3 times by centrifugation followed by resuspension in ASW. Washed samples were diluted and treated with an enzyme as above.

Periodic acid oxidation and reduction

Tetraspore germlings containing mature female gametophytes were fixed in 1% paraformaldehyde in ASW for 30 min at 4°C, and washed in ASW 3 times. Samples were oxidized in 10 mM periodic acid in ASW containing 8.25 mM maleic acid (pH 4.0) for 5 min in the dark at room temperature, washed in ASW 3 times, and reduced in 0.1% sodium borohydride in ASW (pH 9.4) for 10 min in the dark. Two different controls were employed (Table 4). One percent hydrogen peroxide was used in place of periodic acid for non-specific oxidation, and, in the second control, reduction alone was used.

Viability test

The viability of spermatia was examined by both exclusion of Evan's blue (Taylor and West 1980) and fluorescence generated by hydrolysis of fluorescein diacetate (FDA; Sigma; Heslop-Harrison and Heslop-Harrison 1970). Stock solutions of Evan's blue (ca. 5% in $ASP_{12}NTA$ (Provasoli 1963)) and FDA (2 mg ml^{-1} in acetone) were added to cell suspensions to make final concentrations of 0.5% and 4 μg ml^{-1}, respectively. Observations of FDA-stained samples were carried out on an Olympus BH2-RFK epifluorescence microscope using "B-excitation".

To kill the cells for negative controls of the viability test, three methods were employed; 1) spermatia were fixed in 1% GA in seawater for 30 min at 4°C, 2) spermatia were treated with 0.05% saponin for 30 min at 4°C, 3) the spermatial suspension was placed at 70°C for 10 min. Attachment did not occur between these killed spermatia and trichogynes.

TEM preparation and cytochemistry

The method for preparation and observation of the TEM specimen was the same method for enhancement and preservation of spermatial covering and trichogyne coat used

Table 2. Effect of Pronase E pretreatment (5 min) of spermatia on attachment to untreated trichogynes.

Pretreatment	No. of trichogynes	No. of attached spermatia	Spermatia/trichogynes
Control	156	525	3.36
	165	660	4.00
0.01% (w/v) Pronase E	118	73	0.62
	137	41	0.29
0.1% Pronase E	168	18	0.11
	187	20	0.11

Table 3. Effect of trypsin pretreatment (5 min) of spermatia on attachment to untreated trichogynes.

Pretreatment	No. of trichogynes	No. of attached spermatia	Spermatia/trichogynes
Control	256	966	3.77
	271	894	3.30
0.05% (w/v) trypsin	311	483	1.55
	336	473	1.41
0.5% trypsin	257	15	0.06
	354	12	0.03

in Mine and Tatewaki (1994). Compounds containing vicinal glycol residues were cytochemically localized by a periodic acid—thiocarbohydrazide—silver proteinate (PA-TAg) test according to Roland and Vian (1991). Specimens for cytochemistry were fixed in 3% GA, 2% NaCl in cacodylate buffer (pH 7.2), washed in buffer containing NaCl, rinsed in water, dehydrated in ethanol and embedded in LR white (London Resin, Hampshire).

Results

Spermatial covering

The spermatial covering could be detected under the light microscope as ca. 3 μm thick colorless covering which excludes carbon particles of India ink (Fig. 3). The spermatial covering exhibited semisolid, or a gel-like character. The appearance of the covering was not changed even after fixation by GA in seawater. Upon gradual dehydration in ethanol of GA-fixed spermatia, the apparent thickness of the covering decreased (Fig. 6). After a gradual rehydration in water, the covering thickness almost completely recovered (Fig. 7).

The spermatial covering was degraded by proteolytic enzymes. As observed under the light microscope, non-fixed spermatial coverings became thinner in both concentration- and time-dependent manner (Figs. 4, 5, 15, 16). In the presence of 1 mM PMSF, the decrease in the covering thickness by trypsin was partially repressed (Fig. 17). After prolonged enzymatic treatment, e.g. 1-2 h in 1% Pronase E, the coverings were no longer detected around spermatial cell surfaces (Figs. 5, 15). The viability of spermatia after deletion of the coverings by enzymatic treatment was confirmed (Table 1).

In the TEM specimen, a fibrous, reticulated substructure of the spermatial covering was seen on the plasma membrane of spermatia (Fig. 8). The decrease in the covering thickness (Fig. 9) or disappearance of the covering (Fig. 10) by proteolytic enzymes was also observed. In addition, the decrease in the covering thickness by Pronase E (Fig. 18) and trypsin (not shown) also occurred in GA-fixed spermatia.

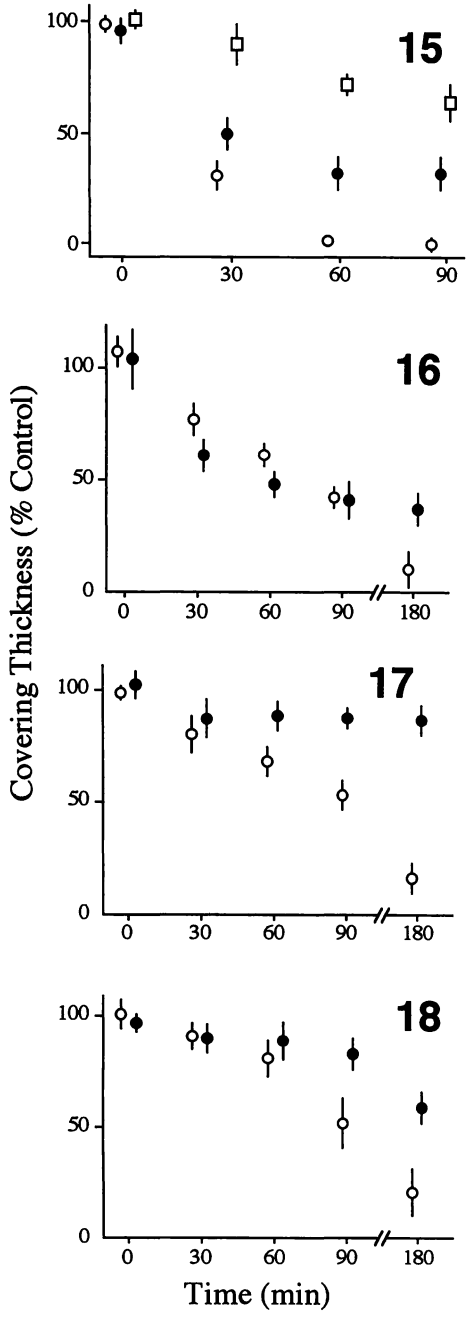
Trichogyne coat

The cell wall surface of the trichogyne was uniformly coated with fibrous structures

Table 4. Effect of degradation of vicinal-glycols of trichogyne coat on gamete attachment.

Oxidative agent used in trichogyne pretreatment	No. of trichogynes	No. of attached spermatia	Spermatia/trichogynes
Periodic acid	185	58	0.31
	76	24	0.32
Hydrogen peroxide	126	570	4.52
	200	671	3.36
None (pH 4.0)	126	977	7.75
	239	387	2.78

(Mine and Tatewaki 1994), and this trichogyne coat was composed of a PATAg-positive material (Figs. 11, 12). This PATAg-positive reaction mostly disappeared after periodic acid oxidation followed by sodium borohydride reduction of chemically fixed trichogynes (Fig. 13), but not after oxidation by hydrogen peroxide and reduction (Fig. 14). The periodic acid-sodium borohydride treatment thus appeared to specifically destroy the PATAg-positive structure, i.e., vicinal glycol residues, of the trichogyne coat.



Inhibition of gamete attachment by gamete pretreatment

The pretreatment, which was expected to destroy the gamete surface structures, inhibited the attachment of spermatia to trichogynes. A brief pretreatment (5 min) of spermatia by proteolytic enzymes disrupted the ability of the spermatia to attach to the trichogynes (Tables 2, 3). The number of attached spermatia per trichogyne decreased remarkably according to the concentrations of both Pronase E and trypsin added to the pretreatment mixture. On the other hand, periodic acid oxidation followed by sodium borohydride reduction of fixed trichogynes also inhibited the gamete attachment significantly (Table 4). In contrast to an unclear difference between the controls without oxidation and those with hydrogen peroxide oxidation, a significantly smaller number of spermatia attached to the periodic acid-oxidated trichogynes.

Discussion

Gamete surfaces

In the present study, the viability and ultrastructure of spermatia were not changed after spermatial covering degradation by proteolytic enzymes. The degradation also oc-

Figs. 15–18. Time course of thickness changes in spermatial coverings of *Palmaria* sp. during treatment with proteolytic enzymes. Data were expressed as % of control. Vertical lines indicate ±1/2 standard deviation. Controls were treated with ASW only. Figs. 15–17. Coverings of non-fixed spermatia. Fig. 15. Treated with 1% (white circle), 0.1% (black circle), or 0.01% (white square) Pronase E. Fig. 16. Treated with 1% trypsin (white circle), or 1% papain (black circle). Fig. 17. Treated with 0.5% trypsin (white circle), or 0.5% trypsin along with 1 mM PMSF (black circle). Fig. 18. Coverings of GA-fixed spermatia treated with 0.5% (white circle), or 0.1% (black circle) Pronase E.

curred in chemically fixed spermatia. Therefore, the decrease in the covering thickness during the enzymatic treatment does not seem to be due to the damage of the covering-generating activity, if present, of the living spermatium. Furthermore, since the degradation was inhibited by a specific protease inhibitor, some protein(s) or polypeptide(s) which can be hydrolyzed by the enzymes should be at least one of the constituents of the covering.

Extracellular proteins have been reported in a red alga (Hanic and Craigie 1969), but a proteinaceous nature of spermatial coverings of red algae has not been demonstrated. Cytochemical studies on the spermatial coverings of other red algae have shown that they consist of acidic and neutral polysaccharides (Peel and Duckett 1975, Cole *et al.* 1985) or mannose residues as detected by binding of lectins (Kim and Fritz 1993a, b). Using histochemical techniques to detect proteins, Peel and Duckett (1975) reported a negative staining in the spermatial covering (as 'spermatial coat'). In *Palmaria* sp., we have found no histochemical evidences in the spermatial covering using several procedures for proteins that have shown positive reaction in the spermatial nucleus and cytoplasm (unpubl. observ.). It is otherwise possible that the proteinaceous component is indispensable for maintaining the covering structure but not the major constituent of the covering. Chemical analysis of the lysate during the spermatial covering proteolysis is in progress.

Although controversial results were obtained in a ceramiacean alga (Kim and Fritz 1993b), we have previously showed that the trichogyne of *Palmaria* sp. was stained with calcofluor (Mine and Tatewaki 1994). Cole *et al.* (1985) reported that the receptive surface ("wall coating") of female gamete of *Bangia* contained vicinal glycol residues as detected by a periodic acid-Shiff test. In the present study, we also demonstrated the PATAg-positive nature of the trichogyne coat in *Palmaria* sp. The trichogyne coat was stained by the PATAg test far more strongly than the trichogyne and thallus cell walls that have been reported to consist of vicinal glycol-containing polysaccharides (Turvey and Williams 1970, as *Palmaria palmata*). This indicates that the trichogyne coat material contains a large quantity of vicinal glycol moieties.

Gamete attachment

There have been SEM studies on the gamete attachment in red algae (Magruder 1984, Cole *et al.* 1985, Mitman and Phinney 1985, Kim and Fritz 1993a). Three examples given above on the bangiacean and ceramiacean algae showed that the spermatia bore specialized appendages (or 'corns') that were apparently responsible for the initial binding to the receptive surface of female gamete. This was further supported by the inhibition of gamete attachment by a lectin and a localization of the lectin binding to the spermatial appendage in a ceramiacean alga (Kim and Fritz 1993a, b). To the contrary, neither SEM study (Mitman and Phinney 1985) nor TEM study (Mine and Tatewaki 1994) showed any appendages on the spermatia of the palmariacean algae throughout the fertilization processes.

Previous experiments have shown that the attachment and fusion of gametes in the intergeneric fertilization were readily observed in palmariacean algae (Mine and Tatewaki 1993). However, no binding occurred between the gametes of *Aglaothamnion neglectum* and other species of related ceramiacean genera (Magruder 1984). The difference in heterologous gamete affinities may be related to the differences in the morphological and chemical properties of the gamete surfaces between ceramiacean and palmariacean algae.

The inhibition of gamete attachment by the brief pretreatment of *Palmaria* spermatia with proteolytic enzymes was probably due to a degradation of the outermost layer of the spermatial covering. It is otherwise possible that other important proteins were disrupted by the proteolytic enzymes and this had a secondary effect on the spermatial attachment as argued in the gamete adhesion of *Chlamydomonas* (Goodenough 1991). On the other hand, the

PATAg-positive compounds in the trichogyne coat appear to be essential for gamete attachment since the attachment was markedly inhibited by a specific chemical degradation of vicinal glycols of the coat. The PATAg-positive entity can be interpreted in various ways (Roland and Vian 1991), but the great majority of positive compounds are polysaccharides containing 1-4 linkages.

There have been many examples that indicate lectin-polysaccharide interactions in the gamete recognition in animals (Rosati 1985, O'Rand 1988), brown algae (Callow 1985, Schmid 1993) and a red alga (Kim and Fritz 1993a). If the PATAg-positive compounds of *Palmaria* trichogynes are polysaccharides, it is likely that the complementary adhesive substance of the spermatial covering is a lectin that binds to the trichogyne coat polysaccharides. An examination of the effect of lectins or specific glycosidases on the gamete attachment will provide further information on the adhesive trichogyne coat containing vicinal glycols.

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峯　一朗・舘脇正和：紅藻ダルスの受精における配偶子表面と接着

紅藻ダルス目ダルス *Palmaria* sp. の配偶子表面の構造の性質を調べた。無固定の不動精子の無色の被膜は，細胞懸濁液に加えられた蛋白質分解酵素により，細胞の生存が損なわれずに分解された。化学固定を施した精子の被膜も同様に酵素的に分解された。受精毛細胞壁の表面は，過ヨウ素酸々化・水素化ホウ素ナトリウム還元処理により破壊される，隣接グリコール基を含む繊維状の構造により覆われていることが観察された。精子被膜の短時間の蛋白質分解酵素処理は，受精毛表層の隣接グリコールの破壊と同様に，配偶子接着に有意な阻害効果を示した。このことは本藻の配偶子の特異的接着が，主にこれらの表面構造により支配されていることを示している。

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Enumeration of the Cyanophyta (blue-green algae) of Japan 2. Nostocales and Stigonematales

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In the present contribution are enumerated all the species of the blue-green algae belonging to the orders of Nostocales and Stigonematales, which were reported to occur in Japan. In the Nostocales are listed 4 families, 28 genera and 161 species. The Microchaetaceae includes 6 genera and 19 species, the Nostocaceae 13 genera and 86 species, the Rivulariaceae 6 genera and 37 species and the Scytonemataceae 3 genera and 19 species. The following two new combinations are established. Nostocaceae: *Hydrocoryne enteromorphoides* (Grun. ex Born. & Flah.) comb. nov. (=*Hormothamnium enteromorphoides* Grun. ex Born. & Flah. 1886), Scytonemataceae: *Scytonematopsis pilosa* (Harv. ex Born. & Flah.) comb. nov. (=*Calothrix pilosa* Harv. ex Born. & Flah. 1886). In the Stigonematales are listed 6 families, 13 genera and 30 species. The Borzinemataceae comprises 2 genera and 2 species, the Capsosiraceae one genus and one species, the Fischerellaceae 2 genera and 5 species, the Mastigocladaceae 5 genera and 11 species, Nostocopsaceae 2 genera and 2 species, and the Stigonemataceae one genus and 9 species.

Key Index words: *blue-green algae—Cyanophyta—Nostocales—Stigonematales—list—Japan*

III. Nostocales (Borzi 1914) Geitl. 1925

1. Microchaetaceae Lemm. 1910

(1) Microchaetoideae Kom. & Anagn. 1989

Fortiea J. De Toni 1936

Syn.: *Leptobasis* Elenk. 1915, non *Leptobasis* Dulac. 1867

F. bossei (Frémy) Desik. 1959

Basion.: *Fremyella Bossei* Frémy 1942

Ref.: Hiramatsu 1967; M. Watanabe and Niiyama 1990

Microchaete Thur. ex Born. & Flah. 1886

Syn.: *Fremyella* J. De Toni 1936

M. bulbosa Copel. 1936

Syn.: *Fremyella bulbosa* (Copel.) J. De Toni 1947

Ref.: Yoneda 1941a, 1952a; Emoto and Yoneda 1941a; Hirose and Hirano 1977

M. grisea Thur. ex Born. & Flah. 1886

Syn.: *Fremyella grisea* (Thur.) J. De Toni 1936

Ref.: Umezaki 1961; Takata and Hirose 1971

M. investiens Frémy 1929

Syn.: *Fremyella investiens* (Frémy) J. De Toni 1936

Ref.: Hirose and Hirano 1977

M. tenera Thur. ex Born. & Flah. 1886

Syn.: *Fremyella tenera* (Thur.) J. De Toni 1936

Ref.: Higashi and Okada 1927; Yoneda 1939a, d, 1952a, 1953a; Emoto and Yoneda 1942; Hiramatsu 1967; Hirose and Hirano 1977

M. thermalis Emoto & Yoneda 1940b

Ref.: Emoto & Yoneda 1940b; Yoneda 1952a; Hirose and Hirano 1977

M. uberrima Cart. 1926

Syn.: *Fremyella uberrima* (Cart.) J. De Toni 1936

Ref.: Akiyama 1961, 1965a

M. vitiensis Ask. ex Born. & Flah. 1886

Syn.: *Fremyella vitiensis* (Ask.) J. De Toni 1936

Ref.: Umezaki 1961

(2) Tolypotrichoideae Kom. & Anagn. 1989

Coleodesmium Borzi ex Geitl. 1942

Syn.: *Desmonema* Berk. & Thw. ex Born. & Flah. 1886

C. sagarmathae Kom. & M. Watanabe 1990
Ref.: Komárek and M. Watanabe 1990

C. wrangelii (Ag.) Born. & Flah. 1886

C. wrangelii var. ***wrangelii***
Ref.: Higashi and Okada 1927

C. wrangelii var. ***floccosum*** (Borzi) Kom. & M. Watanabe 1990
Basion.: *Coleodesmium floccosum* Borzi 1879
Ref.: M. Watanabe et al. 1984 (as *Coleodesmium wrangelii*); Ioriya et al. 1984 (as *Coleodesmium wrangelii*); Komárek and M. Watanabe 1990

Hassallia Berk. ex Born. & Flah. 1886

Syn.: *Tolypothrix* sect. *Hassallina* Kirchn. in Engl. & Prantl 1900

H. byssoidea (Ag.) Hass. ex Born. & Flah. 1886

H. byssoidea var. ***byssoidea***
Syn.: *Tolypothrix byssoidea* (Ag.) Kirchn. in Engl. & Plantl 1900
Ref.: Yoneda 1937, 1950, 1952a; Emoto and Hirose 1940b; Hiramatsu 1967, 1973; Nakano 1970; Yamagishi 1972; Hirose and Hirano 1977

H. byssoidea var. ***saxicola*** Grun. ex Born. & Flah. 1886 (as forma β)
Syn.: *Tolypothrix byssoidea* (Ag.) Kirchn. f. *saxicola* Grun. ex Forti 1907
Ref.: Yoneda 1950

Tolypothrix Kütz. ex Born. & Flah. 1886

T. campylonemoides Ghose 1923
Ref.: Hiramatsu 1973

T. distorta Kütz. ex Born. & Flah. 1886
Ref.: Akiyama 1965a; Hiramatsu 1967; Negoro 1973; Hirose and Hirano 1977; M. Watanabe and Niiyama 1990
Syn.: *Tolypothrix distorta* var. *penicillata* (Ag.) Lemm. 1907
Ref.: Negoro 1973

T. fragilis (Gardn.) Geitl. 1932
Basion.: *Hassallia fragilis* Gardn. 1927 ("*Hassalia*")
Ref.: Akiyama 1965b; Hirose and Hirano 1977

T. lanata (Desv.) Ag. ex Born. & Flah. 1886
Ref.: Hirose 1938; Yoneda 1953a; Horikawa et al. 1969; Hirose and Hirano 1977

T. limbata Thur. ex Born. & Flah. 1886
Ref.: Akiyama 1965a; Hirose and Hirano 1977
Syn.: *Tolypothrix limbata* var. *cylindrica* Ghose 1932
Ref.: Mori 1971

T. rechingeri (Wille) Geitl. 1925 ("*Rechingeri*")
Ref.: Higashi and Okada 1927

T. tenuis Kütz. ex Born. & Flah. 1886

T. tenuis var. ***tenuis***
Ref.: Hirose 1938; Yoneda 1939a, d, 1953a; Kobayasi 1958; Hirano 1960; Kobayasi et al. 1962; Akiyama 1965a; Hiramatsu 1967, 1973; A. Watanabe 1970; Negoro 1973; Hirose and Hirano 1977; Yamagishi 1972, 1985

T. tenuis var. ***wartmanniana*** (Rabenh.) Hansg. 1892 ("*Wartmanniana*")
Ref.: Hirose 1938; Hirose and Hirano 1977

Petalonema Berk. ex Kirchn. 1898

Syn.: *Croatella* Erceg. 1925

P. densum A. Br. ex Mig. 1907
Ref.: Yoneda 1939a
Syn.: *Scytonema densum* (A. Br.) Born. ex Born. & Flah. 1886
Ref.: Hirose and Hirano 1977

2. Nostocaceae Dumort. 1829

(1) Anabaenoideae (Born. & Flah.) Kirchn. 1900

Anabaena Bory ("*Anabaina*") ex Born. & Flah. 1886

A. aequalis Borge 1906
Ref.: Fukushima 1952, 1954; Hirano 1963; Mizuno 1964; Hirose and Hirano 1977

A. affinis Lemm. 1897
Ref.: Akatsuka 1951; Yamaguti 1956; Mizuno 1964; Akiyama 1965a; Muraya-

ma and Saisho 1967; Hirose and Hirano 1977; Imazu 1979, 1981, 1986, 1987; M. Watanabe and Chihara 1980; M. Watanabe 1984; Negoro 1991a

Syn.: *Anabaena catenula* (Kütz.) Born. & Flah. var. *affinis* (Lemm.) Geitl. 1932

Ref.: Fukushima 1951; M. Watanabe 1971

A. augstumalis Schmidle 1899

A. augstumalis var. ***augstumalis***

Ref.: Hirose 1938; Yoneda 1953a; Hirano 1956a, 1958; Hirose and Hirano 1977

A. augstumalis var. ***marchica*** Lemm. 1905

Ref.: Yoneda 1953a; Hirano 1962; Mizuno 1964; Hirose and Hirano 1977

A. ballygungii Banerji 1938

Ref.: Akiyama 1977

A. circinalis Rabenh. ex Born. & Flah. 1886

Ref.: Hirano 1956b; M. Watanabe 1971; M. Watanabe and Niiyama 1990

Syn.: *Anabaena Hassallii* Wittr. ex Lemm. 1907

Ref.: Okada 1939b; Akatsuka 1951

A. citrispora M. Watanabe 1992

Ref.: M. Watanabe 1992

A. crassa (Lemm.) Kom.-Legn. & Cronb. 1992

Basion.: *Anabaena spiroides* var. *crassa* Lemm. 1898

Syn.: *Anabaena spiroides* f. *crassa* (Lemm.) Elenk. 1938

Ref.: Okada 1939b; Kokubo 1944; Yamaguti 1956; Iwai 1963; Mizuno 1964; Negoro 1968, 1971, 1991a; M. Watanabe 1971, 1984; Hirose and Hirano 1977; M. Watanabe and Chihara 1980; M. Watanabe and Niiyama 1990

A. cylindrica Lemm. 1896

Ref.: T. Watanabe 1956; M. Watanabe 1971; Hirose and Hirano 1977

A. flos-aquae Bréb. ex Born. & Flah. 1886 (*"Flos-aquae"*)

A. flos-aquae f. ***flos-aquae***

Ref.: Hattori 1908; Higashi and Okada 1927; Ueno 1934; Yamada 1935; Miyauchi 1935; Negoro 1937a, 1973; Kokubo 1944; Kokubo and Kawamura 1948; Hirose 1950; Akatsuka 1951; Yoneda 1953b; Hirano 1956a, 1960; Hada 1960; Mizuno 1964; M. Watanabe 1971; Kurasawa and Okino 1975; Hirose and Hirano 1977; M. Watanabe and Chihara 1980

Syn.: *Anabaena circinalis* (Kütz.) Hansg. ex Lemm. 1907

Ref.: Ueno 1933; Akatsuka 1951; Ochiai 1962a; Fukushima 1954; Mizuno 1964; Hirose and Hirano 1977

Syn.: *Anabaena flos-aquae* Bréb. var. *gracilis* Kleb. 1895

Ref.: M. Watanabe 1971

Syn.: *Anabaena flos-aquae* Bréb. var. *intermedia* Woron. f. *spiroides* Woron. 1923

Ref.: Akatsuka 1951; M. Watanabe 1971

A. iyengarii Bharadw. 1935 (*"Iyengarii"*)

A. iyengarii Bharadw. var. ***tenuis*** C. B. Rao 1937

Ref.: Emoto and Hirose 1942e; Yoneda 1952a; Hirose and Hirano 1977

A. lapponica Borge 1913

Ref.: Kobayasi 1958; Kobayasi et al. 1962; Hirano 1962; Mizuno 1964; M. Watanabe 1971; Hirose and Hirano 1977

A. laxa A. Br. ex Born. & Flah. 1886

Syn.: *Anabaena inaequalis* (Kütz.) Born. & Flah. 1886

Ref.: Fukushima 1952, 1954; Nakano 1970; M. Watanabe 1971; Hiramatsu 1973; Hirose and Hirano 1977

A. lemmermannii P. Richt. 1903 (*"Lemmermannii"*)

Syn.: *Anabaena flos-aquae* f. *lemmermannii* (P. Richt.) Canab. 1929 (*"Lemmermannii"*)

Ref.: Akatsuka 1951

A. macrospora Kleb. 1895

A. macrospora var. ***macrospora***

Ref.: Negoro 1936, 1959, 1967, 1973; Akatsuka 1951; Hirose and Hirano 1977; M. Watanabe et al. 1985

A. macrospora var. ***crassa*** Kleb. 1895

Ref.: Negoro 1968; Hirose and Hirano 1977

A. mendotae Trelease 1889

Syn.: *Anabaena flos-aquae* Bréb. f. *treleasii* (Born. & Flah.) Elenk. 1938 (*"Treleasii"*)

Ref.: Negoro 1937a; T. Watanabe 1956; M. Watanabe 1971, 1984; M. Watanabe and Niiyama 1990

A. minderi Huber-Pestal. 1938 (*"Minderi"*)
Ref. Negoro 1973

A. oscillarioides Bory ex Born. & Flah. 1886

A. oscillarioides var. ***oscillarioides***
Ref.: Okada 1936, 1939b; Yoneda 1953a; Onuki 1950; Hiramatsu 1967; Hirose and Hirano 1977

A. oscillarioides var. ***stenospora*** Born. & Flah. 1886
Ref.: M. Watanabe 1971

A. planctonica Brunnth. 1903
Syn.: *Anabaena solitaria* f. *planctonica* (Brunnth.) Kom. 1958
Ref.: Kokubo 1944; Hirose 1950; Onuki 1950; Akatsuka 1951; Mizuno 1964; Akiyama 1965a; Negoro 1973; Hirose and Hirano 1977; Yamagishi et al. 1982; M. Watanabe 1971 (as *A. scheremetievi* f. *ovospora*), 1984, 1992; M. Watanabe and Niiyama 1990
Syn.: *Anabaena limnetica* G. M. Smith 1916
Ref.: Akatsuka 1951
Syn.: *Anabaena solitaria* f. *solitaria* sensu Kom. 1958
Ref.: M. Watanabe and Chihara 1980

A. saaremaaensis Skuja 1929
Ref.: M. Watanabe 1971

A. sedovii Kossinsk. 1933 (*"Sedovii"*)
Ref.: Kokubo 1944

A. smithii (Kom.) M. Watanabe 1992
Basion.: *Anabaena solitaria* Kleb. f. *smithii* Kom. 1958
Ref.: M. Watanabe 1971 (as *A. scheremetievi* var. *recta* f. *ovalispora* Elenk.), 1984, 1992; Hirose and Hirano 1977 (as *A. scheremetievi*)
Syn.: *Anabaena Scheremetievi* Elenk. var. *recta* Elenk. f. *rotundospora* Elenk. 1938
Ref.: Negoro 1937a; Okada 1939b; Hirano 1954; T. Watanabe 1968b

A. solitaria Kleb. 1895
Ref.: Umezaki 1983

A. sphaerica Born. & Flah. 1886
Ref.: Kobayasi 1958; Kobayasi et al. 1962; Hirose and Hirano 1977

A. spiroides Kleb. 1895
Ref.: Hirose 1938; Kokubo and Kawamura 1948; Yoneda 1953b; Onuki 1950; Akatsuka 1951; Hirano 1956b; Negoro 1967, 1973; M. Watanabe 1971; Akiyama 1977; Hirose and Hirano 1977; Wakabayashi and Ichise 1982; M. Watanabe and Chihara 1980; M. Watanabe 1984

A. subcylindrica Borge 1921
Ref.: T. Watanabe 1956; Akiyama 1965a; M. Watanabe 1971; Hirose and Hirano 1977

A. torulosa (Carm.) Lagerh. ex Born. & Flah. 1886
Ref.: Imazu and Hirose 1961; Hirose and Hirano 1977

A. verrucosa Peters. 1928
Ref.: Kobayasi 1958; Kobayasi et al. 1962; Hirano 1962; Hirose and Hirano 1977

A. viguieri Denis & Frémy 1923 (*"Viguieri"*)
Syn.: *Anabaena affinis* f. *viguieri* (Denis & Frémy) Kom. 1958
Ref.: Hirose and Hirano 1977; M. Watanabe 1992

Anabaenopsis (Wolosz.) Mill. 1923

A. arnoldii Aptek. 1926 (*"Arnoldii"*)
Ref.: Okada 1936, 1939b; Negoro 1973; Hirose and Hirano 1977; Umezaki 1983
Syn.: *Anabaenopsis doliiformis* Noda 1963
Ref.: Noda 1963

A. circularis (G. S. West) Wolosz. & Mill. in Mill. 1923
Basion.: *Anabaena flos-aquae* Bréb. ex Born. & Flah. var. *circularis* G. S. West 1907
Ref.: Akatsuka 1951; A. Watanabe and Yamamoto 1967; Negoro 1973
Syn.: *Anabaenopsis circularis* (G. S. West) Mill. f. *recta* Fukushima 1954
Ref.: Fukushima 1954

A. elenkinii Mill. 1923 (*"Elenkini"*)
Ref.: Akatsuka 1951

A. milleri Woron. 1929 (*"Milleri"*)
Ref.: Akatsuka 1951

A. nadsonii Woron. 1929 (*"Nadsonii"*)
Ref.: Akatsuka 1951

A. tanganyikae (G. S. West) Mill. 1923
Basion.: *Anabaena tanganyikae* G. S. West 1907
Ref.: Akatsuka 1951

Aphanizomenon Morr. ex Born. & Flah. 1886

A. aphanizomenoides (Forti) Horec. & Kom. 1979
Basion.: *Anabaena aphanizomenoides* Forti 1912
Ref.: Akatsuka 1951; Akiyama 1977; Hirose and Hirano 1977; Negoro and Aoki 1991

A. elenkinii Kisel. 1951 (*"Elenkinii"*)
Syn.: *Aphanizomenon elenkinii* Kisel. var. *gracile* Kascht. 1955
Ref.: Hirano 1958

A. flos-aquae Ralfs ex Born. & Flash. 1886 (*"Flos-aquae"*)

A. flos-aquae var. ***flos-aquae***
Ref.: Higashi and Okada 1927; Higashi 1933c; Miyauchi 1935; Kokubo 1944; Hirose 1950; Akatsuka 1951; Hirano 1956b; Mizuno 1964; Negoro 1973; Akiyama 1977; Hirose and Hirano 1977; M. Watanabe and Chihara 1980; Umezaki 1987; M. Watanabe 1991

A. gracile Lemm. 1907
Basion.: *Aphanizomenon Flos-aquae* var. *gracile* Lemm. 1890
Ref.: M. Watanabe and Chihara 1980; Yamagishi et al. 1982
Syn.: *Aphanizomenon Flos-aquae* var. *Klebahnii* Elenk. 1909
Ref.: Negoro 1937a; Hirose 1950; Hirano 1960; Hirose and Hirano 1977; M. Watanabe 1991

A. paraflexuosum M. Watanabe 1991
Ref.: M. Watanabe 1991

A. yezoense M. Watanabe 1991
Ref.: M. Watanabe 1991

Cylindrospermopsis Seenayya & Subba Raju 1972

C. raciborskii (Wolosz.) Seenayya & Subba Raju 1972
Basion.: *Anabaenopsis Raciborskii* Wolosz. ex Geitl. 1925
Ref.: Negoro 1935, 1936, 1973, 1991b; Akatsuka 1951; Fukushima 1949, 1955a; Ochiai 1960; Hirose and Hirano 1977; Umezaki 1992

Cylindrospermum Kütz. ex Born. & Flah. 1886

C. alatosporum Fritsch 1918
Ref.: Hirose and Hirano 1977
Syn.: *Cylindrospermum oblongum* Yoneda 1942a
Ref.: Yoneda 1942a

C. catenatum Ralfs ex Born. & Flah. 1886
Ref.: Yoneda 1942a; Hirose and Hirano 1977

C. licheniforme (Bory) Kütz. ex Born. & Flah. 1886
Ref.: Yoneda 1938b, 1952a; Hirose and Hirano 1977

C. majus Kütz. ex Born. & Flah. 1886
Ref.: Hirose 1938; Yoneda 1942a, 1952a; Akiyama 1965a, b; Hiramatsu 1967; Hirose and Hirano 1977; M. Watanabe and Niiyama 1990

C. muscicola Kütz. ex Born. & Flah. 1886

C. muscicola var. ***muscicola***
Ref.: Yoneda 1938b, 1952a; Ochiai 1962b

C. stagnale (Kütz.) Born. & Flah. 1886
Ref.: Higashi and Okada 1927; Yoneda 1938a, 1952a, 1953a; Hirose 1938; Fukushima 1952, 1954; Hirano 1962; Hiramatsu 1967, 1973; Negoro 1973; Hirose and Hirano 1977; Yamagishi 1985
Syn.; *Cylindrospermum echigoense* Noda 1971
Ref.: Noda 1971

C. tropicum W. & G. S. West 1902
Ref.: Akatsuka 1951

Hydrocoryne Schwabe ex Born. & Flah. 1886
Syn.: *Hormothamnium* Grun. ex Born. & Flah. 1886 (*"Hormothamnion"*), *Anabaenothrix* Randh. 1936

H. enteromorphoides (Grun. ex Born. & Flah.) comb. nov.
Basion.: *Hormothamnium enteromorphoides* Grun. ex Born. & Flah., Ann. Sci. Nat. VII. Bot. 7: 260, 1886
Ref.: Higashi and Okada 1927; Umezaki 1961; Umezaki and Kamura 1977

H. spongiosa Schwabe ex Born. & Flah. 1886
Ref.: Higashi and Okada 1927; Hirose 1938; Hirose and Hirano 1977

Raphidiopsis Fritsch & Rich 1929

R. mediterranea Skuja f. ***major*** Yoneda 1953b
Ref.: Yoneda 1953b
Syn.: *Raphidiopsis mediterranea* var. *grandis* Hill 1970
Ref.: M. Watanabe and Chihara 1980; M. Watanabe 1985

Richelia Johs.-Schmidt 1901

R. intracellularis Johs.-Schmidt 1901
Ref.: Okamura 1916; Higashi and Okada 1927; Akatsuka 1951; Tokida and Masaki 1959; Umezaki 1961; Marumo 1966; Yoneda 1966; Yabu 1971; Yamaji 1984

Wollea Born. & Flah. 1886

W. saccta (Wolle) Born. & Flah. 1886
Ref.: Higashi and Okada 1927

(2) Nostocoideae (Borzi 1914) Kom. & Anagn. 1989

Aulosira Kirchn. ex Born. & Flah. 1888

A. fertilissima Ghose 1923
Ref.: Hiramatsu 1973

A. implexa Born. & Flah. 1886
Ref.: Yoneda 1942a, 1952a, 1953a, 1962a; Emoto and Yoneda 1941b; Hirose and Hirano 1977; Mifune and Hirose 1983a

A. laxa Kirchn. ex Born. & Flah. 1886
Ref.: Akiyama 1965a

A. major Emoto & Hirose 1940a
Ref.: Emoto and Hirose 1940a; Yoneda 1952a; Hirose and Hirano 1977

A. prolifera Bharadw. 1933
Ref.: Akiyama 1965b; Mori 1971; Hirose and Hirano 1977

Nodularia Mert. ex Born. & Flah. 1886

N. harveyana (Thw. in Harv.) Thur. ex Born. & Flah. 1886 (*"Harveyana"*)
Ref.: Umezaki 1961; Hirose 1964; Mizuno 1964; Hiramatsu 1967; Hirose and Hirano 1977
Syn.: *Nodularia Harveyana* var. *sphaerocarpa* (Born. & Flah.) Elenk. 1916
Ref.: Negoro 1936, 1973; Hirose and Hirano 1977

N. spumigena Mert. ex Born. & Flah. 1886
Ref.: Yoneda 1937; Okada 1939b; Akatsuka 1951; Mizuno 1964; Akiyama 1965a, b; Nakano 1970; Negoro 1973
Syn.: *Nodularia spumigena* var. *major* (Kütz.) Born. & Flah. 1886
Ref.: Hirose and Hirano 1977
Syn.: *Noduralia spumigena* var. *minor* Fritsch 1912
Ref.: Higashi and Okada 1927

Nostoc Vauch. ex Born. & Flah. 1886
(as *Nostoc* Geoffroy ex Linn. pro synon. 1753, according to Drouet 1978, p. 21)

N. carneum (Lyngb.) Ag. ex Born. & Flah. 1886
Ref.: Yoneda 1938b, c, 1952a; Emoto and Hirose 1942a; Hirose 1962; Hiramatsu 1967; Hirose and Hirano 1977

N. coeruleum Lyngb. ex Born. & Flah. 1886
Ref.: Yoneda 1941a, 1953a; Hirose 1962; Hirano 1962; Mori 1971; Hirose and Hirano 1977; Yamagishi 1985

N. commune Vauch. ex Born. & Flah. 1886

N. commune var. ***commune***
Ref.: Martens 1866; Toyama 1890; Okamura 1902, 1936; Matsumura 1904; Higashi and Okada 1927; Higashi 1933a; Hirose 1938, 1962, 1965; Yoneda 1938a, 1950, 1953a, 1962b, 1966; Okada 1939b, 1953b; Kobayasi 1958; Dawson 1959 (Harvey's manuscript); Umezaki 1961; Akiyama 1961, 1965a; Kobayasi et al. 1962; Nakano 1970; A. Watanabe 1970; Negoro 1973; Hirose and Hirano 1977; Yamagishi 1985

N. commune var. ***flagelliforme*** (Berk. & Curt.) Born. & Flah. 1886
Syn.: *Nostoc flagelliforme* Berk. & Curt. 1857
Ref.: Yendo 1912; Okamura 1913, 1934b; Hisauchi 1969; S. Ueda et al. 1963; Hirose 1965; Yoneda 1966; A. Watanabe 1970

N. conglomeratum Hirose 1962
Ref.: Hirose 1962; Hirose and Hirano 1977

N. ellipsosporum (Dasmaz.) Rabenh. ex Born. & Flah. 1886

Ref.: Yoneda 1941a; Emoto and Hirose 1942c (as *Nostoc carneum* Ag.); Hirose 1962; Hiramatsu 1967, 1973; Hirose and Hirano 1977

*N. **kihlmanii*** Lemm. 1900 ("*Kihlmani*")

*N. **kihlmanii*** var. ***doliiforme*** Hirose 1962

Ref.: Hirose 1938 (as *Nostoc kihlmani* Lemm.), 1962; Hirose and Hirano 1977

*N. **kihlmanii*** var. ***vaginatum*** Hirose 1962

Ref.: Hirose 1962; Mizuno 1964; Hirose and Hirano 1977

*N. **linckia*** (Roth) Born. ex Born. & Flah. 1886 ("*Linckia*")

Ref.: Hirose 1938, 1962; Yoneda 1941a, 1953a; Fukushima 1952; Mizuno 1964; Hiramatsu 1967; Hirose and Hirano 1977; Noda 1987

*N. **macrosporum*** Menegh. ex Born. & Flah. 1886

Ref.: Yoneda 1939a, 1952a; Emoto and Yoneda 1941a; Hirose 1962; Hirose and Hirano 1977

*N. **microscopicum*** Carm. ex Born. & Flah. 1886

Ref.: Yoneda 1939a; Hirose 1962; Mifune et al. 1966; T. Watanabe 1968a; Nakano 1970; Hiramatsu 1973; Hirose and Hirano 1977

*N. **minutum*** Desmaz. ex Born. & Flah. 1886

Ref.: Hirano 1962; Mori 1971

*N. **muscorum*** Ag. ex Born. & Flah. 1886

Ref.: Yoneda 1942a, e, 1952a; Emoto and Yoneda 1942; Hirose 1962; Hirose and Hirano 1977

*N. **paludosum*** Kütz. ex Born. & Flah. 1886

Ref.: Dickie 1877; Matsumura 1904; Yoneda 1938a, 1953a; Hirano 1954, 1962; Hirose 1962; Mizuno 1964; T. Watanabe 1968a; Mori 1971; Yamagishi 1972; Hirose and Hirano 1977

*N. **parmelioides*** Kütz. ex Born. & Flah. 1886

Ref.: Fukushima 1952; Hirose 1962; Akiyama 1965a; Hiramatsu 1967; T. Watanabe 1968c; Hirose and Hirano 1977

*N. **planctonicum*** Poretz. & Tschern. 1929

Ref.: Negoro 1973

*N. **pruniforme*** Ag. ex Born. & Flah. 1886

Ref.: Yoneda 1966

*N. **punctiforme*** (Kütz.) Hariot 1891

Ref.: Emoto and Hirose 1942c; Yoneda 1952a, 1953a; Hirose 1962; Hiramatsu 1973; Hirose and Hirano 1977

*N. **rivulare*** Kütz. ex Born. & Flah. 1886

Ref.: Yoneda 1938a; Hirose 1962; Negoro 1973; Hirose and Hirano 1977

*N. **sphaericum*** Vauch. ex Born. & Flah. 1886

*N. **sphaericum*** var. ***sphaericum***

Ref.: Yoneda 1938a, 1950; Hirose 1938, 1962; Fukushima 1952; Hirano 1962; T. Watanabe 1968c; Mori 1971; Hirose and Hirano 1977

*N. **sphaericum*** var. ***cylindrosporum*** Hirose 1962

Ref.: Hirose 1962; Hirose and Hirano 1977

*N. **spongiaeforme*** Ag. ex Born. & Flah. 1886

Ref.: Yoneda 1940a; Hirose 1962; Hiramatsu 1967; Negoro 1973

*N. **torulosum*** Hirose 1962

Ref.: Hirose 1962; Mizuno 1964; Hirose and Hirano 1977

*N. **verrucosum*** Vauch. ex Born. & Flah. 1886

Ref.: Tomaya 1890; Koizumi 1919; Higashi 1933a; Kobayasi and Watari 1934; Okada 1939b; Yoneda 1939a, 1962b, 1966; Mifune 1957; Hirose 1962; Kobayasi et al. 1962; Akiyama 1965a; Hiramatsu 1967; A. Watanabe 1970; Negoro 1973; Hirose and Hirano 1977

Trichormus (Ralfs ex Born. & Flah.) Kom. & Anagn. 1989

Basion.: *Anabaena* Bory sect. *Trichormus* Ralfs ex Born. & Flah. 1886

*T. **azollae*** (Strasb.) Kom. & Anagn. 1989

Basion.: *Anabaena Azollae* Strasb. ex Wittr., Nordst. & Lagerh. 1896

Ref.: Okamura 1902; Matsumura 1904; Kobayasi and Watari 1934; Okada 1953b; Akiyama 1965a; S. Ueda et al. 1963; Yoneda 1966; Hiramatsu 1973; Negoro 1973; Hirose and Hirano 1977

*T. **catenulus*** (Kütz. ex Born. & Flah.) Kom. & Anagn. 1989

Basion.: *Anabaena catenula* (Kütz.) Born. & Flah. 1886

Ref.: Fukushima 1951, 1954; Yoneda

1953b; Mizuno 1964

T. cycadearum (Reinke) Kom. & Anagn. 1989
Basion.: *Anabaena Cycadearum* Reinke in Tilden 1896
Ref.: Higashi and Okada 1927; Yamada 1935; Okada 1953b; S. Ueda et al. 1963; Yoneda 1966; Nakano 1970; Negoro 1973; Hirose and Hirano 1977
Syn.: *Nostoc cycadae* A. Watanabe & Kiyohara 1963, nom. nud.
Ref.: A. Watanabe and Kiyohara 1963

T. thermalis (Vouk) Kom. & Anagn. 1989
Basion.: *Anabaena thermalis* Vouk 1916
Syn.: *Anabaena Voukii* J. De Toni 1936
Ref.: Emoto and Hirose 1942f; Yoneda 1952a; Mifune et al. 1959; Akiyama 1965a; Hirose and Hirano 1977

T. variabilis (Kütz. ex Born. & Flah.) Kom. & Anagn. 1989
Basion.: *Anabaena variabilis* Kütz. ex Born. & Flah. 1886
Ref.: Yoneda 1938b, c, 1952a; Hirose and Hirano 1977

3. Rivulariaceae Kütz. 1843

Calothrix Ag. ex Born. & Flah. 1886

C. africana Schmidle 1901
Ref.: Hirose and Hirano 1977

C. braunii Born. & Flah. 1886 ("*Braunii*")
Ref.: Hirose 1937; Yoneda 1942c, 1952a, 1953a; Fukushima 1949; Akiyama 1965a; Horikawa et al. 1969; Nakano 1970; Hirose and Hirano 1977

C. brevissima G. S. West 1907
Ref.: Yoneda 1938b, c, 1952a; Emoto and Hirose 1952a; Hirose and Hirano 1977
Syn.: *Calothrix brevissima* var. *moniliforme* Ghose 1927
Ref.: Emoto and Hirose 1940a

C. confervicola Ag. ex Born. & Flah. 1886
Ref.: Okamura 1902, 1916; Ueda and Okada 1934; Umezaki 1961; Hagihara et al. 1970; Noda 1975
Syn.: *Calothrix nodulosa* Setch. & Gardn. 1924
Ref.: Umezaki 1953a, b; Noda 1974

C. coriacea Copel. 1936
Ref.: Emoto and Hirose 1952a; Hirose and Hirano 1977

C. crustacea Thur. ex Born. & Flah. 1886
Ref.: De Toni 1895; Okamura 1902, 1916; Matsumura 1904; Hirose 1957; Umezaki 1961; Hiramatsu 1967; Takata and Hirose 1971; M. M. Watanabe and Kurogi 1975; Noda 1974, 1987
Syn.: *Calothrix aeruginea* Thur. ex Born. & Flah. 1886
Ref.: Okamura 1902, 1916; Umezaki 1954, 1956b; Noda 1974, 1987

C. fusca (Kütz.) Born. & Flah. 1886
Ref.: Hirose 1937; Yoneda 1941b, 1942a, b, 1952a, 1953a; Emoto and Yoneda 1941b; Akiyama 1961, 1965a; Hiramatsu 1967, 1973; M. Watanabe et al. 1985
Syn.: *Calothrix fusca* (Kütz.) Born. & Flah. var. *crassa* C. S. Rao 1939
Ref.: Mori 1971
Syn.: *Calothrix longissima* Hirose 1937
Ref.: Hirose 1937

C. fusco-violacea Crouan ex Born. & Flah. 1886
Ref.: Noda 1974, 1987

C. kuntzei P. Richt. in Kuntze 1898 ("*Kuntzei*")
Ref.: Yoneda 1941b, 1942b; Emoto and Hirose 1942c; Hirose and Hirano 1977

C. marchica Lemm. 1914
Ref.: Higashi and Okada 1927; Hirose and Hirano 1977
Syn.: *Calothrix marchica* Lemm. var. *crassa* C. B. Rao 1937
Ref.: Emoto and Hirose 1942c; Mori 1971
Syn.: *Calothrix marchica* Lemm. var. *intermedia* C. B. Rao 1937
Ref.: Emoto and Hirose 1952a

C. membranacea Schmidle 1901
Ref.: Hiramatsu 1967

C. parasitica (Chauv.) Thur. ex Born. & Flah. 1886
Ref.: Yoneda 1940a; Hirose 1957, 1958; Umezaki 1961; Funahashi 1967; Noda 1974, 1987; Suzuki 1986
Syn.: *Calothrix codicola* Setch. & Gardn. 1930
Ref.: Umezaki 1953a, 1961; Noda 1987

Syn.: *Calothrix nidulans* Setch. & Gardn. 1924
Ref.: Umezaki 1956c; Noda 1987

C. parietina (Näg.) Thur. ex Born. & Flah. 1886
Ref.: Yoneda 1939a, d, 1952a; 1953a; Emoto and Yoneda 1941a; Emoto and Hirose 1942a, f, 1943b; Akiyama 1965a; Mifune et al. 1959, 1966; Negoro 1973; Hirose and Hirano 1977; Mifune and Hirose 1983a; M. Watanabe et al. 1985
Syn.: *Calothrix thermalis* (Schwabe) Hansg. ex Born. & Flah. 1886
Ref.: Yoneda 1938b, c, 1942c, g, 1952a; Emoto and Hirose 1943a
Syn.: *Calothrix parietina* var. *thermalis* G. S. West 1902
Ref.: Negoro 1973

C. rhizosoleniae Lemm. 1899 ("*Rhizosoleniae*")
Ref.: Akatsuka 1951; Marumo 1966

C. scopulorum (Web. & Mohr.) Ag. ex Born. & Flah. 1886
Ref.: Okamura 1902, 1916; Matsumura 1904; Hirose 1957; Umezaki 1961; Hiramatsu 1967; Noda 1974, 1987; M. M. Watanabe and Kurogi 1975

C. stagnalis Gom. 1895
Ref.: Negoro 1973

C. turfosa Geitl. 1933
Ref.: Emoto and Hirose 1942d; Yoneda 1952a; Hirose and Hirano 1977

Dichothrix Zanard. ex Born. & Flah. 1886

D. gypsophila (Kütz.) Born. & Flah. 1886
Ref.: Higashi and Okada 1927; Yoneda 1953a; Hirano 1962; Horikawa et al. 1969; Negoro 1973; Hirose and Hirano 1977

D. meneghiniana (Kütz.) Forti 1907 ("*Meneghiniana*")
Ref.: Hirano 1960

Gardnerula J. De Toni 1936

Syn.: *Polythrix* Zanard. ex Born. & Flah. 1886, non *Polythrix* Nees 1847

G. corymbosa (Harv.) J. De Toni 1936
Basion.: *Polythrix corymbosa* (Harv.) Grun. ex Born. & Flah. 1886
Ref.: Higashi and Okada 1927; Umezaki 1956a, b, 1961; Umezaki and Kamura 1977

Gloeotrichia J. Ag. ex Born. & Flah. 1886

G. echinulata (Smith & Sowerby) P. Richt. 1894
Ref.: Yoneda 1938a; Akatsuka 1951; Hirano 1956b; Ochiai 1962b; Mizuno 1964; Negoro 1973; Hirose and Hirano 1977; Imazu 1981
Syn.: *Rivularia echinata* Smith & Sowerby ex Agardh 1824
Ref.: Akatsuka 1951

G. pisum (Ag.) Thur. ex Born. & Flah. 1886 ("*Pisum*")
Ref.: Okamura 1902; Akiyama 1965a; Hirose and Hirano 1977
Syn.: *Rivularia Lens* Menegh. 1843
Ref.: Martens 1866; Okamura 1902
Syn.: *Rivularia Pisum* Ag. 1824
Ref.: Matsumura 1904

G. longiarticulata G. S. West 1907
Ref.: Imazu 1979

G. natans (Hedw.) Rabenh. ex Born. & Flah. 1886
Ref.: Higashi and Okada 1927; Yoneda 1937, 1938c, 1952a; Okada 1939b; Akatsuka 1951; Hirano 1963; Mori 1966; Negoro 1973; Hirose and Hirano 1977; Imazu 1979; Yamagishi 1985
Syn.: *Rivularia natans* Welwitsch ex Born. & Flah. 1886
Ref.: Akatsuka 1951

Isactis Thur. ex Born. & Flah. 1886

I. nipponica Hirose 1937
Syn.: *Rivularia nipponica* (Hirose) Bourr. 1970
Ref.: Hirose 1937

I. plana (Harv.) Thur. ex Born. & Flah. 1886
Ref.: Higashi and Okada 1927; Hirose 1957; Umezaki 1961; Noda 1974, 1987; Hiramatsu 1967; Kajimura 1975

Rivularia (Roth) Ag. ex Born. & Flah. 1886

R. aquatica De Wild. 1897
Syn.: *Rivularia globiceps* G. S. West 1907
Ref.: Hirose 1937; Akiyama 1965a; Hirose and Hirano 1977

Syn.: *Rivularia globiceps* var. *longissima* Hirose 1937
Ref.: Hirose 1937; Hirose and Hirano 1977

R. atra Roth ex Born. & Flah. 1886

R. atra var. ***atra***
Ref.: De Toni 1895; Okamura 1902, 1916; Matsumura 1904; Akatsuka 1951; Tanaka 1956; Hirose 1957 and 1958 (as *Rivularia beccariana*); Umezaki 1961; Hiramatsu 1967; Noda 1974, 1987
Syn.: *Rivularia opaca* Harv. 1859
Ref.: Harvey 1859; Dawson 1959 (Harvey's manuscript)

R. atra var. ***confluens*** Born. 1892
Ref.: Umezaki 1961

R. atra var. ***hemisphaerica*** (Kütz.) Born. & Flah. 1886
Ref.: Yamada and Tanaka 1934; Umezaki 1961

R. beccariana (De Not.) Born. & Flah. 1886 ("*Beccariana*")
Ref.: Hirose 1937; Yoneda 1940a; Hiramatsu 1967, 1973; Negoro 1973; Hirose and Hirano 1977

R. biasolettiana Menegh. ex Born. & Flah. 1886 ("*Biasolettiana*")
Ref.: Yoneda 1952a

R. borealis Richt. 1899
Ref.: Negoro 1973

R. dura Roth ex Born. & Flah. 1886
Ref.: Negoro 1973

R. haematites (Lam. & De Candl.) Ag. ex Born. & Flah. 1886
Ref.: Akiyama 1965a; Negoro 1973; Bando and Nakano 1983

R. nitida Ag. ex Born. & Flah. 1886
Ref.: Kawashima 1957; Umezaki 1961; Funahashi 1967; Hagihara et al. 1970; Noda 1974, 1987

R. planctonica Elenk. 1921
Ref.: Kokubo and Kawamura 1949

R. polyotis (J. Ag.) Born. & Flah. 1886
Ref.: Umezaki 1961; Hiramatsu 1967; Umezaki and Kamura 1977

R. sphaerica Hirose 1937
Ref.: Hirose 1937; Hirose and Hirano 1977

4. Scytonemataceae Kütz. 1843

Kyrtuthrix Erceg. 1929

K. maculans (Gom.) Umezaki 1958
Basion.: *Brachytrichia maculans* Gom. 1901
Ref.: Okamura 1916
Syn.: *Kyrtuthrix maculans* Erceg. 1929
Ref.: Umezaki 1958, 1961; Hirose 1957, 1958; Hiramatsu 1967

Scytonema Ag. ex Born. & Flah. 1886

S. arcangelii Born. & Flah. 1886 ("*Arcangelii*")
Ref.: Hiramatsu 1967

S. burmanicum Skuja 1949
Ref.: Hiramatsu 1973

S. cincinnatum (Kütz.) Thur. ex Born. & Flah. 1886
Syn.: *Scytonema crispum* (Ag.) Born. 1889
Ref.: Hirose 1938; Emoto and Hirose 1940, 1943b, 1952b; Yoneda 1941a, 1952a; Kobayasi 1958; Kobayasi et al. 1962; Hiramatsu 1973; Hirose and Hirano 1977; Bando and Nakano 1983; M. Watanabe and Niiyama 1990

S. coactile Mont. ex Born. & Flah. 1886

S. coactile var. ***coactile***
Ref.: Hiramatsu 1967

S. coactile var. ***minus*** Wille 1913 ("*minor*")
Ref.: Emoto and Hirose 1943b (as *minor*); Yoneda 1952a (as *minor*); Hirose and Hirano 1977 (as *minor*)

S. coactile var. ***thermale*** Geitl. 1933
Ref.: Emoto and Hirose 1942b, c, d; Yoneda 1952a; Hirose and Hirano 1977

S. hofmannii Ag. ex Born. & Flah. 1887 ("*Hofmannii*")

S. hofmannii var. ***hofmannii***
Ref.: Emoto and Hirose 1943a; Yoneda 1951; Akiyama 1961, 1965a; Hiramatsu 1967; Mori 1971; Hirose and Hirano 1977; Bando and Nakano 1983

S. hofmannii var. ***crassum*** Bharadw. 1934 ("*crassa*")
Ref.: Emoto and Hirose 1942d, 1943a; Yoneda 1952a; Hirose and Hirano 1977

S. hofmannii var. ***synplocoides*** (Reinsch) Born. & Flah. 1886 ("*Symplocoides*")
Ref.: Hirose and Hirano 1977

S. javanicum (Kütz.) Born. ex Born. & Flah.

1887
Ref.: Yoneda 1951; Hiramatsu 1973

S. millei Born. ex Born. & Flah. 1886 ("*Millei*")
Ref.: Nakano 1970; Hirose and Hirano 1977

S. mirabile (Dillw.) Born. 1889
Ref.: Higashi and Okada 1927; Yoneda 1937, 1953a; Hirose 1938; Fukushima 1952, 1954; Akiyama 1961, 1965a; Kobayasi 1958; Kobayasi et al. 1962; Hirano 1962; Nakano 1970, 1971; Yamagishi 1967, 1972; Hiramatsu 1967, 1973; Negoro 1973; Hirose and Hirano 1977; Imazu 1979
Syn.: *Scytonema figuratum* Ag. ex Born. & Flah. 1886
Ref.: Okamura 1902

S. myochrous (Dillw.) Ag. ex Born. & Flah. 1886 ("*Myochrous*")
Ref.: Yoneda 1939a; Yamaguti 1956; Hiramatsu 1967; Mori 1971; Hirose and Hirano 1977

S. ocellatum Lyngb. ex Born. & Flah. 1886
Ref.: Okamura 1902; Emoto and Hirose 1940b; Emoto and Yoneda 1941a, b; Yoneda 1950, 1951; Mizuno 1964; Akiyama 1965a; Hirose and Hirano 1977; Yamagishi 1972, 1985

S. pascheri Bharadw. 1934 ("*Pascheri*")
Ref.: Hiramatsu 1973

S. polycystum Born. & Flah. 1886
Ref.: De Toni 1895; Okamura 1902, 1916; Matsumura 1904; Umezaki 1961
Syn.: *Lyngbya effusa* Harv. 1859
Ref.: Harvey 1859; Okamura 1902

S. saleyerense Weber-van Bosse 1913 ("*saleyerensis*")
Ref.: Hiramatsu 1973

S. stuposum (Kütz.) Born. ex Born. & Flah. 1886
Ref.: Yoneda 1941a, 1951, 1952a; Emoto and Yoneda 1941a, b; Hirose and Hirano 1977
Syn.: *Scytonema caldarium* Setch., 1899
Ref.: Emoto and Hirose 1942a, c, e; Yoneda 1952a; Hirose and Hirano 1977

S. tolypothrichoides Kütz. ex Born. & Flah. 1886 ("*tolypotrichoides*")
Ref.: Ochiai 1962b; Hiramatsu 1973

S. varium Kütz. ex Born. & Flah. 1886
Ref.: Yoneda 1938b, c, 1952a; Hirose and Hirano 1977

Scytonematopsis E. Kissel. 1930
Syn.: *Tildenia* Kossinsk. 1926, *Setchelliella* J. De Toni 1936

S. ambigua Emoto & Hirose 1952b
Ref.: Emoto and Hirose 1952b

S. pilosa (Harv.) comb. nov.
Basion.: *Calothrix pilosa* Harv. ex Born. & Flah., Ann. Sci. Nat. VII. Bot. 3: 363, 1886
Syn.: *Tildenia pilosa* (Harv.) Poljansky, Izv. Glavn. Bot. Sada URSS 27(3): 327, 1928, *Setchelliella pilosa* (Harv.) J. De Toni, Noterelle di nomenclatura algologica, VIII, p. 6, 1936
Ref.: Umezaki 1961; Hiramatsu 1967; Noda 1974, 1987

The following species without Latin diagnosis and other descriptions are listed in Yoneda's paper (Yoneda, Y.: A general consideration of the thermal Cyanophyceae of Japan. Mem. Coll. Agr., Kyoto Univ. 62: 1-20, 1952). Rivulariaceae: *Calothrix itibionensis* Yoneda nom nud., *Dichothrix caldaria* Yoneda nom. nud. Scytonemataceae: *Scytonematopsis variabilis* Yoneda nom. nud.

IV. Stigonematales Geitl. 1925

1. Borzinemataceae Geitl. 1942

Borzinema J. De Toni 1936

B. rupicola (Borzi) J. De Toni 1936
Basion.: *Diplonema rupicola* Borzi 1916
Ref.: Mori 1971

Spelaeopogon Borzi 1905
Syn.: *Pseudospelaeopogon* Elenk. 1949

S. koidzumianum Yoneda 1942f ("*Koidzumianum*")
Ref.: Yoneda 1942f

2. Capsosiraceae (Borzi) Geitl. 1925

Capsosira Kütz. ex Born. & Flah. 1886

C. brebissonii Kütz. ex Born. & Flah. 1887 ("*Brebissonii*")
Ref.: Higashi and Okada 1927; Hirose 1937; Yoneda 1953a; Hirose and Hirano 1977

3. Fischerellaceae Anagn. & Kom. 1990

Fischerella (Born. & Flah.) Gom. 1895
Syn.: *Fischera* S. H. Schwabe 1837, *Sommierella* Borzi 1907

F. ambigua (Näg.) Gom. 1895
Basion.: *Scytonema ambiguum* Näg. ex Born. & Flah. 1886
Ref.: Emoto and Hirose 1940b; Yoneda 1952a; Hirano 1962; Yamagishi 1967; Hirose and Hirano 1977

F. major Gom. 1902
Ref.: Yoneda 1938a; Hirose and Hirano 1977

F. muscicola (Thur.) Gom. var. ***minor*** Peters. 1928
Ref.: Higashi and Okada 1927

F. thermalis (Schwabe) Born. & Flah. 1887
Ref.: Yoneda 1938b, c, 1952a

Westiellopsis M. Janet 1941

W. prolifica M. Janet 1941
Ref.: Akiyama 1965b; Akiyama and Nishigami 1967; Hirose and Hirano 1977

4. Mastigocladaceae Geitl. 1925

(1) Mastigocladoideae Anagn. & Kom. 1990

Hapalosiphon Näg. in Kütz. ex Born. & Flah. 1887

H. arboreus W. & G. S. West 1895
Ref.: Yoneda 1937; Hirose and Hirano 1977

H. fontinalis (Ag.) Born. 1889
Ref.: Yoneda 1938b, c, 1952a, 1953a; Emoto and Yoneda 1941a, b; Hirano 1962; Negoro 1973; Hirose and Hirano 1977
Syn.: *Hapalosiphon pumilus* Kirchn. ex Born. & Flah. 1886
Ref.: Okamura 1902

H. hibernicus W. & G. S. West 1896
Ref.: Higashi and Okada 1927; Yoneda 1937, 1941b, 1952a, 1953a, 1954b; Hirose 1937; Negoro 1937b, 1973; Emoto and Hirose 1940b; Hirano 1959b, 1962; Ochiai 1962b; Mizuno 1964; Imada 1970; Yamagishi 1972; Hirose and Hirano 1977; Imazu 1977, 1986

H. intricatus W. & G. S. West 1895
Ref.: Hirano 1962; Akiyama 1965a; Hiramatsu 1967; Yamagishi 1967; Nakano 1971; Hirose and Hirano 1977

H. luteolus W. & G. S. West 1897
Ref.: Hiramatsu 1967

H. stuhlmannii Hieron. 1895 ("*Stuhlmannii*")
Ref.: Akiyama 1965a; Hiramatsu 1967; Hirose and Hirano 1977

H. welwitschii W. & G. S. West 1897 ("*Welwitschii*")
Ref.: Akiyama 1965b; Hiramatsu 1967, 1973; Hirose and Hirano 1977

Mastigocladus Cohn 1862

M. laminosus Cohn 1862
Ref.: Molisch 1926; Yoneda 1938b, c, 1939b, c, 1940b, c, 1941b, 1942, 1952a; Emoto and Hirose 1940a, b, c, 1941, 1942a, b, d, e, f, 1943a, b, 1949, 1952a, b, c; Fukushima 1950; Ikoma and Doi 1955; Akiyama 1965a; Hirose 1966; Negoro 1973; Hirose and Hirano 1977; Mifune and Hirose 1982, 1983a, b
Syn.: *Mastigocladus laminosus* var. *anabaenoides* (B. Peters.) Copel. 1936
Ref.: Yoneda 1952a
Syn.: *Mastigocladus laminosus* var. *phormidioides* (B. Peters.) Copel. 1936
Ref.: Emoto and Yoneda 1942; Yoneda 1952a

Thalpophila Borzi 1906

T. caldaria Emoto & Yoneda 1941b
Ref.: Emoto and Yoneda 1941b; Yoneda 1952a

Umezakia M. Watanabe 1987

U. natans M. Watanabe 1987

Ref.: M. Watanabe 1987

(2) Brachytrichoideae (Born. & Flah.) Fritsch 1945

Syn.: Sub-trib. Rivulariaceae Kütz. ex. Born. & Flah. 1886, sectio Brachytricieae Born. & Flah. 1886, Scytonemataceae Rabenh. 1865 subfam. Brachytrichieae Fritsch 1945, Brachytrichiaceae Watenberg 1872, Brachytrichiaceae Hirose 1965, nom. nud.

Brachytrichia Zanard. ex Born. & Flah. 1886

B. quojii (Ag.) Born. & Flah. (*"Quoyi"*)

Basion.: *Nostoc Quojii* Ag. 1924 (*"Quoji"*)

Syn.: *Brachytrichia Balanii* Born. & Flah. 1886, *Brachytrichia rivularioides* Zanard. 1872, *Brachytrichia affinis* Setch. & Gardn. in Gardn. 1918, *Brachytrichia Codii* Setch. 1926, *Brachytrichia Balanii* f. *purpurea* Frémy 1932

Ref.: Okamura 1915, 1936; Higashi and Okada 1927; Higashi 1933a; Umezaki 1952a, 1955b, 1956b, c, 1958, 1961; Hirose 1957 (as *Brachytrichia quoyi* f. *quoyi* Umezaki), 1958; Kida 1964; Umezaki and Kamura 1977; Hiramatsu 1967; Noda 1974, 1987

5. Nostochopsaceae Geitl. 1925

Syn.: Mastigocladopsaceae Iyeng. & Desik. 1946 (false Mastigocladopsidaceae)

Mastigocoleus Lagerh. ex Born. & Flah. 1886

M. testarum Lagerh. ex Born. & Flah. 1886

Ref.: Okamra 1922; Higashi and Okada 1927; Umezaki 1961; Akimoto et al. 1972

Nostochopsis Wood ex Born. & Flah. 1886

N. lobatus Wood ex Born. & Flah. 1886

Ref.: Higashi and Okada 1927; Hada 1937; Yoneda 1952a; Akiyama 1965a; Hiramatsu 1967; Negoro 1973

Syn.: *Nostochopsis Wichmannii* Weber van Bosse 1913

Ref.: Yoneda 1938c, 1939a; Hirose and Hirano 1977

6. Stigonemataceae (Hass.) Kirchn. 1898

Stigonema Ag. ex Born. & Flah. 1886

Syn.: *Sirosiphon* Kütz. 1843

S. aerugineum Tild. 1910

Ref.: Hiramatsu 1967, 1973

S. hormoides (Kütz.) Born. & Flah. 1886

Ref.: Akiyama 1961, 1965a; Horikawa et al. 1969; Nakano 1971; Hiramatsu 1973; Hirose and Hirano 1977; Bando and Nakano 1983

S. informe Kütz. ex Born. & Flah. 1886

Ref.: Higashi and Okada 1927

S. mamillosum (Lyngb.) Ag. ex Born. & Flah. 1886

Ref.: Yoneda 1937; Hirano 1962; Nakano 1971; Negoro 1973; Hirose and Hirano 1977; Bando and Nakano 1983

S. mesentericum Geitl. 1925

Ref.: Hiramatsu 1967

S. minutum (Ag.) Hass. ex Born. & Flah. 1886

Ref.: Hirose 1937; Yoneda 1939a, 1949, 1950; Fukushima 1952, 1954; Akiyama 1961, 1965a; Horikawa et al. 1969; Negoro 1973; Hirose and Hirano 1977

S. ocellatum (Dillw.) Thur. ex Born. & Flah. 1886

S. ocellatum f. ***ocellatum***

Ref.: Yoneda 1937, 1951, 1953a, 1954b; Fukushima 1952, 1954; Hirano 1959a, 1962; Ochiai 1962b; Mizuno 1964; Akiyama 1961, 1965a, b; Hiramatsu 1967; Yamagishi 1967, 1972; Nakano 1971; Negoro 1973; Hirose and Hirano 1977

Syn.: *Sirosiphon vermicularis* Suring. 1870, *Stigonema vermicularis* (Suring.) Forti 1907

Ref.: Suringer 1870; Okamura 1902; Matsumura 1904

S. ocallatum f. ***tomentosum*** (Kütz.) Elenk. 1938

Basion.: *Stigonema tomentosum* (Kütz.) Hieron. 1895

Ref.: Emoto and Hirose 1942c; Yoneda 1952a; Hirose and Hirano 1977

S. panniforme (Ag.) Born. & Flah. 1886

Ref.: Hiramatsu 1967

S. turfaceum Cooke ex Born. & Flah. 1886
Ref.: Yoneda 1937; Akiyama 1965a; Hiramatsu 1967; Hirose and Hirano 1977

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梅崎　勇*・渡辺眞之**：日本産藍藻類目録 2. ネンジュモ目及びスチゴネマ目

本報告は日本から報告された藍藻類のネンジュモ目とスチゴネマ目の種をリストしたものである。ネンジュモ目は4科28属161種あった。その内訳は，ミクロケト科は6属19種，ネンジュモ科は13属86種，ヒゲモ科は6属37種，スキトネマ科は3属19種であった。ネンジュモ科とスキトネマ科にそれぞれ1新組合せ種がつくられた。ネンジュモ科：*Hydrocoryne enteromorphoides* (Grun. ex Born. & Flah.) comb. nov. (＝*Hormothamnium enteromorphoides* Grun. ex Born. & Flah. 1886)，スキトネマ科：*Scytonematopsis pilosa* (Harv. ex Born. & Flah.) comb. nov. (＝*Calothrix pilosa* Harv. ex Born. & Flah. 1886)。スチゴネマ目は6科13属30種がリストされた。その内訳は，ボルジネマ科は2属2種，カプソシラ科は1属1種，フィッシェレラ科は2属5種，イデユアイミドリ科は5属11種，ノストコプシス科は2属2種，スチゴネマ科は1属9種であった（*917 小浜市学園町1-1　福井県立大学生物資源学部海洋生物資源学科，**305 つくば市天久保4-1-1　国立科学博物館　植物研究部）

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Effect of temperature on growth rate and agar quality of a new member of Japanese *Gracilaria* in Tosa Bay, southern Japan.

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Growth of *Gracilaria* sp. growing much in Uranouchi Inlet at Tosa Bay recently, was conducted in the aquatron culture system at various temperatures of 13, 16, 20, 23, 25 and 28°C with a photon flux density of $100\pm10\ \mu M\cdot m^{-2}\cdot s^{-1}$, in a light regime of 12L : 12D hours. Daily growth rate of thalli attained maximum and minimum values of $2.47\pm1.05\%$ at 16°C and $1.20\pm0.27\%$ at 28°C, respectively. Physical properties of agar of the cultured thalli were also determined after 2 h treatment with 5% NaOH at 80°C. Agar yields attained between 24.2 ± 0.2 and $28.4\pm0.6\%$. Measurement of the gel strength of 1.5% agar gave a highest value of $755\pm15\ g\cdot cm^{-2}$ at 16°C. The lowest gel strength recorded was $437\pm48\ g\cdot cm^{-2}$ at 25°C. Viscosities of 1.5% agar sol obtained maximum value of 73.9 ± 0.6 cP at 16°C and minimum values of 16.4 ± 0.8 cP at 25°C. Gelling temperatures ranged from 48°C to 49°C. This *Gracilaria* sp. indicated high growth rate and best agar quality at 16°C.

Key Index Words: New Japanese Gracilaria—*growth rate—agar quality—temperature.*

Gracilaria sp. occurring along the coast of Kyushu Island, south Ise Bay, and other inland seas in Japan has been reported as a new Japanese *Gracilaria* (Chirapart *et al.* 1994). In recent year, large quantities of this *Gracilaria* have been harvested (more than 2000 t dry weight per year) for the production of agar and salad vegetable. Algal biomass and physical properties of this *Gracilaria* sp. have been reported to be seasonal and high gel strength obtained from the winter collected seaweed in Tosa Bay (Chirapart and Ohno, 1993b). Property of agar commonly has been reported in relation to environmental factors of plant growth (Craigie and Wen 1984; Friedlander *et al.* 1987; Christeller and Laing 1989). Moreover, growth of *Gracilaria* spp. from Tosa Bay has been reported under different environmental factors in a close-recirculating system or aquatron (Orosco and Ohno 1992). However, there have been no report on effect of environmental factor on growth and agar quality of this new Japanese *Gracilaria* under culture conditions. This study was carried out in order to examine effect of temperature on growth and agar quality of this seaweed under controlled culture conditions.

Materials and Methods

Growth rate

Gracilaria samples were collected from Uranouchi Inlet in Tosa Bay in 1992. Growth of the algae was determined in a close-recirculating system (aquatron) at various temperatures (cf. Ohno, 1977). collected samples were allowed to adapt to each set of experimental conditions for one week. After which 0.9 to 1 g of healthy thallus (10 replicates per treatment temperature) were fixed to glass rods with fine lines and incubated at 13, 16, 20, 23, 25 and 28°C with a photon flux density of $100\pm10\ \mu M\cdot m^{-2}\cdot s^{-1}$, in a light regime of 12L:12D hours. Fresh weight was measured every 7 days and growth rates assessed. One third of the unenriched cul-

tured seawater was replaced every 2-3 days. Data represent the first week of incubation. Experiments were conducted in duplicate. Daily growth rates were calculated as the increase in fresh weight in percentage following the formula of Penniman et al. (1986)

$$G=[(W_t/W_o)^{1/t}-1]\times 100$$

where G is % increase in fresh weight per day, W_o is initial weight and W_t is weight after t days.

Agar quality

The effect of temperature on agar properties of the *Gracilaria* sp. was also determined. Healthy thalli, 50 to 60 g (10 replicates per treatment temperature), were incubated in the aquatron at the temperatures and culture conditions described above. After two weeks incubations, fresh weight was measured and the samples were sun-dried prior to extraction.

Dried samples (50 g), were incubated in 2 *l* of 5% NaOH solution in 80°C water bath for 2 hr and washed in tap water for 30 min. The samples were neutralized in 1 *l* of 1.5% H_2SO_4 solution for 1 hr, and then washed in tap water for 2 hr. The treated samples were boiled for 2 hr using a Bunsen burner with 1.5 *l* of distilled water in 2 *l* Erlenmeyer flask equipped with reflux condenser. The agar extract was filtered through muslin cloth.

A 1.5% agar solution was prepared from the extracted agar by boiling 9 g of agar powder in 600 m*l* of distilled water for 30 min. Viscosities of the solution at 80°C were determined using a Brookfield viscometer (Spindle No. 1 at 60 rpm; Tokyo keki). Gel strength (3 replicates per sample) were measured using a 1 cm^2 plunger (Nikkansui Shiki gelometer, Kiya Seisakusho, Tokyo) and gel pH was measured using an electronic pH meter. Gelling temperature was determined according to Kim (1970).

Results

The physical and chemical characteristics of seawater in the experimental chamber are shown in Table 1. Thalli were cultured in water temperatures of 13, 16, 20, 23, 25 and 28°C. Water salinity fluctuated from 33.85±0.08 to 36.40±0.04. Total dissolved inorganic nitrogen (DIN) and PO_4-P concentrations varied from 0.52±0.18 to 4.21±2.65 $\mu g\cdot at\cdot l^{-1}$ and 0.12±0.03 to 0.30±0.03 $\mu g\cdot at\cdot l^{-1}$, respectively.

Table 1. Physical and chemical characteristics of seawater in the aquatron during culture period.

Temperature treatment (°C)	Salinity	PO_4-P ($\mu g\cdot at\cdot l^{-1}$)	DIN ($\mu g\cdot at\cdot l^{-1}$)
13	34.10±0.10	0.13±0.03	0.94±0.55
16	35.53±0.04	0.30±0.03	0.58±0.22
20	33.85±0.08	0.16±0.06	1.15±0.52
23	34.32±0.06	0.18±0.06	0.52±0.18
25	33.97±0.31	0.24±0.11	1.13±0.94
28	36.40±0.04	0.12±0.03	4.21±2.65

Daily growth rates of thalli grown in the

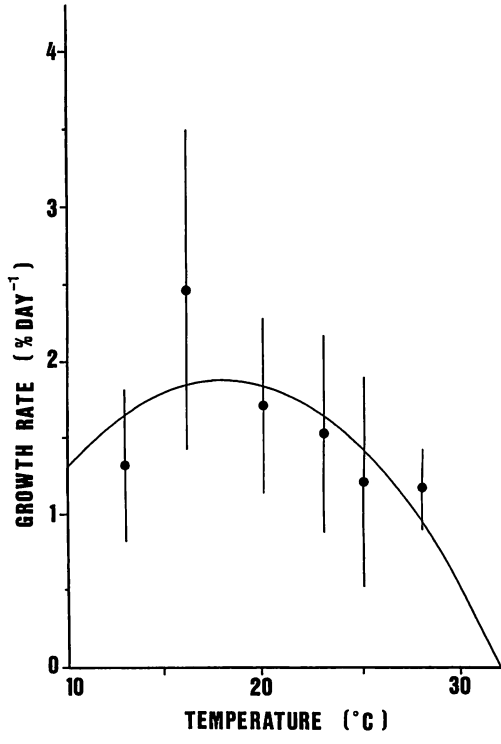

Fig. 1. Growth rates of *Gracilaria* sp. in the aquatron culture system at various temperatures. Lines represent standard deviations. Polynomial curve represent predicted growth rates.

Table 2. Agar yield, gelling temperature and gel pH of agar obtained from *Gracilaria* sp. incubated at various temperatures in the aquatron culture system, after treatment for 2 h with 5% NaOH at 80°C.

Temperature treatments (°C)	Agar yield of crude extract (%)	1.5% agar product	
		Gelling temperature (°C)	Gel pH
13	24.3±0.1	48	6.5
16	24.2±0.2	49	6.5
20	27.7±0.3	49	6.4
23	26.6±0.0	49	6.5
25	28.4±0.6	49	6.7

aquatron at various temperatures are shown in Fig. 1. The greatest growth was observed at temperature between 16°C and 20°C. The cultured plants were healthy with dark reddish color, branching, and no epiphytes. Maximum daily growth rate attained was 2.47±1.05% at 16°C. Increasing cultured temperatures over than 20°C, growth rates were gradually decreased and obtained minimum value of 1.20±0.27% at 28°C. At high temperature, the cultured thalli were not healthy, much epiphytized.

Properties of agar obtained from *Gracilaria*, after incubation in the aquatron at various temperatures, are given in Table 2. Agar yields varied between 24.2±0.2 and 28.4±0.6%. Gelling temperatures were

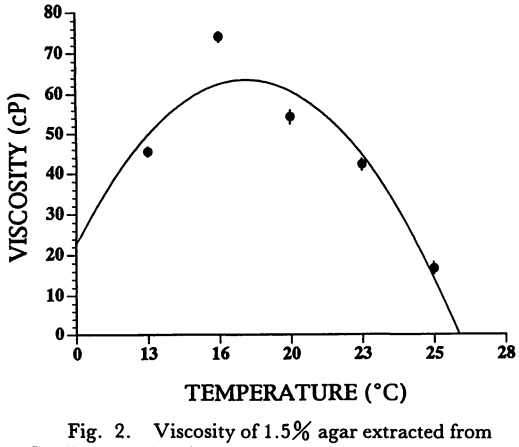

Fig. 2. Viscosity of 1.5% agar extracted from *Gracilaria* sp. incubated at various temperatures in the aquatron culture system. Lines represent standard deviations. Polynomial curve represent predicted viscosity.

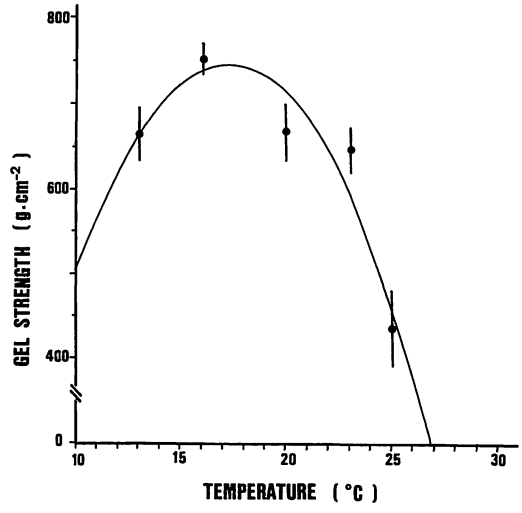

Fig. 3. Gel strength of 1.5% agar extracted from *Gracilaria* sp. incubated at various temperatures in the aquatron culture system. Lines represent standard deviations. Polynomial curve represent predicted gel strengthe.

rather stable between 48°C and 49°C and gel pH of 1.5% agar gel ranged from 6.4 to 6.7. Viscosity of 1.5% agar sol attained maximum value of 73.9±0.6 cP from sample cultured at 16°C (Fig. 2). The values were decreased after increasing water temperature and obtained minimum value of 16.4±0.8 cP in plant cultured at 25°C. The viscosity values corresponded to agar gel strength values obtained in this study. Gel strength of 1.5% agar gel (Fig. 3) obtained highest values of 755±15 $g \cdot cm^{-2}$ at a temperature of about 16-17°C while the lowest value of 437±48 $g \cdot cm^{-2}$ occurred at 25°C. Increasing water temperature over than 20°C, gel strengths were descreased.

Temperature being tested in the cultured conditions had no effect on the yield of agars and gelling temperatures whereas low temperature (16-20°C) had effect on agar gel strength and viscosity values. The higher gel strength and viscosity values also corresponded with higher growth rates of the cultured thalli.

Discussion

Growth of *Gracilaria* sp. showed positive

relationship with temperature up to 20°C, and obtained maximum growth rate at a temperature between 16°C and 17°C. This result indicated the optimum temperature similar to a previous study of *G. chorda* (15°C) in the same culture system (Orosco and Ohno 1992). However, a previous study on growth of *Gracilaria* spp. from southeast Asian water using the same aquatron system, has been reported maximum growth at 25°C for *G. "verrucosa"* and *G. fisheri* and at 27°C for *G. salicornia* and *G. firma* (Chirapart and Ohno 1993a). Present study, agar gel strength of the *Gracilaria* sp. showed inverse relationship with increasing temperature in the culture system, and positive correlation with growth rate. Similar result had been reported in long-term experiments in outdoor culture of *Gracilaria* cf. *conferta* in Israel, which showed increased gel strength under high growth rate conditions (Friedlander et al. 1987). However, the Israel strain obtained high gel strength at high temperatures in contrast to the present study wherein alkali-treated agars attained from the cultured *Gracilaria* showed the best gel at low temperatures (16–17°C). There results correspond with those of the gel of *Gracilaria* collected from natural environment, which showed a maximum gel strength value in winter, when seawater temperatures were 15–17°C (Chirapart and Ohno 1993b). This may be confirmed by the hypothesis of Craigie and Wen (1984) that growth rate may have more effect on gel strength than the particular environmental factor being tested. Craigie and Wen (1984) also suggested that chemical composition varied with the part of the thallus from which it was extracted and with the temperature at which the alga was grown. They also reported that *Gracilaria tikvahiae* showed the highest 3,6-anhydrogalactose content from alkali-modified agar of the thalli grown at 17°C, and young parts of thallus contained a higher proportion of 3,6-anhydrogalactose than mature parts (Craigie and Wen 1984). This, then, may in part explain our observed correlations between gel strength and growth rate at low temperature in the aquatron culture system. Moreover, there have been reports of gel strenghts increased with increasing temperature, and decreased with increasing nitrogen level (Christeller and Laing 1989). Conversely, lower gel strengths also have been reported during summer or in high temperatures with high level of sulfation (Cote and Hanisak 1986, Miller and Furneaux 1987).

In conclusion, optimum temperature for growth of the *Gracilaria* sp. was 16–17°C. At this low temperature condition, the algae also can produce the best gel. Both growth rates and culture temperature are considered to be effect on agar quality of this seaweed. Under certain conditions the cultured new Japanese *Gracilaria* produced comparable yields and agar properties to those of natural-grown plants and its higher agar gel strength obtained within the range (gel strength more than $500\,g \cdot cm^{-2}$) of commercial grade agars. This new Japanese *Gracilaria* species has a high potential as an essential source of agar for food industry gels.

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Anong Chirapart*・大野正夫・沢村正義*・楠瀬博三*：土佐湾の新産オゴノリ類の成長と寒天品質におよぼす温度の影響**

高知県浦の内湾に，最近大量に生育し始めたオゴノリ類の一種について，アクアトロン培養（光量は，100±10 μM m^{-2} s^{-1}，12時間照射）により，13，16，20，23，25と28°Cの温度条件で，成長速度を調べた。日間成長率は16°Cでもっとも高く，2.47±1.05%を示し，28°Cで最も低く，1.20±0.27%であった。

培養された葉体について，80°C，5%，NaOH 2時間処理により寒天の物理的特性を調べた。寒天の収率は，24.2±0.2から28.4±0.6%の範囲であった。ゲル強度は，16°Cで最も高い値，755±15 g cm^{-2}，25°Cで最も低い値，437±48 cm^{-2}をしめした。ゲル寒天の粘度は，16°Cで最も高く73.9±0.5 cP，25°Cで最も低く16.4±0.8 cP，を示した。ゲル化温度は48–49°Cであった。これらの結果から16°Cで最も成長が良く，寒天の品質ももっとも良かった。（*783 高知県南国市物部乙-200 高知大学農学部生物資源科学科，**781-11 高知県土佐市宇佐町井の尻194 高知大学海洋生物教育研究センター）

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Hirotoshi Yamamoto, Masao Ohno and Nguyen Huu Dinh: *In vitro* life histories and spermatangial types of two *Gracilaria* species from Vietnam, *G. heteroclada* and *G. firma* (Gracilariaceae, Rhodophyta)

Key Index Words: Gracilaria—G. firma—G. heteroclada—*life history—spermatangium—spermatangial type—Rhodophyta.*
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On Vietnamese species of the genus *Gracilaria*, several researchers conducted taxonomic studies (Dawson 1954, Pham 1969, Nguyen 1969, 1972). Recently Nguyen (1991) reexamined their herbaria and listed 15 species. However, more information is needed for decisive identification of some taxa. The information on male structures is indispensable for basically grouping *Gracilaria* species.

A taxon (Taxon A) called tentatively *Gracilaria bursa-pastoris* (Gmelin) Silva or *G. heteroclada* Zhang and Xia in Vietnam has been increasingly used in pond culture for agar materials of good quality. However, since the male structures were not known, identification remained provisional. Another taxon (Taxon B), which is mixed up with *G. salicornia* (C. Agardh) Dawson in Vietnam, seemed close to *G. changii* (Xia and Abbott) Abbott, Zhang and Xia or *G. firma* Chang and Xia in morphology but the accurate identification was also suspended owing to the lack of information on the males. Accordingly, we attempted to complete the life histories of the two taxa to confirm their male structures and to finalize their names.

Ohno and Nguyen collected several mature female fronds of both Taxon A (Ha Tien, Kien Giang Prov.) and Taxon B (Dong Xauan, Phu Yen Prov.) in Vietnam in February, 1993 and Ohno brought them back to Japan for *in vitro* culture. The culture experiments were conducted by the first author of this paper at the laboratory in Faculty of Fisheries, Hokkaido University.

Several cystocarps were cut off from the fronds and shaken with sterile sand to remove surface contamination (*cf.* Yamamoto and Sasaki 1987). Each of these cystocarps was placed overnight in Petri dish with sterile seawater. Fifteen to twenty spores released were transferred to each of 20 m*l* glass bottles by pipette for establishing unialgal culture. Six sporelings of *ca* 5 mm in length (*ca* 40 days culture) were detached from the bottom of the glass bottles and transferred into each of 500 m*l* flasks for free-living culture.

Culture conditions: Temperature of 26–27°C, light of *ca* 75 μE $m^{-2}s^{-1}$ of cool white fluorescent lamps, a photoperiod of 14 h (light)-10 h (dark) and aeration (*ca* 0.2 *l*/min) only in free-living culture. PES medium (1/2 concentration of original prescription) without vitamins was changed about once a week throughout free-living culture. Spores from raised fronds were cultured under the same conditions.

Taxon A: Carpospore-derived fronds grew up to 15–20 cm in length and released tetraspores in about 70 days after carpospores were transferred to glass bottles. Tetrasporophytes were terete and irregularly branched. Branches were long, but often spinous in upper parts of axes. Color was pale green. Tetraspore-derived fronds gave rise to male

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(10–15 cm long) and female (*ca* 5 cm long) fronds in 60–70 days (Figs. 1 and 2). These gametophytes were the same as wild tetrasporophytes in general appearance and color.

Spermatangia were formed superficially (*Chorda* type, *cf.* Yamamoto 1975) all over the fronds except basal and apical portions. Cystocarps appeared all over the fronds except apical portions, up to 1 mm high and 1 mm in diameter. Traversing filaments in cystocarps are absent. Released carpospores developed normally and completed the life history of typical *Polysiphonia* type in about 140 days from the initial culture.

Taxon B: Carpospore-derived fronds grew up to 5–7 cm and released tetraspores in about 120 days after carpospores were transferred to glass bottles. Tetraspores released developed into male and female fronds in about 100 days (Figs. 3 and 4). Both tetrasporophytes and gametophytes were terete, irregularly branched and dark to blackish brown in color. Branches were more or less inflated in middle portion and branch bases were markedly constricted and sometimes stipitate (Figs. 3 and 4). The fronds were small but similar to wild ones in morphology. Tetrasporangia, spermatangia and cystocarps were formed all over the fronds except basal and apical portions.

Figs. 1 and 2. Habit of *Gracilaria heteroclada* raised in culture, showing characteristic spinous branchlets. Fig. 1. Female. Fig. 2. Male. Scale bars: 2 cm for 1 and 3 cm for 2.

Figs. 3 and 4. Habit of *Gracilaria firma* raised in culture, showing distinctive constriction (rather stipitate) of basal part of branches. Fig. 3. Male. Fig. 4. Female. Scale bars: 2 cm for 3 and 4.

Male structure is *Verrucosa* type (*cf.* Yamamoto 1975). Life history was completed in about 250 days and showed typical *Polysiphonia* type.

Taxonomy

Taxon A: Nguyen (1991) thought that *G. heteroclada* was similar to plants he had earlier identified as *G. bursa-pastoris* (Nguyen 1969, 1972), but he did not have spermatangial material.

Our culture experiment showed that male type of Taxon A coincided with that of *G. heteroclada* and not *G. bursa-pastoris* (*Textorii* type, *cf.* Yamamoto 1975). Raised Taxon A was almost the same morphologically as the former in having spinous branchlets (Zhang and Xia 1988, Fig. 2) and having pale green color. *G. heteroclada* was identified by Zhang and Xia as having *Chorda* type spermatangia.

The distribution of *G. heteroclada* was confirmed to range as far west as Vietnam from Hainan island, China (type locality).

Taxon B: Taxon B was sometimes included in *G. salicornia* or *G. firma* owing to not understanding the morphological variation, and also sometimes considered as *G. changii*. Morphology of raised fronds almost coincides with that of *G. firma* with few second order branches and *Verrucosa* type male structure. The plants never showed characteristic branch constrictions of *G. salicornia*. Taxon B is basically different from *G. changii* which has male structures of *Polycavernosa* type (Xia and Abbott 1987).

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山本弘敏*・大野正夫**・Nguyen Huu Dinh***:ベトナム産オゴノリ属植物2種 *Gracilaria heteroclada, G. firma* の生活史と雄性生殖器官の型

ベトナム産オゴノリ属2種の種名は雄性生殖器官が不明なため確定していなかった。この2種について，室内培養により果胞子からイトグサ型の生活史を完結させると共にそれぞれの雄性生殖器官の型を確認した。その結果，表層型 (*Chorda* type) を示す種を *Gracilaria heteroclada*, 深いツボ型の種を *G. firma* と同定した。(*041 函館市港町3-1-1 北海道大学水産学部，**781-11 土佐市宇佐町 高知大学海洋生物教育研究センター，*** National Center for Scientific Research of Vietnam, Union for Science, Nhatrang, Vietnam)

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Jpn. J. Phycol. (Sôrui) 42: 335–339, September 20, 1994

Shigeo Kawaguchi: The reproductive morphology of *Prionitis articulata* Okamura (Halymeniaceae, Rhodophyta) from Japan

Key Index Words: Carpopeltis articulata—*Halymeniaceae*—Prionitis articulata—*reproductive morphology*—*Rhodophyta.*

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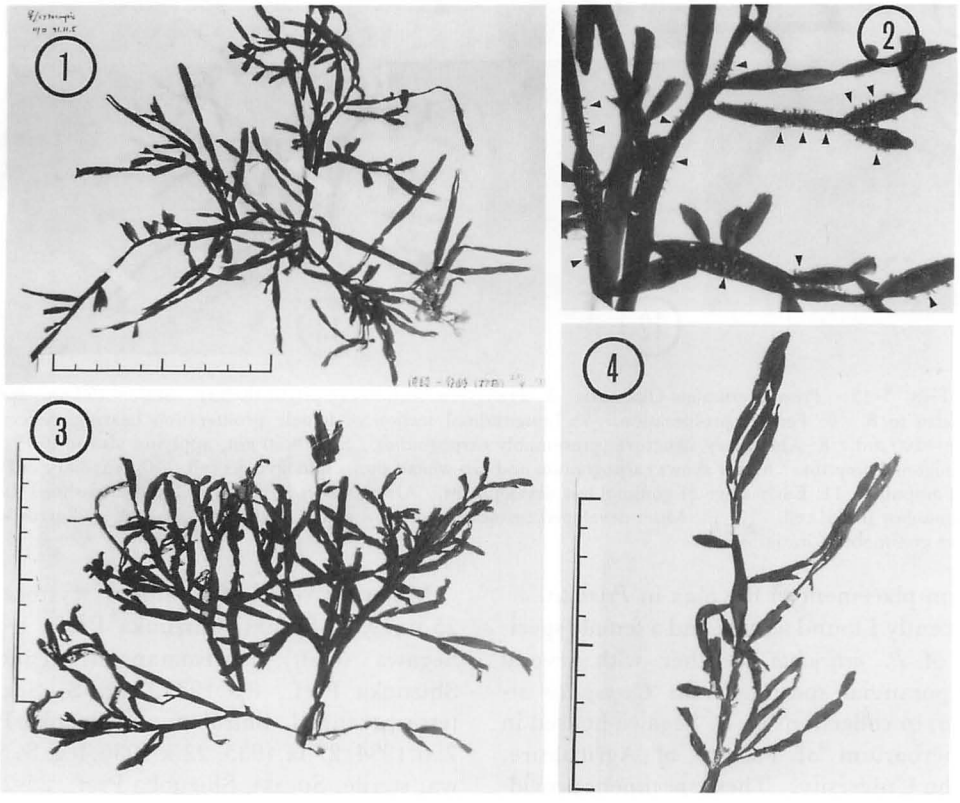
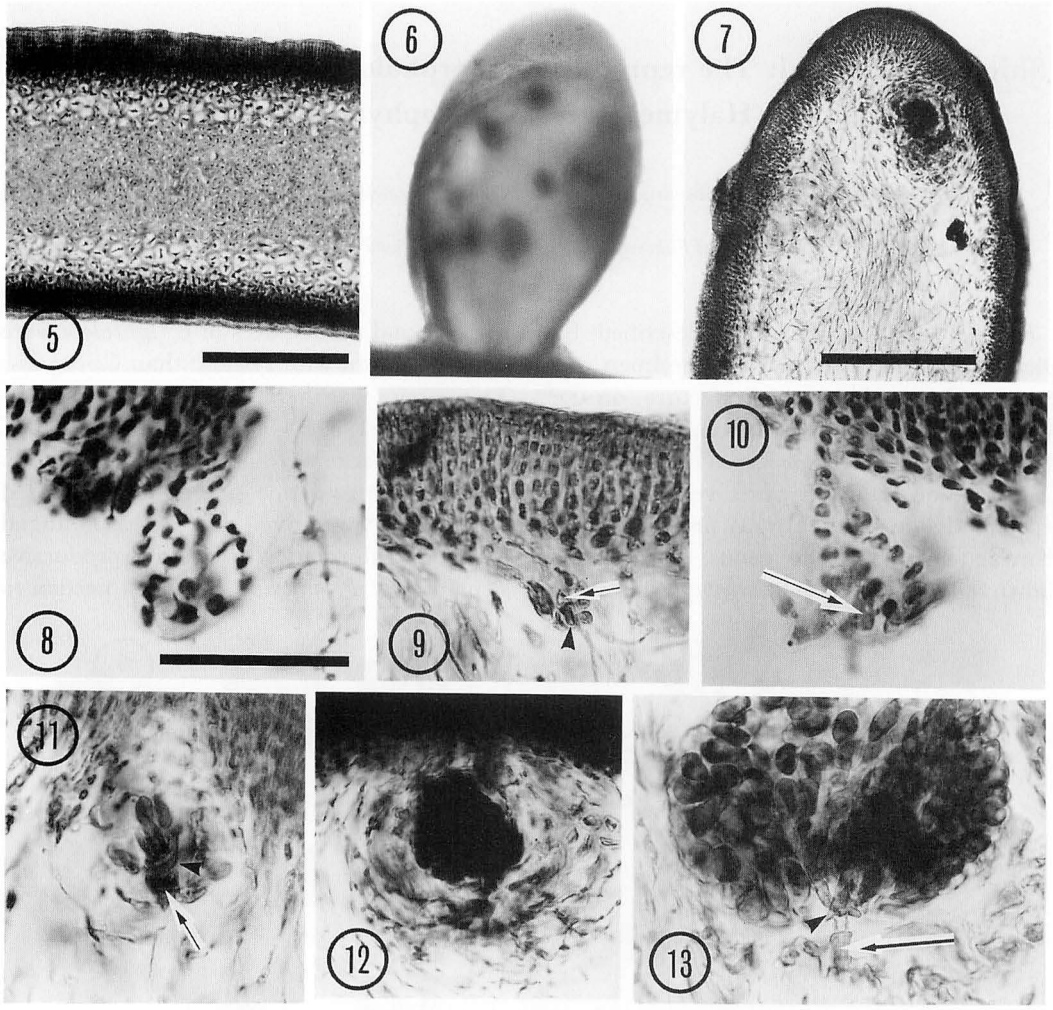
Prionitis articulata was first described by Okamura (1899, P.5.) from a specimen collected at Iragozaki, Aichi Prefecture, on the central Pacific coast of Japan. Okamura (1909) subsequently transferred this species to *Carpopeltis* on the basis of its vegetative and reproductive features. In my previous paper (Kawaguchi 1989), the genus *Prionitis* was shown to be distinct from *Carpopeltis* in several respects and the features of *C. articulata* were more in accord with *Prionitis* than *Carpopeltis*. This species was therefore restored to *Prionitis* (Kawaguchi 1989). However, due to its rarity, sexual plants were not available for study at that time and my discussion was based solely on vegetative and tetrasporangial features. Information on sexual reproductive structures of *P. articulata* has been needed to



Figs. 1–4. Herbarium specimens of *Prionitis articulata* Okamura collected by S. Segawa and deposited in the Herbarium, Faculty of Agriculture, Kyushu University. Scale=10 cm. 1: Female specimen collected at Susaki on 25 September 1935. 2: Magnification of Fig. 1. Arrowheads show minute reproductive proliferations. 3: Tetrasporangial specimen collected at Shirahama on 22 October 1936. 4: Male specimen collected at Tanoura on 8 October 1935.

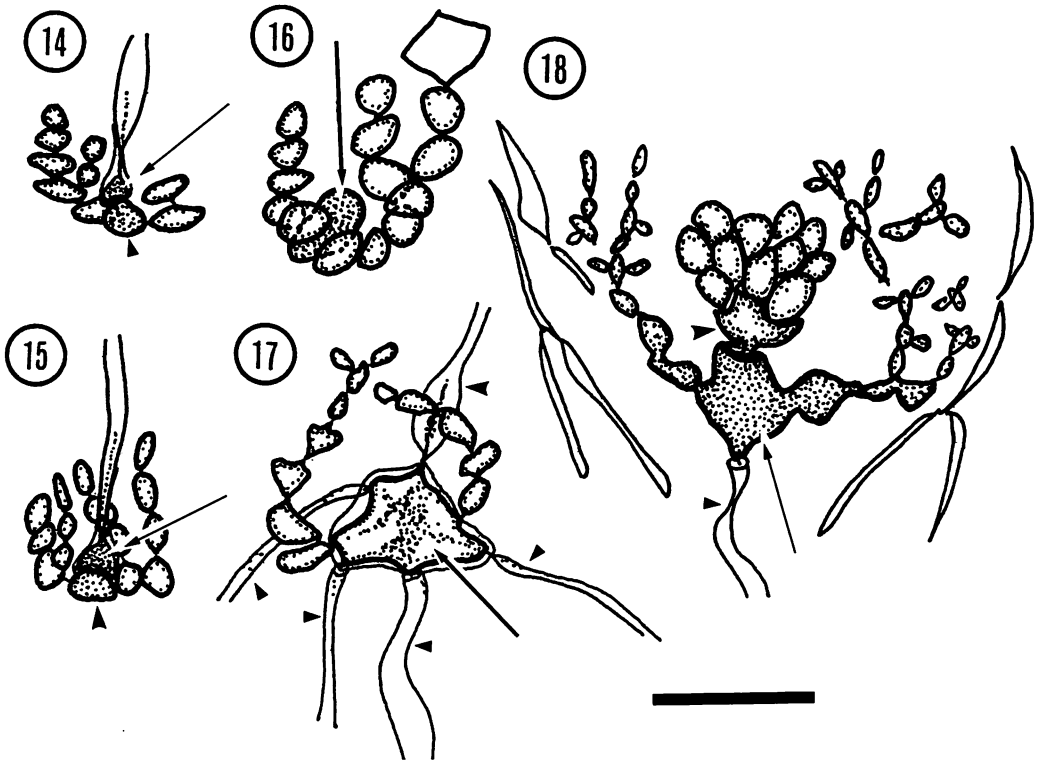


Figs. 5–13. *Prionitis articulata* Okamura. 5: Transverse section of upright thallus. Scale=150 μm, applying also to 6. 6: Female proliferation. 7: Longitudinal section of female proliferation bearing cystocarp. Scale=100 μm. 8: Ampullary structure (presumably carpogonial). Scale=50 μm, applying also to 9–13. 9: Carpogonial ampulla. Arrow shows carpogonium and arrowhead shows hypogynous cell. 10: Auxiliary cell (arrow) ampulla. 11: Early stage of gonimoblast development. Arrow shows auxiliary cell and arrowhead shows gonimoblast initial cell. 12, 13: More developed cystocarps. Arrow shows auxiliary fusion cell and arrowhead shows gonimoblast initial cell.

confirm placement of the alga in *Prionitis*.

Recently I found a male and a female specimen of *P. articulata* together with several tetrasporangial specimens (as *Carpopeltis articulata*) in collections by S. Segawa housed in the herbarium of Faculty of Agriculture, Kyushu University. These specimens provided the opportunity to describe sexual reproductive features of *P. articulata* for the first time and to make additional observations on vegetative and tetrasporangial structures.

Materials used for study: cystocarpic, 25.ix.1935, Susaki, Shizuoka Pref., leg. S. Segawa (drift); spermatangial, Tanoura, Shizuoka Pref., 8.x.1935, leg. S. Segawa; tetrasporangial, Shirahama, Shizuoka Pref., 7.xi.1934, 27.ix.1935, 22.x.1936, leg. S. Segawa; sterile, Susaki, Shizuoka Pref., 25–27.iii, 30.xi, 1935, leg. S. Segawa; sterile, Shirahama, Shizuoka Pref., 7.ix.1934, leg. S. Segawa; sterile, Tanoura, Shizuoka Pref., ii.1938, leg. S. Segawa.



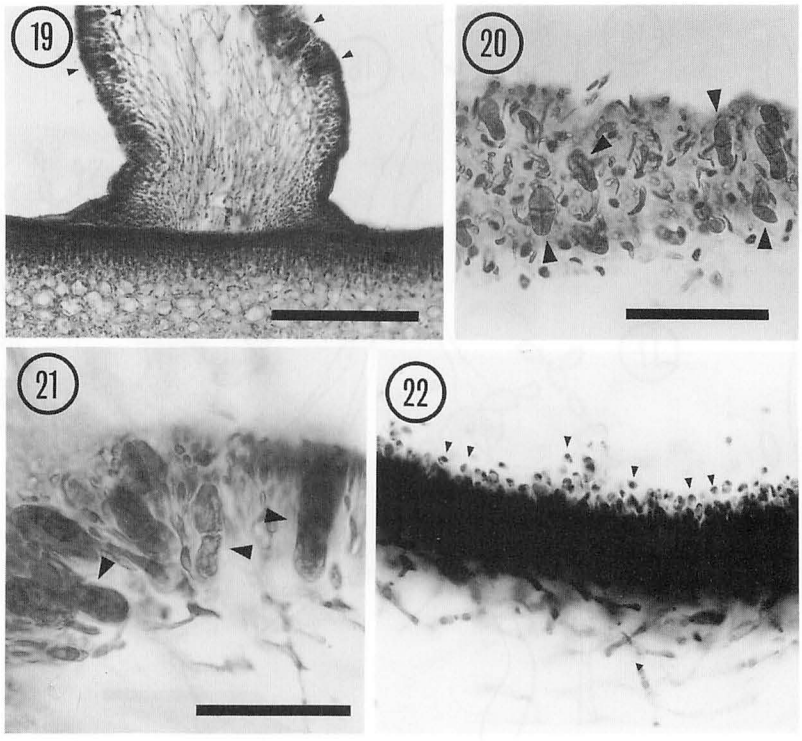
Figs. 14–18. *Prionitis articulata* Okamura. Scale=200 μm. 14, 15: Carpogonial ampulla. Arrow shows capogonium and arrowhead shows hypogynous cell. 16: Auxiliary cell (arrow) ampulla. 17: Production of connecting filaments (small arrowhead) from carpogonial fusion complex (arrow) with trichogyne (large arrowhead). 18: Cystocarp development. Arrow shows auxiliary fusion complex with connecting filament (small arrowhead) and large arrowhead shows gonomoblast initial. Note that lateral filaments are produced from ampullary cells.

Hand sections were made with a razor blade from small pieces excised from the dried specimens and resoaked in seawater. Sections were stained with a 0.5% cotton blue solution (Kawaguchi and Masuda 1984) and mounted in a glycerol/seawater mixture. Microscope slides used for study are held by the author.

The fertile specimens used in this study were 8–20 cm long. Several upright thalli developed from a scutate holdfast, each having a short terete stipe to 3–4 mm long. Upright thalli are compressed throughout, and are repeatedly articulated into cuneate or ellipsoid segments, 1–5 cm long × 3–5 mm wide. Branching is di-or trichotomous, or irregularly proliferous from the margin or the surface of the thallus, occasionally giving rise to a very entangled appearance (Figs. 1, 3, 4).

The upright thallus is up to 500 μm thick in section and consists of a compact cortex and a dense filamentous medulla. The outer cortex consists of small, isodiametric cells tightly arranged in anticlinal rows 7 to 8 cells deep. This layer connects to an inner layer of larger, polygonal to rounded cells, also tightly packed and connected laterally by secondary pit-connections. The medulla consists of densely interwoven filaments and occupies about one third of the thallus (Fig. 5).

Male and female reproductive structures are confined to minute reproductive proliferations, as are tetrasporangia (Figs. 6, 7). These proliferations develop from the surfaces or the margins of the thalli in the upper portion of a plant (Fig. 2). The male proliferations are spindle-shaped, 400–500 μm wide × 700–800 μm long. The female proliferations are spindle-shaped or occasionally slightly compressed, 750–900 μm wide × 800–



Figs. 19–22. *Prionitis articulata* Okamura. 19: Longitudinal section of tetrasporangial proliferation through vegetative segment. Arrowhead shows tetrasporangium. Scale=200 μm. 20: Tetrasporangia (arrowhead) scattered in the proliferation. Scale=100 μm. 21: Tetrasporangium (arrowhead) formation. Scale=50 μm, applying also to 22. 22: Spermatium (arrowhead) formation.

1100 μm long (Fig. 6). The tetrasporangial proliferations are circular in outline, 1000–1300 μm wide × 1200–1400 μm long × 250–300 μm thick (Fig. 19). The medullary filaments of reproductive proliferations are more laxly arranged than in vegetative segments (Figs. 7, 19).

Spermatangia are formed from outermost cortical cells, and are 4–5 μm long × 2–3 μm wide (Fig. 22). Carpogonial branches and auxiliary cells are separately formed in ampullary cell clusters (Figs. 8–10, 14–16). Carpogonial ampullae were rare in the specimen at hand, but a carpogonial branch was observed to consist of a carpogonium and a hypogynous cell (Figs. 9, 14, 15). Auxiliary cell ampullae were common and sparingly branched to the second order (Figs. 10, 16). Auxiliary cells are slightly larger than other ampullary cells and are centrally located in the bottom of the ampulla (Fig. 16). After putative fertilization, several connecting filaments are cut off from a large cell, presumably a carpogonial fusion complex (Fig. 17). A connecting filament fuses with an auxiliary cell which subsequently produce gonimoblasts toward the thallus surface (Figs. 11, 18). Whether the connecting filament ceased to grow at the fusion point or further grew to another auxiliary cell was not ascertained in the specimen at hand. During gonimoblast development ampullary cells produce lateral filaments (Fig. 18). Mature cystocarps are reniform to rounded, 120–150 μm in diameter, and deeply submerged in the medulla (Figs. 12, 13). Pericarps are scarcely evident in the mature cystocarps (Fig. 13). Tetrasporangia are scattered in the proliferations (Figs. 20, 21) and are narrowly ellipsoidal, 40–50 μm long × 10–15 μm wide.

The presence of carpogonial branches and auxiliary cells within separate ampullary cell

clusters clearly places *P. articulata* within the Halymeniaceae (Chiang 1970). As discussed in my previous paper (Kawaguchi 1989), *Prionitis* is characterized by a combination of the following features: 1) rigid, cartilaginous thalli, 2) compact cortical and medullary layers, 3) absence of refractive medullary cells, 4) confinement of reproductive structures to distal segments and/or to proliferations. Vegetative features and the presence of minute tetrasporangial proliferations of *P. articulata* were consistent with this circumscription and the species was therefore placed in this genus (Kawaguchi 1989). The present study has confirmed that spermatangia and cystocarps are also confined to minute reproductive proliferations, and that auxiliary cells are formed in sparingly branched ampullae. The last feature is not exclusive to *Prionitis* within this family, but is considered to be a distinctive reproductive feature of this genus (Chiang 1970). *P. articulata* is therefore confirmed as a typical member of *Prionitis* on the basis of both vegetative and reproductive features.

Acknowledgements

I wish to express my thanks to Mr. J. A. Lewis of the University of Melbourne for his assistance in improving the manuscript.

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川口栄男：フシキントキ（紅藻，ムカデノリ科）の生殖器官

これまで栄養体と四分胞子体についてのみ記載されていたフシキントキ *Prionitis articulata* Okamura の雌雄生殖器官の観察を，九州大学農学部に保存されている標本に基づいて行なった。本種の雌雄生殖器官は，四分胞子嚢と同様，藻体表面及び縁辺から生じる微小な生殖のための副枝 (minute reproductive proliferation) に形成される。造果枝と助細胞は離れてフラスコ状の細胞糸 (ampulla) 内に生じ，助細胞 ampulla はまばらに分枝する。

これらの特徴は，本種がまちがいなくムカデノリ科に属し，栄養体の構造と四分胞子嚢の形成位置により本種をキントキ属の種であるとした見解（川口 1989）を，雌性生殖器官の点からも支持することを示す。（812 福岡市東区箱崎 6 丁目　九州大学農学部水産学第二教室）

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Keitaro Kiyosawa: Beyond the Hodgkin-Huxley phenomenological analysis for excitation in squid axons: From studies on excitation in characean internodal cells

Excitation phenomena observed in animal nerves have been studied mainly using squid axons. Phenomenological analysis and explanation of the excitation in squid axons was done by Hodgkin *et al.* (1952), and Hodgkin and Huxley (1952) by a voltage clamp method. However, they were able to explain only excitation of a short duration of ca. 1 ms. Thus, these analyses are not likely to be valid for explaining excitations of slow and long duration of 1s–3s, such as that in characean internodal cells. Presented here are some important findings on excitation in characean internodal cells that contradict Hodgkin-Huxley's phenomenological analysis and equation on excitation in squid axons.

Key Index Words: Action potential—Charophyta—electroneutrality—excitation—Hodgkin-Huxley hypothesis.

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The extended Hodgkin-Huxley hypothesis on excitation in nerves is composed of the following assumptions and explanations. The electrical membrane current I is composed of that carried by ions, I_i, and flowing to charge up the electrical membrane capacitance, C_M, i.e., $I=I_i+C_M$ (dV/dt). Thus, since (dV/dt)=0 under voltage clamp condition, $I=I_i$. I_i is carried by an ion which creates a rapid inward current in the initial phase dut to the rapid increase in the electrical membrane conductance of the nerve cell membrane for the ion, followed by a late outward current carried by another ion due to the late, gradual increase in the electrical membrane conductance of the nerve cell membrane for the ion. However, in characean internodal cells which have much slower and longer action potential than that in nerves, the fundamental assumption that $I=I_i+C_M$ (dV/dt) does not hold. Ions which should carry the early rapid current and other ions which should carry the late, somewhat slow current in the Hodgkin-Huxley hypothesis, flow almost simultaneously across the characean cell membrane during a propagating excitation. In this review, I would like to point some important problems from the viewpoint of the electroneutrality rule in electrolyte solutions and transport phenomena of ions in and/or through synthetic membranes together with results obtained from experiments on excitation in characean internodal cells.

I. Invalidity of the basic Hodgkin-Huxley assumption on electrical membrane current across the voltage-clamped axon plasma membrane against that across the characean cell membrane

The Hodgkin-Huxley analysis had its theoretical and experimental bases on the assumption that the total electrical current I across the cell membrane is composed of electrical current I_i carried by ions (ionic current) and the electrical current which flows through a capacitance of the cell membrane C_M due to the change in the electrical membrane potential dv/dt (capacity current, $C_M\frac{dV}{dt}$) (Hodgkin *et al.* 1952), that is,

$$I=I_i+C_M\frac{dV}{dt} \qquad (1)$$

Phenomenologically, this assumption is superficially reasonable because it has been shown that the cell membrane has an electrical membrane capacitance C_M measured as 0.9 μF cm^{-2} with the voltage clamp method (Hodgkin *et al.* 1952) and the transient electrical membrane current is observed much later (200 μs) when a short electrical pulse higher than the threshold is applied across the axonal

membrane under a voltage clamp. This electrical current should be carried by charged particles (ions), i.e., I_i which is not affected by the initial electrical pulse inducing the current (Hodgkin *et al.* 1952). Since dv/dt=0 under a voltage clamp, Eq. (1) becomes

$$I=I_i \quad (2)$$

Although an externally applied electrical pulse can induce an electrical current amounting to I across the axonal membrane in the initial phase, no net electrical current should keep flowing, i.e., I=0 200 μs after the short electrical pulse in a non-propagating action potential without a voltage clamp. Therefore, with a non-propagating action potential without a voltage clamp, Eq. (1) becomes

$$I_i=-C_M\frac{dV}{dt} \quad (3)$$

Eq. (3) indicates that with a non-propagating action potential without a voltage clamp, the transient electrical current across the axonal membrane 200 μs after the short pulse flows as if it were charged with the electrical capacitance of the axonal membrane itself. This phenomenological relation derived from Eq (1) can explain the non-propagating action potential in squid axons without a voltage clamp (cf. Hodgkin *et al.* 1952).

In turn, Eq (2) indicates that all of the electrical current across the axonal cell membrane 200 μs after a short electrical pulse should be carried by only ions under a voltage clamp (Hodgkin *et al.* 1952). Based on this assumption, Hodgkin et al (1952) and Hodgkin and Huxley (1952a-d) developed their experiments and were able to successfully explain the action potential in squid axon in terms of an early rapid increase in Na^+ conductance, followed by a rapid decrease and later a somewhat slow increase in K^+ conductance, all of which are expressed with mathematically complicated formulae as functions of time and membrane potential.

However, my analysis of Kishimoto's experiments (1966) indicated that Eq. (1), the most fundamental and important assumption for Hodgkin *et al.* (1952) and Hodgkin and Huxley (1952a-d), was not valid for the action potential in *Nitella* internodal cells using a voltage clamp method. Kishimoto showed that a transient inward current across the cell membrane of the *Nitella* internode on excitation in artificial pond water (0.05 mM KCl, 0.05 mM NaH_2PO_4, 0.2 mM NaCl, 0.5 mM $Ca(NO_3)_2$, 0.1 mM $MgSO_4$) reached 3-9 μA cm^{-2} at its peak under a voltage clamp. He calculated values of dV/dt during a non-propagating action potential and found the product of the electrical membrane capacitance C_M of the *Nitella* internode and the (dV/dt) values assuming $C_M=1$ μF cm^{-2} as a function of time, having transient inward C_M (dV/dt) values peaking at 0.18-0.3 μA cm^{-2}. Namely, the transient inward current in characean internodal cells under a voltage clamp is much larger than C_M (dV/dt) calculated from the (dv/dt) values in a non-propagating action potential. Kishimoto's results, if we assume the transient inward current in a *Nitella* internodal cell under a voltage clamp is I_i in the Hodgkin *et al.* (1952) analysis of the transient inward current in a squid axon under a voltage clamp, indicate that the assumption of Hodgkin *et al.* (1952) and Hodgkin and Huxley (1952a-d) of

$$I=I_i+C_M\,(dV/dt) \quad (4)$$

would not be valid for the action potential in *Nitella* internodal cells which have a duration 1000-3000 times as long as that in squid axons because $I_i \neq C_M$ (dV/dt), in which I_i is measured by the voltage clamp method while C_M (dV/dt) is calculated from (dV/dt) values during a non-propagating action potential, in *Characeae* internodal cells.

In other words, Eq. (4) is phenomenologically valid for the action potential in squid axons having a very short duration and thus has large (dV/dt) values, but is invalid for the action potential in *Nitella* internodal cells which have much longer duration and thus small (dV/dt) values. These findings and analysis suggest the need to examine the physicochemical molecular bases of the phenomenological terms I_i and C_M (dV/dt) in excitation phenomena which are well-defined

in electrotechnology.

II. Alternative definitions of the electrical conductances for Na^+, g_{Na}, and K^+, g_K.

Hodgkin and Huxley (1952b) determined the electrical conductances of the axonal cell membrane for Na^+, g_{Na}, and for K^+, g_K, assuming that

$$I_{Na}(t)=g_{Na}(t)(V-E_{Na}) \quad (5)$$

$$I_K(t)=g_K(t)(V-E_K) \quad (6)$$

where V, E_{Na}, E_K, $I_{Na}(t)$ and $I_K(t)$ are the membrane potentials clamped by a voltage clamp method, the equilibrium potentials for Na^+ and K^+ being expressed by the equations (Hodgkin and Huxley 1952a)

$$E_{Na}=-\frac{RT}{F}\ln\frac{[Na^+]^i}{[Na^+]^o} \quad (7)$$

$$E_K=-\frac{RT}{F}\ln\frac{[K^+]^i}{[K^+]^o} \quad (8)$$

where R, T and F are the gas constant, absolute temperature and Faraday constant, respectively; superscripts i and o indicate the inside and outside of the cell, respectively, and $I_i(t)$ as functions of time measured in artificial sea water containing Na^+ and $I_i(t)$ measured in Na^+-lacking choline sea water, because V, E_{Na} and E_K are assumed to be constant in an intact squid axon under a voltage clamp.

From the Hodgkin and Huxley (1952a, b) assumption that E_{Na} and E_K should be determined by the Na^+ and K^+ concentrations in the external solution and the cytoplasm of the axon, and having V clamped at an arbitrarily constant value, we can obtain $g_{Na}(t)$ and $g_K(t)$ as a rapid transient increasing function and a slowly increasing function from Eqs. (5) and (6) in that $I_{Na}(t)$ and $I_K(t)$ change in such a manner in artificial sea water containing and not containing Na^+, respectively, and the electrical membrane potential difference across the cell membrane should be maintained at a constant value (V-E).

Kishimoto (1968) has tried to express the equivalent electrical circuit for the *Nitella* cell membrane on excitation as Fig. 1. This means that phenomenologically the equivalent circuit for the *Nitella* membrane can or only can be expressed as a membrane electromotive force, E, in series with a membrane resistance, r (reciprocal of a membrane conductance, g) which are functions of time, t, and membrane potential, V, during excitation; the membrane potential actually measured is the potential difference across such a series circuit as shown in Fig. 1. If Ohm's law is applicable even during excitation, the following equation should hold (cf. Tasaki and Spyropoulos 1958):

$$I_i(t)=g(t)(V\text{-}E(t)) \quad (9)$$

where V is the electrical membrane potential clamped by a voltage clamp method; E(t) is the putative electro-motive force of the characean cell membrane which may change with time t even under clamped electrical potential V, and g(t) is the electrical membrane conductance evaluated by the equation

$$g(t)=\frac{\Delta I(t)}{\Delta V} \quad (10)$$

where ΔV is a superimposed sinusoidal potential on the clamped potential V and $\Delta I(t)$ is a measured sinusoidal current in response to the externally applied V (Fig. 2). Kishimoto

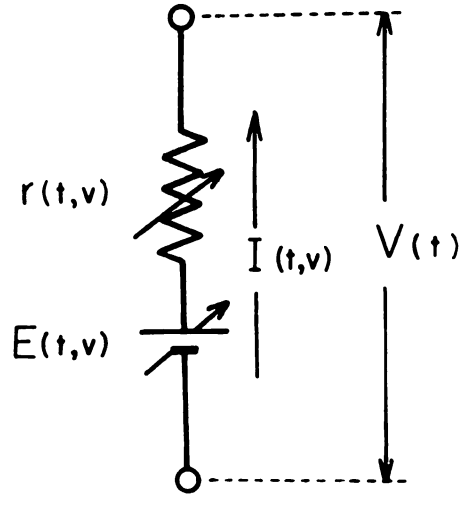

Fig. 1. Equivalent electrical circuit adopted by Kishimoto (1968) for the *Nitella* membrane.

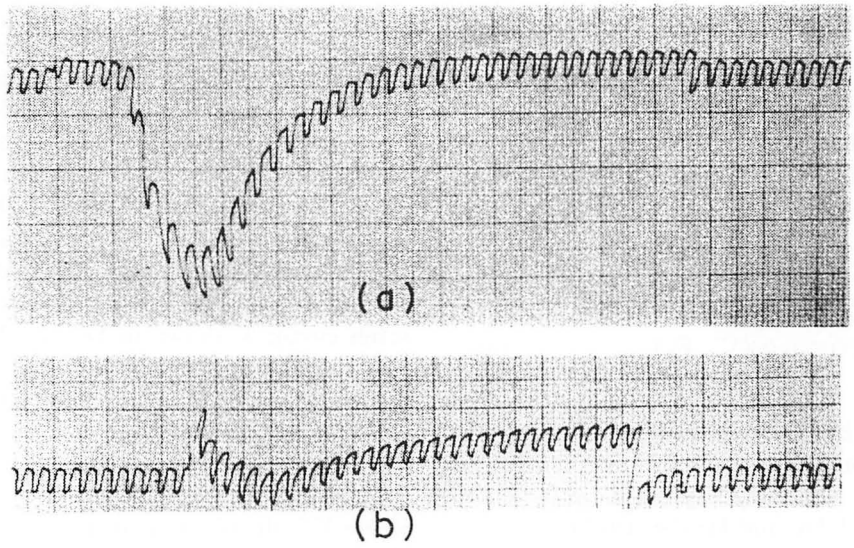

Fig. 2. Patterns of ionic current for depolarizations by 17 mV (a) and 78 mV (b), respectively. The superimposed small change in the current curve is caused by superposition of potential pulses of a small constant amplitude (Kishimoto 1968).

(1968) assumed that the electrical membrane potential difference could not alwasy be maintained at a constant value (V-E) in a voltage clamp method, but should change with time as (V-E(t)). He measured the electrical membrane conductance g(t) from a superimposed sinusoidal potential (Fig. 2) independently from the voltage clamped electrical membrane potential difference (V-E) used by Hodgkin and Huxley (1952b). Here we should note the difference in the difinition of the electrical membrane conductance g(t) between Hodgkin *et al.* (1952) and Hodgkin and Huxley (1952b) (cf. Eqs. (5), (6), (11) and (12)) and that of Tasaki and Spyropoulos (1958) and Kishimoto (1968) (cf. Eq. (10)).

The analysis by Kishimoto (1968) gave $I_i(t)$ as not being continuous for step potential change, but E(t) and g(t) as being continuous; E(t) has a transient characteristic, rising to a peak which is followed by a lower steady state level; the peak of E(t) coincides with the peak of the action potential, and the peak of g(t) is attained earlier than that of E(t) (Fig. 3).

In brief, the definition of Hodgkin *et al.* (1952) and Hodgekin and Huxley (1952b, d) of the electrical membrane conductance by Eqs. (5) and (6) is not the only possible one. Another possibility is that of Tasaki and Spyropoulos (1958) and Kishimoto (1968) using Eq. (10). Furthermore, the equivalent circuit for squid axonal membrane expressed in terms of capacity, C, inductance, L, and resistance, R, (Cole 1941, 1969; Fig. 4) is an alternative to that of Hodgkin and Huxley's (1952a-d) on the electrical properties of the axonal cell membrane (Fig. 5).

III. Argument against separate movement of Na^+ and K^+ across the axonal cell membrane inducing the ionic current I_i as different functions of time without a voltage clamp using reversible electrodes.

Hodgkin *et al.* (1952) and Hodgkin and Huxley (1952a), after showing the inward transient electrical current followed by a late outward current across the axonal cell membrane in sea water under a voltage clamp (Hodgkin *et al.* 1952), presented the following findings: (1) the early inward current disappeared in sodium-free choline sea water (ca. 484 mM choline$^+$, ca. 10 mM K^+, ca. 11 mM Ca^{2+}, ca. 54 mM Mg^{2+}, ca. 621 mM Cl^-, ca. 3 mM HCO_3^-); (2) the late outward current was only slightly altered in the sodium-free solution; (3) the changes were reversed when

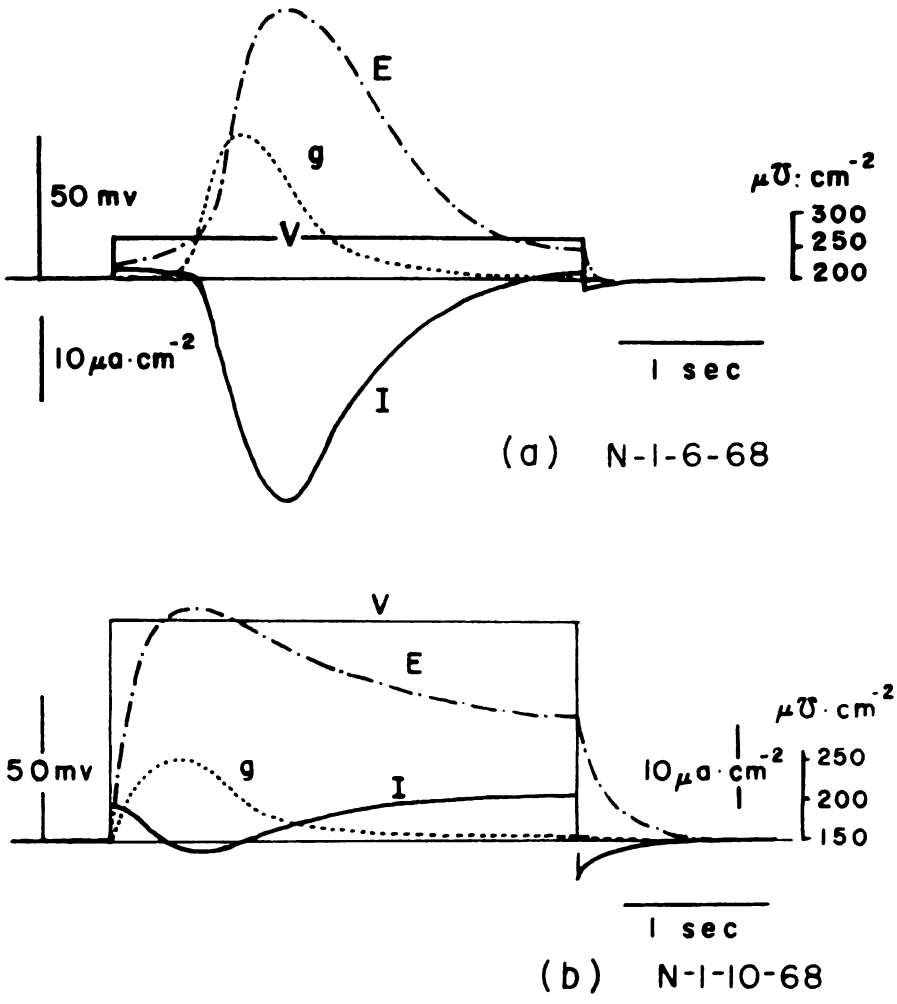

Fig. 3. Electromotive force, E, and conductance, g, defined by Eq. (9).

sea water was replaced; (4) the 'sodium potential' E_{Na} could be expressed by Eq. (7).

Hodgkin and Huxley separated the ionic current I_i into I_{Na} (I_i carried by Na^+) and I_K (I_i carried by K^+) by comparing the currents when the axon was in sea water with those in the low sodium solution under the assumptions that (1) the time course of I_K was the same in both cases; (2) the time course of I_{Na} was similar in the two cases with the amplitude and sometimes the direction being changed, but not the time scale or the form of the time course; (3) $dI_K/dt=0$ initially for a period about one-third of that taken by I_{Na} to reach its maximum (Hodgkin and Huxley 1952a, b).

Thus, Hodgkin and Huxley (1952b) expressed I_i in terms of eletrical conductances $g_{Na}(t)$ and $g_K(t)$ by the equations

$$g_{Na}(t)=I_{Na}(t)/(V-E_{Na}) \qquad (11)$$

$$g_K(t)=I_K(t)/(V-E_K) \qquad (12)$$

as functions of time. The origin of the propagating action potential is described as follows: (1) current from the neighbouring active region depolarizes the membrane by spreading along the cable structure of the fibre ('local circuit') (Fig. 6a). (2) As a result of this depolarization, sodium current I_{Na}

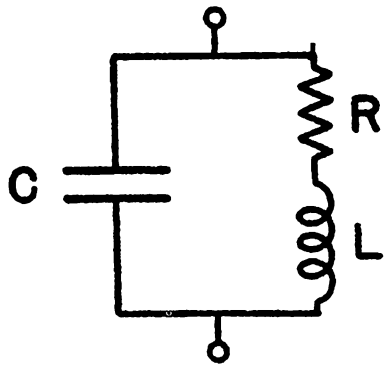

Fig. 4. Equivalent electrical curcuit for squid giant axons expressed by Cole (1941).

is allowed to flow. Since the external sodium concentration is several times greater than the internal one, this current is directed inward and depolarizes the membrane still further, until the membrane potential reverses its sign and approaches the value at which sodium ions are in equilibrium (Fig. 6b). (3) As a delayed result of the depolarization, the potassium current I_K increases and the ability of the membrane to pass sodium current decreases. Since the internal potassium concentration is greater than the external one, the potassium current is directed outwards (Fig. 6c). When it exceeds the sodium current, it repolarizes the membrane, raising the membrane potential to the neighbourhood of the resting potential (Fig. 6d), at which time potassium ions inside and outside the fibre approach an equilibrium.

Their conclusions have two important problems from physicochemical viewpoints. One is whether or not the ionic currents, $I_{Na}(t)$ and $I_K(t)$, carried by Na^+ and K^+ can

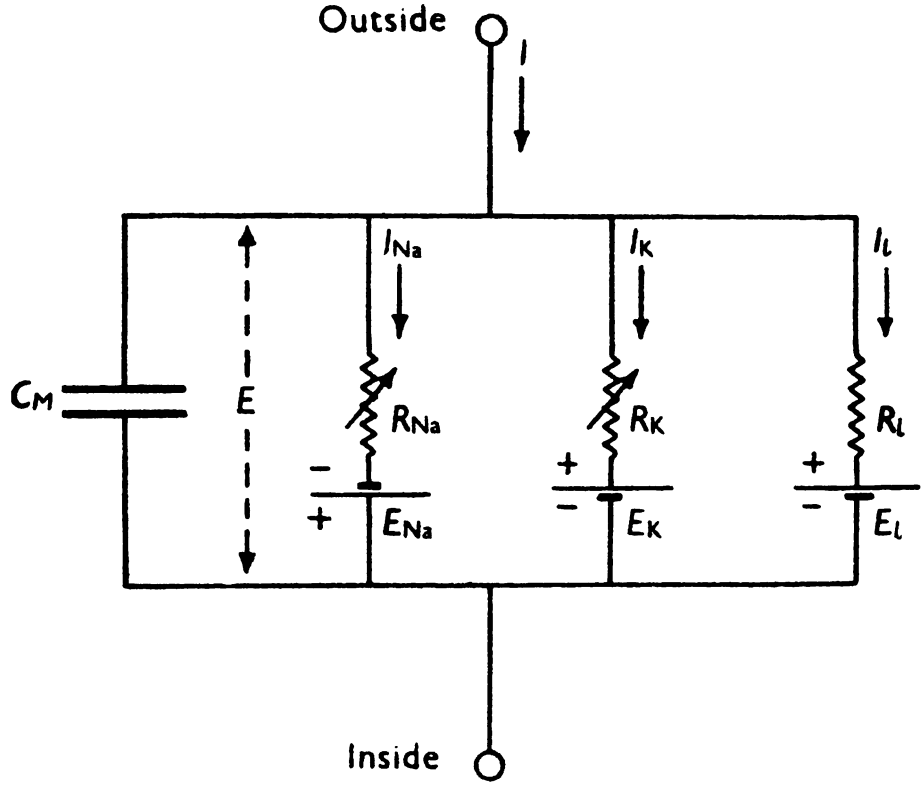

Fig. 5. Electrical circuit representing the axonal cell membrane expressed by Hodgkin and Huxley (1952). $R_{Na}=1/g_{Na}$; $R_K=1/g_K$; $R_l=1/g_l$. I_l, R_l and E_l are the leakage current, electrical resistance to leakage current, and electrical membrane potential for generating leakage current, respectively. E_K, E_{Na} and C_M are 'potassium potential', 'sodium potential' and the membrane capacity, respectively. R_{Na} and R_K vary with time and membrane potential; the other components are constant.

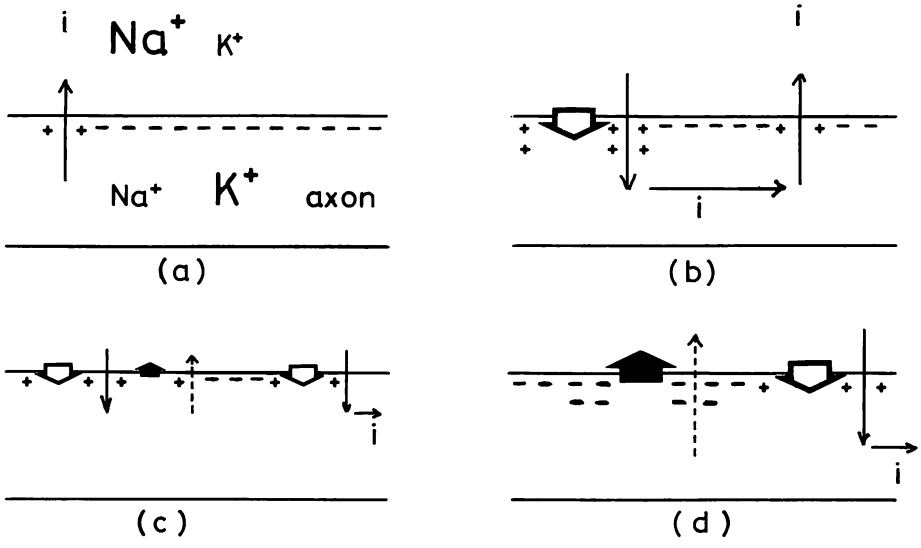

Fig. 6. Schematic illustration of Hodgkin-Huxley phenomenological explanation of propagating action potentials in squid giant axon. (a), (b), (c) and (d) indicate successive processes of Na^+ and K^+ flows, ionic currents and electrical currents across the axonal cell membrane as a function of time. ⇩ and ⇧ indicate Na^+ and K^+ flows across the axonal cell membrane, respectively, and their sizes indicate relative magnitudes of their flows. Thin solid and dashed arrows beside ⇩ and ⇧ without a letter i are Na^+ and K^+ ionic currents: their sizes indicate their relative magnitudes; thin arrows with a letter i are electrical currents in an axon and/or across the axonal cell membrane. Symbols + and − near the axonal cell membrane inside the axon indicate "depolarization" of the resting potential and its being a negative potential against the external solution, respectively. Large letters of Na^+ and K^+ and their small letters indicate Na^+ and K^+ of high and low concentrations, respectively.

actually flow across the cell membrane due to Na^+ and K^+ concentration differences or their electrochemical potential differences between the outside and inside of the axon during non-propagating action potentials, respectively. The other is whether or not the inward sodium current assumed to be carrieed by Na^+ flows into the axon first, then the potassium current assumed to be carried by K^+ flows out of it in the later phase of the non-propagating action potential.

1. Diffusional fluxes of ions across the cell membrane flow to maintain the electroneutrality rule, thus generating no ionic current.

The ionic current amounting to I_i flows, when an electrical potential difference is externally applied across the axonal cell membrane, for a short period due to a supply of energy from outside the axon by voltage clamping equipment through reversible electrodes. If, however, only Na^+ or K^+ can permeate the membrane, the ionic current I_i should produce just the corresponding unequal distribution of cations and anions across the cell membrane creating an electrical potential difference, polarization, against the externally applied potential across it, which would finally stop the electrical current flowing across the cell membrane.

In all recent theories on membrane transport across synthetic membranes under no externally applied electrical potential difference, the electroneutrality rule is assumed to be

$$0=\Sigma I_p = I_{Na+}+I_{K+}+I_{H+}+I_{Ca^{2+}}+I_{Cl^-}+\ldots \quad (13)$$

where I_p is the electrical current carried by the p-th ion transported across the membrane ($p=K^+, Na^+, H^+, Ca^{2+}, Mg^{2+}, Cl^-, NO_3^-$ and $H_2PO_4^-$ etc.; Kobatake *et al.* 1965, Lakshminarayanaiah 1969, 1984, Hanai 1988; cf. Kiyosawa and Okihara 1988, Kiyosawa 1993) and

$$I_p = -z_p F c_p u'_p \left(RT \frac{d\ln c_p}{dx} + z_p F \frac{dV}{dt} \right) \quad (14)$$

$$c_+ = c_- + X \quad (15)$$

where z_p, u'_p, c_+, c_- and X are the valence of the p-th ion, the mobility of the p-th ion in the membrane, the concentrations of cations and anions in the membrane and fixed charge of the membrane, respectively. The x-axis is taken in the direction of the membrane thickness from the outside to the inside of the cell.

When there is no ATP consumption by AT-Pases in the cell membrane, the positive charge due to all cations to be transported should be equal to the negative charge due to all anions to be transported if the externally supplied electrical current is zero (cf. Kiyosawa and Okihara 1988, Kiyosawa 1993). In other words, when a cation flows from the inside of the cell to the external solution, an anion having the correspondengly equal negative charge must be transported together with the cation, or another cation having the correspondingly equal positive charge in the external solution must enter the cell across the cell membrane in exchange for the outgoing cation.

Since this electroneutrality rule, first applied to electrolyte solutions, is very strict, Na^+ or K^+ cannot move freely across the cell membrane independently of other anions or cations to create an electrical current when there is no ATP consumption or externally supplied electrical energy. This indicates that diffusional ion fluxes across the cell membrane cannot create an electrical current without active transport accompanied by ATP consumption or without energy supply from a voltage clamp equipment. Since total membrane current density I is negligible in non-propagating action potential at time periods greater than 200 μs after a short pulse to induce it (Hogkin *et al.* 1952), what occurs in or across the axonal membrane is diffusional processes of ions such as Na^+, K^+, Cl^- etc. The diffusional processes themselves cannot create any electrical current amounting to I_i.

From this point of view, Kishimoto (1966) has found very interesting and important phenomena on a non-propagating action potential in *Nitella* internodal cells which

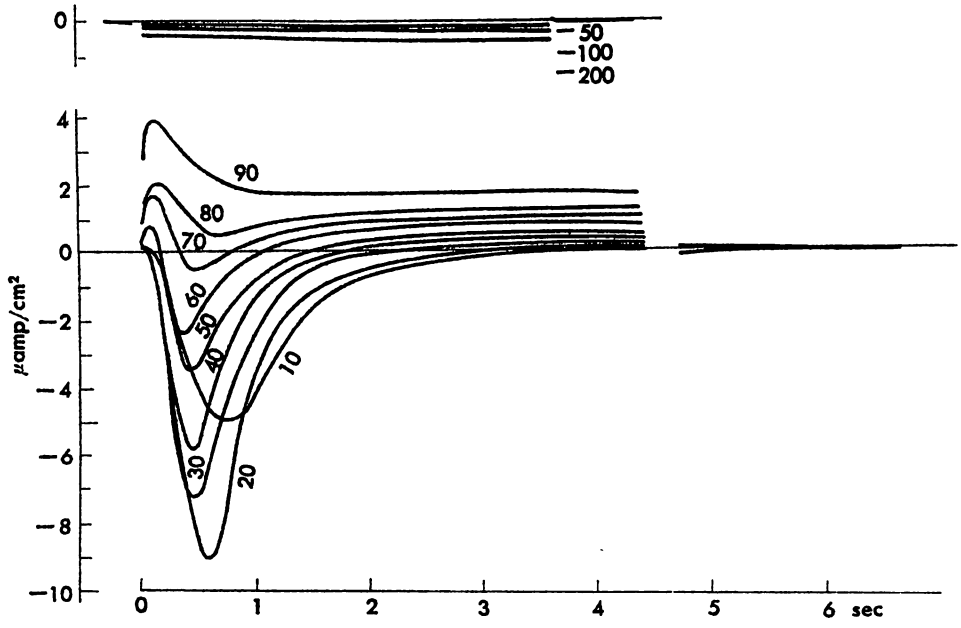

Fig. 7. Patterns of membrane currents at various levels of clamped membrane potential. The number attached to each curve indicates the amount of depolarization (lower curve) or hyperpolarization (upper figure) from the resting membrane potential (Kishimoto 1966).

generate much slower and longer action potential than that in squid axon. For moderate depolarization, the transient inward current was followed by a slowly rising outward current; for larger depolarization, a transient outward current preceded the transient inward current, and only monotonic inward currents were observed for hyperpolarizations (Fig. 7). When these curves were replotted against the potential level, the parameter being time in this case, the temporal variation of the current-voltage relation (I-V curve) was obtained (Fig. 8a). The transient inward current was the largest at about 0.5 s after the step change of the potential. The pattern, however, was not constant with time, but decayed and moved leftward along the voltage axis (V-axis) and finally converged into a steady delayed rectification curve. The potential at which the largest I-V curve crosses the V-axis corresponds almost exactly to the potential at the peak of the action potential, and the temporal locus of the potential at which a series of the I-V curves crosses the V-axis, i.e., $I=0$ coincided approximately with the potential change which actually occurred during the action potential (Fig. 8b). This finding indicates that the actual non-propagating action potential is a membrane phenomenon which occurs at $I=0$ in the temporal I-V curve obtained under voltage clamp method. In other words, the actual non-propagating action potential is phenomenon which occurs with electroneutrality being maintained.

2. Reports of experiments showing simultaneous outflows of K^+ and Cl^- during excitation in characean internodal cells

Tsutsui *et al.* (1986) found that when the I-V curve of the *Chara* cell membrane was obtained by applying a slow ramp hyperpolarization to the internodal cell, the transient early inward current component disappeared almost completely under La^{3+} treatment while no effect was observed on the late outward current. They interpreted these

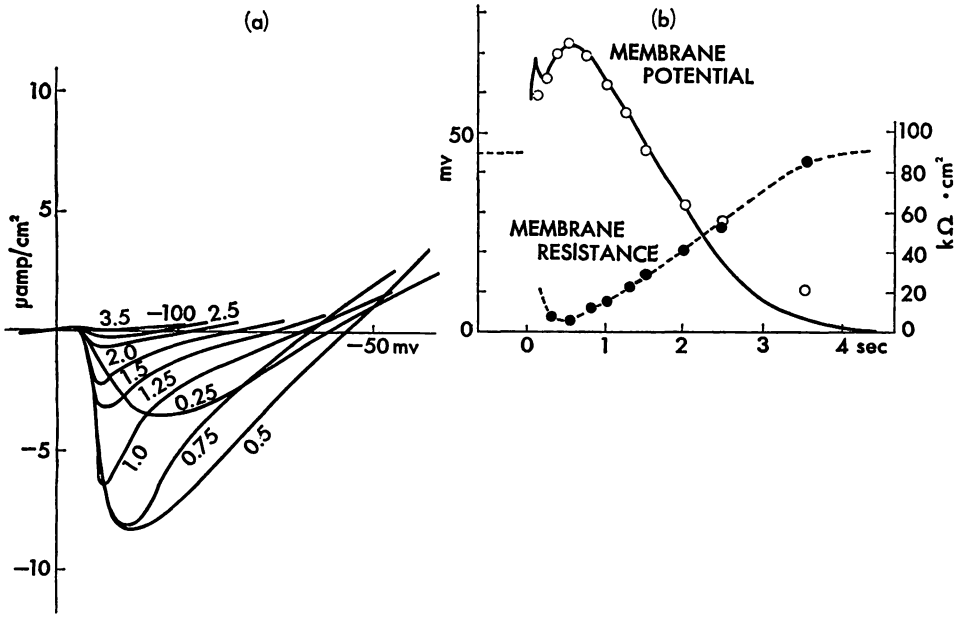

Fig. 8. a: Membrane currents during step potential changes in Fig. 7, replotted against the membrane potential level, the parameter being time here. The number attached to each curve is time in seconds after the step potential change. These curves show the temporal change of the I–V relation of the *Nitella* internode after stimulation. b: Temporal change of the potential at which a series of the I–V curves crosses the potential axis (open circles) coincides approximately with the action potential (full line). The temporal change of the membrane resistance (black circles) is obtained from the slope of the I–V curve at each intersection with the V-axis (Kishimoto 1966).

phenomena, as being similar to the Hodgkin-Huxley phenomenological analysis, that the transient early inward current is mainly carried by the efflux of Cl^- and the late large outward current is mainly carried by the efflux of K^+; both ions exist predominantly in the internodal cell.

However, as stated in the Introduction and other sections, excitation in the *Characeae* internodal cell is of much slower and longer duration than that in the squid axon. Therefore, ion fluxes can be separately measured during excitation. If the Hodgkin and Huxley theory were also true for characean internodal cells, Cl^- in the internodal cell should go out first, followed by a later K^+ outflow, as Tsutsui *et al.* (1986) suggest.

To examine this hypothesis, Oda (1975, 1976) constructed an apparatus having a groove in which a *Characeae* internodal cell could be placed and K^+-free artificial pond water could be kept flowing to a flame photometer to detect the K^+ leaving the internodal cell during excitation. In the groove, he placed two sets of two Ag-AgCl electrodes to measure the Cl^- leaving the same internodal cell during excitation and the excitation itself. He detected simultaneous K^+ and Cl^- effluxes of almost equal amount on excitation.

Later, Williamson and Ashley (1982) reported that *Chara* cells have a low free Ca^{2+} concentration, comparable with those of animal cells, and that action potentials which inhibit cytoplasmic streaming substantially increase this Ca^{2+} concentration. Kikuyama *et al.* (1984) showed that on excitation, *Chara* and *Nitellopsis* internodal cells produced a large amount of K^+ efflux but some cells showed action potentials without a detectable increase in Cl^- efflux; they assumed Ca^{2+} influx to be a candidate for the exchange with the K^+ efflux during excitation in cases where no Cl^- outflow was detectable. Recently, Hayama *et al.* (1979), Kikuyama and Tazawa (1983) and Kikuyama *et al.* (1993) have shown that Ca^{2+} in the external solution transiently enter the *Characeae* internodal cell during excitation using $^{45}Ca^{2+}$ and aequorin, respectively.

These phenomena observed in characean internodal cells disagree with the Hodgkin-Huxley hypothesis which assumes separate Na^+ inflow and K^+ outflow as different functions of time. Thus, further study is needed to establish a universal theory with equations that can explain excitation phenomena in both squid axons and characean internodal cells, i.e., excitation phenomena of short and long duration.

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清沢桂太郎：神経の興奮に関する Hodgkin-Huxley 説を超えて
車軸藻節間細胞での研究から見た一私見

イカの巨大神経は，静止時には内部の電位は外部に対し −60 mV を示すが，刺激により，一過性に +40 mV に達した後，元の値に戻る。Hodgkin ら，Hodgkin and Haxleg（以下，H-H と記す）は，この現象は刺激により，まず Na^+ に対する透過性が，一過性に増大し，外部の Na^+ が一過性に流入，その後，Na^+ に対する透過性が減少，一方 K^+ に対する透過性が増大し，内部の K^+ が外部に出ていくためであると説明した。岸本は，H-H の仮説は，一つの現象論としては，全く異論をはさむ余地はないが，実際にその通りの事が起こっているのかどうかは別であるとし，車軸藻節間細胞に，H-H と同様の膜電位固定法を適用し，彼らとは異なった表現法を提出した。小田は車軸藻節間細胞での興奮現象を H-H 流に説明すると，まず，細胞内の Cl^- が出て，遅れて K^+ が出て行くことになるが，実測すると，Cl^- と K^+ はほとんど同時に出ることを示した。ここではこれらの実験の紹介を含め，H-H の仮説は，単なる一つの現象論であって，実際に起こっている現象とは別である可能性があることを膜に関する物理化学的法則を基に論証した。（560 豊中市待兼山町1-3　大阪大学基礎工学部生物工学科）

藻類 Jpn. J. Phycol. 42: 353–356, September 20, 1994

奥田一雄：第5回国際藻類学会議報告

K. Okuda: Report on the Fifth International Phycological Congress in Qingdao

本会議は国際藻類学会が主催となり，これまでにニューファンドランド（カナダ），コペンハーゲン（デンマーク），メルボルン（オーストラリア），ダーラム（アメリカ）の順番で3年毎に開催されてきている。今回の第5回国際藻類学会議は中国科学院海洋研究所がホストとなってチンタオで1994年6月26日から7月2日までの7日間にわたって開催された。出席者総数は名簿がないので正確にはわからないが約500名位であろうと思われた。1週間の会期のうち4日間（6月27日，28日，30日，7月1日）で，基調講演4，シンポジウム11，ワークショップ4を含め約300の演題（うちポスター発表109)について発表・討論が行なわれた。アブストラクト集から抽出した参加国別の演題数は次の通りであった（国際間の共同発表は重複してカウントした）：中国（95），日本（33），アメリカ（31），ドイツ（16），韓国（15），イギリス（11），オーストラリア（11），イタリア（8），メキシコ（8），フランス（8），イスラエル（8），スウェーデン（8），カナダ（7），ロシア（6），スペイン（5），台湾（5），ベルギー（4），オランダ（4），ノルウェー（4），ギリシア（3），チリ（3），デンマーク（3），南アフリカ（3），ホンコン（2），フィリピン（2），オーストリア（2），インド（2），フィンランド（2），ブラジル（2），ポルトガル（2），マレーシア（1），ハンガリー（1），スイス（1），ウクライナ（1），ニュージーランド（1），スロベニア（1），タイ（1），フィジー（1），アイルランド（1）。

チンタオは既に夏の真盛りであった。会議初日の26日は前日に続いて会議登録の受付が行なわれたが，夕方からは歓迎会が催され参加者の顔ぶれをおたがいに確認しあった。27日の朝，W. J. Woelkerling 議長の下，Z. S. Yu チンタオ市長，C. K. Tseng 中国科学院海洋研究所名誉所長，千原光雄 IPS 会長の挨拶によって開会式が挙行され，会議が開始された。最初発表会場には暗幕がなくスライドがよく見えない状態であったが，後にへやを暗くする工夫がなされスライド投影の環境はやや改善した。ポスター会場は，2階のホールであったが，中央に大きな吹き抜け部分があり全体的に狭く，また照明が暗いように感じた。会議参加者は A, B, C, D の4つのホテルに滞在し，朝と夕方にそれぞれのホテルと発表会場のある人民会館の間で送迎バスが運行された。朝食はそれぞれのホテルで取り，昼食は発表会場で弁当が配られた。28日の夕方には中国藻類学会主催の banquet があり，中華料理のフルコースが出た。

チンタオはかつてドイツ領であったことから，現在でも当時建設されたヨーロッパ風のブリック造りの建物が数多く残されている。有名なチンタオビールは1缶 (350 ml) 3元（39円）で売られ，結構おいしい。また，チンタオは海浜都市であるので新鮮な海産物が豊富である。市中の多くのレストランにはアサリ，ツブガイ，マテガイなどを入れた生け簀が陳列され，注文するとすぐにその生け簀から生きている貝を取って調理してくれ，また非常に安価である（1品10–20元）。しかしながら，いくら新鮮な材料が使われても，その料理が外国人にとって体に合うかどうかは別問題である。会議参加者の多くの人が日本人に限らずおなかの不調を訴えていた。ある人は油のせいであると言い，別の人は水が原因だと言っていた。しかし，多くの人がおなかを壊す中で見事にチンタオ料理に適応した人が居たことも事実であった。急速に発展しているこの国を反映するように，チンタオもホテルなどが建設ラッシュで街は人々の活気で満ちているのはよいが，けたたましく警笛を鳴らす車と交通マナーの悪さ（運転者だけでなく歩行者も）には閉口した。

会議なかびの29日には，行き先別に5つのグループに分かれて見学旅行が行なわれたが，当日は生憎びったりと終日雷雨という天候であった。筆者の参加した North Mount Laoshan へのツアーでは，日本人を含む物好きな幾人かがせっかく来たのだからといって強風の中，雨に叩き付けられながら徒歩で山に登った。山から見る展望はすばらしかった。しかしながら，登山口にある建物のトイレはそれは使える使えないという問題以前の物凄いもので，これについてはひとしきり話題の種になった。

30日の晩には，Entertainment として Peking Opera（京劇）を観賞した。劇場には一般市民も多数入場し，大変賑やかであった。しかしながら，歌謡ショウなど

の前座が長時間続いたので，途中で眠りに落ちてしまい，取りである肝心の京劇を見れずじまいであった人もいた。

7月1日には，チンタオで最も高級と目されるホテルで Congress Banquet と閉会式が行なわれた。このとき，千原光雄 IPS 会長によってポスターセッションにおける受賞ポスターの発表と表彰が取り行なわれた。今回は，異なる3つの研究分野からそれぞれ1点，計3点の受賞ポスターが選ばれたが，残念ながら日本人のものは選から漏れた。次回の第6回国際藻類学会議がオランダのライデンで開催されるということで，ライデンの街の様子がスライドによって簡単に紹介された。国際間の和やかな歓談と再会を期する握手のうちに宴は閉じられた。

以下に基調講演と日本人が発表した講演題目を記す。

6月27日（月）

Plenary lecture:

C. K. Tseng: Marine phycoculture and its prospect in China.

SYMPOSIUM 1: BIOLOGY OF GIANT UNICELLULAR ALGAE

10:15 I. Shihira-Ishikawa and D. M. Y. Yano: Accumulation of ribosomes preceding cap differentiation in *Acetabularia caliculus*.

10:45 T. Hishinuma, K. Tsubura and S. Wada: Cell polarity in a giant unicellular green alga, *Bryopsis plumosa*.

SYMPOSIUM 2: SEAWEED CULTIVATION

11:15 M. Ohno: The ecology of cultivated *Monostroma*, green algae.

POSTER GROUP 1: ECOLOGY AND BIOGEOGRAPHY OF FRESHWATER MICROALGAE

14:00–15:15

X. M. Zhang, M. M. Watanabe, I. Inouye and M. Chihara: A survey of mixotrophy in thirty freshwater chrysophytes.

E. A. Lobo, Y. Aruga and K. Katoh: Epilithic diatom assemblages response to water pollution in rivers of Tokyo, Japan.

E. Takahashi and A. Kuzmina: The chrysophyte flora in Lake Baikal, Russia, in Summer 1992.

POSTER GROUP 3: ECOLOGY OF MICROALGAE IN LAKES, SNOW AND ICE ZONES

14:00–15:15

T. Matsusaka and S. Ohtani: Species composition and seasonal variation of the attached diatoms from brackish lakes of Shinjiko and Nakaumi, Japan.

S. Ohtani: Taxonomy and ecology of snow algae on King George Island, Antarctica.

青島の新聞（青島日報，Qingdao Ribao 1994年6月25日発行）に掲載された学会風景

SESSION 1: CYTOLOGY AND PHYSIOLOGY OF GIANT UNICELLULAR ALGAE

15:45 K. Sugimoto, T. Maekawa and R. Nagai: Light-induced translocation of the cytoplasm in coenocytic green alga *Dichotomosiphon*.

16:05 K. Okuda: The roles of cortical microtubules on cell growth in marine coenocytic green algae.

16:25 S. Miyamura and T. Hori: Pyrenoid as a chloroplast nucleoid in *Caulerpa*.

SESSION 3: ECOLOGY OF MICROALGAE IN LAKES, WETLANDS AND GLACIERS

16:25 M. M. Watanabe and H. Nozaki: Diversity of benthic algae in two small moorland pools.

17:25 Y. Yoshimura and S. Kohshima: Cryovegetation of a Himalayan glacier, Yala glacier, Langtang region, Nepal.

6月28日（火）

Plenary lecture:

D. J. Chapman: Biochemical evolution in algae: Looking beyond the trees.

WORKSHOP 2: ALGAL CULTURE METHODOLOGIES

10:00 A. Miura: Consideration on the culture methodologies of the cultivation of *Porphyra yezoensis* in China.

11:00 N. Saga: Strain- and cryo-preservation in algal tissue culture.

11:30 M. Notoya: Tissue culture method of blade pieces excised from young sporophytes of Laminariales species.

12:00 M. Tatewaki and M. Suzuki: Unsaturated fatty acids as allelochemicals on the spore-attachment and development of red seaweeds.

WORKSHOP 3: PROCHLORON AND ITS ALLIES

11:30 A. Shimada, S. Kanai and T. Maruyama: Rubisco amino-acid sequences and the phylogeny of *Prochloron* and *Prochlorococcus* (prochlorales).

POSTER GROUP 6: MORPHOLO-GY, DEVELOPMENT AND CYTOLOGY OF MARINE MACROALGAE

14:00–15:15

T. Kobara: Peculiar method of asexual reproduction in Helgoland *Bryopsis hypnoides*.

POSTER GROUP 7: PHYSIOLOGY OF MICROALGAE

14:00–15:15

Z. Gombos, H. Wada, E. Hideq and N. Murata: Unsaturation of membrane lipids stabilizes photosynthesis against heat stress.

6月30日（木）

Plenary lecture:

M. H. Hommersand: A new era in algal systematics: Rhodophyta.

SYMPOSIUM 7: ALGAL HORMONES AND TOXINS

12:00 M. Yotsu-Yamashita, T. Seki, V. J. Paul and T. Yasumoto: Polycavernosides, probable causes of *Gracilaria* poisoning in Guam.

SYMPOSIUM 9: SYSTEMATICS OF FRESHWATER ALGAE

11:30 H. Nozaki: Systematics and life cycle of the Volvocales (Chlorophyta) based on cultured material.

POSTER GROUP 11: CYTOLOGY, TAXONOMY AND SYSTEMATICS OF MICROALGAE

14:00–15:15

T. Hori and J. C. Green: MTOC occur on mitochondrial surfaces during cell division of a prymnesiophyte.

S. Mayama and I. Shihira-Ishikawa: Observations on the scattered chloroplast nucleoids in three *Pinnularia* species, *P. major, P. viridis* and *P. viridiformis* (Bacillariophyceae).

H. Kobayashi, S. Mayama and K. Terao: Observations on the structures of *Cymbella amoyensis* and two related species.

SESSION 12: BIOCHEMISTRY, NATURAL PRODUCTS AND THEIR USES OF MACROALGAE

16:45 A. Chirapart, Y. Katoh, H. Ukeda, M. Sawamura and H. Kusunose: Chemical and rheological properties of agar from a Japanese *Gracilaria, G. lemaneiformis* (Bory) Weber-van Boss.

7月1日（金）

Plenary lecture:

B. Kloareg: Biotechnological approaches in basic and applied phycology.

SYMPOSIUM 10: MICROALGAL AND MACRO-

ALGAL BIOTECHNOLOGY

10:00 Y. Fujita: Genetic improvement of *Porphyra* by protoplast fusion.

SYMPOSIUM 11: CHROMOPHYTE ALGAE

9:30 I. Inouye, X. Zhang and D. Honda: Absolute cell organization and systematics of chromophyte algae.

SESSION 15: BIOGEOGRAPHY, TAXONOMY AND SYSTEMATICS OF RED MACROALGAE

11:00 I. A. Abbott and M. Yoshizaki: Systematics and evolution within the Liagoraceae (Nemaliales).

SESSION 17: TAXONOMY AND SYSTEMATICS OF BROWN MACROALGAE

11:00 T. Ajisaka: Studies on *Sargassum opacum* J. G. Agardh from Okinawa prefecture, Japan.

11:40 H. Kawai and W. F. Prud'homme van Reine: Life history and systematic position of Japanese *Stypocaulon dura* (Sphacelariales, Phaeophyceae).

WORKSHOP 4: BIOGEOGRAPHY OF FRESHWATER ALGAE

14:00 T. Ichimura: Genome rearrangement and speciation.

SESSION 20: PHYSIOLOGY AND CULTIVATION OF MARINE MACROALGAE

15:00 J. Rebello and M. Ohno: Growth rates and agar quality of *Gracilaria lemaneiformis* (Bory) Weber-van Bosse (Gracilariales, Rhodophyta) from South Africa (Namibia) in Tosa Bay, Japan.

(780 高知市曙町2-5-1 高知大学理学部生物学教室)

新刊紹介

Irvine, L. M. and Chamberlain, Y. M.: Seaweeds of the British Isles. Vol. 1. Rhodophyta, Part 2B Corallinales, Hildenbrandiales. vii＋276 pp. 1994. The Natural History Museum, London. ISBN 0 11 3100167. 価格30ポンド。
HMSO Books, PO Box 276. London SW8 5DT. Credit Card Order: Fax 071-873-8200.

イギリス海藻誌 Seaweeds of the British Isles のシリーズの紅藻の部分は5部に分けられ，そのうち第4番目にサンゴモ目 Corallinales とベニマダラ目 Hildenbrandiales を扱った Part 2B が新しく出版された。あと Part 3B のウシケノリ綱 Bangiophyceae で紅藻が完成する。

この分冊は Irvine と Chamberlain の共編で，そのうち有節サンゴモについては Johansen が協力している。記述の体裁はこれまでの分冊と同様である。

30ページにわたる Introduction は Corallinales についての詳しい解説で，その形態と生態，研究史などが適切に纏められている。

各論では，サンゴモ科 Corallinaceae の5つの亜科の14属，すなわち *Choreonema, Corallina* サンゴモ属，*Haliptilon, Jania* モサズキ属，*Lithophyllum* イシゴロモ属，*Titanoderma* ノリマキ属，*Hydrolithon, Pneophyllum* モカサ属，*Exilicrusta, Leptophytum, Lithothamnion* イシモ属，*Melobesia* サビ属，*Mesophyllum, Phymatolithon* に含まれる44種について，検索表とともに詳細な記載と図解が与えられている。また，タイプ標本についての情報も含まれている。これらの属は日本にも産するものが多い。最近，属のタイプ種のタイプ標本の再検討が行われ，属の定義の見直しが進んできて，そのため，命名上にも多くの変更がなされてきている。この出版物でも，*Hydrolithon* が *Fosliella* よりも古い正名とされている。また，1993年の国際植物科学会議（横浜）で採択された保留属名の一つに *Phymatolithon* があり，*Apora* に対して保留された。これらは日本産の種の取り扱いにも影響がある。

ベニマダラ科 Hildenbrandiaceae も目のレベルで取り扱われている。

この分冊もこれまでに出版された分冊と同様，非常に高度なモノグラフである。21ページにわたる引用文献の表とともに，術語の解説もあってサンゴモ科に独特な用語についての理解もえられる。ただ，一つだけ間違いを指摘すると，Fig. 118 の A と B が逆になっている。

まだ完成していない分冊（紅藻の Bangiophyceae，褐藻の半分，Cyanophyta, Prymnesiophyta, Bacillariophyta）の発行が待たれる。

（北大・理・生　吉田忠生）

新刊紹介

Christensen, T.: ALGAE A taxonomic survey. xi+472 pp. 1980–1994. AiO Print Ltd., Odense, Denmark

第1巻 (Fasc. 1.) paper bound 115 デンマーククローネ (DKK) (1980)

第2巻 (Fasc. 2.) paper bound 125 DKK (1994)

第1巻 + 第2巻 (Fasc. 1+2) paper bound in 2 volumes 200 DKK (1980, 1994)

第1·2巻合本版 (Fasc. 1+2) in one bound volume (hard cover) 260 DKK (1980–1994)

本書はデンマークの Christensen 博士による英語で書かれた藻類の系統分類の総説書であり，上であげたようないくつかの形で販売される。前編に当たる第1巻 (Fasc. 1.) はすでに1980年に刊行されており，今回後編にあたる第2巻 (Fasc. 2.) が刊行された。さらに第1巻と第2巻を合本したハードカバーのものも販売されるが，このハードカバー版はなかなか不思議な成り立ちの本である。すなわち前編に相当する部分は1980年に刊行された第1巻の本文部分がそのままとじ込まれており，後半部分とは紙質も明らかに異なっている。従ってすでに第1巻を持っておられる方は第2巻を購入すれば十分で，合本版を買っても前半部分に全く変更はない。

内容については，本書は良い意味でも悪い意味でもきわめてオーソドックスな藻類学の教科書である。全体を通してさまざまな藻類の系統群についての形態，生活史，および分類などが記述されている。図版は光学顕微鏡レベルの線画がほとんどで写真の図版はない。しかし単に教科書的な知識と他の研究者の最近の研究成果をただわかりやすく紹介したカタログ的な教科書ではなく，進化・系統群としての藻類全体をどうとらえるかという筆者自身の主張も強く感じられる。ちなみに筆者は1966年にデンマーク語で書かれた藻類学の教科書 (Botanik, Bind II Systematisk Botanik Nr. 2 Alger, 180 pp., Munksgaard, Kobenhavn) を出版しておられるが，本書 (Algae) はその改訂・英語版に相当し，図版もかなりの部分がこのデンマーク語版から採録されている。らん藻（シアノバクテリア）を含む藻類全体が Cyanophyta（1綱），Rhodophyta（1綱），Chromophyta（9綱），Chlorophyta（6綱）に分けて紹介されているが，このうち Chromophyta の Glaucocystophyceae と，Chlorophyta が今回の第2巻に納められている。

第1巻は出版当時の藻類学における新知見を積極的に紹介しており非常に参考になったが，その出典（著者・論文・雑誌名など）が示されていないという欠点があった。今回の第2巻ではこの欠点をおぎなうべく，第1巻の内容も含めて関連する文献のリストと図版の出典があげられている。リストは本文のページ順にでており，とってつけたような印象をあたえ必ずしも使いやすいとはいえないが，やはり有用である。また第1巻が発行されてから14年もたってから第2巻が刊行されているためか，第2巻（または合本版の後半部分）には第1巻の内容に関するかなり充実した補遺が載せられている。これは結果的にこの十数年の間に出版された主な藻類学の研究成果に関するレビューになっており，非常に参考になる。また，第2巻は付録（？）としてほとんどの藻類の属の名の語源集が載っており，著者のラテン語・ギリシャ語などの古典語への造詣の深さがうかがえる。（神戸大理学部・川井浩史）

―学　会　録　事―

―会　員　移　動―

新　入　会　員

住所変更

退　会　者

ニ　ュ　ー　ス

国際生物学賞シンポジウム—生物の多様性と進化—の開催

第10回国際生物学賞に関連して，生物の多様性と進化（Biodiversity and Evolution）と題するシンポジウムが下記のように行なわれます。藻類関係では，メルコニアン先生やガバリエルースミス先生の講演が予定されています。

参加は無料です。

詳しいことは生物科学ニュースをご覧ください。

記

日　時：11月29日（火）・30日（水）

場　所：東京上野公園内　日本学士院（ホール）

日本学術会議だより　No.33

第15期最後の総会開催される

平成6年6月　日本学術会議広報委員会

今回の日本学術会議だよりでは，5月25日から27日まで開催された第118回総会の概要と同総会で採択された「新しい方式の国際研究所の設立について(勧告)」，「公的機関の保有する情報の学術的利用について(要望)」，「女性科学研究者の環境改善の緊急性についての提言(声明)」についてお知らせします。

日本学術会議第118回総会報告

日本学術会議第118回総会（第15期・第6回）が，5月25日～27日の3日間にわたって開催されました。

総会の初日（25日）の午前は，会長からの前回総会以降の経過報告に続いて，各部，各委員会等の報告が行われました。次いで，今回総会に提案されている13案件について，それぞれ提案説明と質疑応答が行われました。午後からは，各部会が開催され，総会提案案件の審議及び各部会個別案件について審議が行われました。

総会2日目（26日）の午前は，前日提案された13案件のうち，9案件の審議・採択が順次行われました。

まず，「日本学術会議会則の一部を改正する規則」，「日本学術会議の運営の細則に関する内規の一部改正」，「日本学術会議の行う国際学術交流事業の実施に関する内規の一部改正」，「副会長世話担当研究連絡委員会の運営について（申合せ）の一部改正」及び「第16期における研究連絡委員会委員の在任期間等に関する規定の適用について（申合せ）」について一括して討論が行われ，採決の結果，いずれも可決されました。これらの会則，内規等の改正は，

1．運営審議会の構成員等の見直し

常置委員会と運営審議会の連絡を緊密にし，運営審議会の議論をより充実させるため，常置委員会委員長が常時運営審議会に出席することとし，併せて，運営審議会の構成員の見直しを行うこと。

2．第7常置委員会の設置及び第16期に向けての研連の見直し

国際対応委員会の改組について（申合せ）（平成5年4月22日第116回総会決定）に沿って第7常置委員会を設置し，併せて，各部等での検討結果を踏まえ，第16期へ向けての研連の見直しを行うこと。

3．研連委員の在任期間等関係

研連委員の在任期間に関する運営内規の解釈をより一層明確化するとともに，将来に向けての研連活動の継続的発展・活性化を図るため，研連委員の在任期間等についての関係規定を整備すること。

を趣旨とするものです。

次に，「運営審議会附置会員推薦手続検討委員会の設置」についての討論・採決が行われ，可決されました。これは，会員推薦制度導入以来，今回で4度目となり，会員推薦手続の過程において，幾つかの問題点がみられたことから，これらの諸問題について審議するため，新たな委員会を運営審議会に附置するものです。

続いて，「新しい方式の国際研究所の設立について（勧告)」，「公的機関の保有する情報の学術的利用について（要望)」，「女性科学研究者の環境改善の緊急性についての提言（声明)」についての討論・採決が行われ，可決されました。午後は，「第6常置委員会報告～国際学術交流・協力の飛躍的発展のために～」，「人口・食糧・土地利用特別委員会報告～21世紀の人口・食糧問題に対する全人類的取組に向けて～」，「学術国際貢献特別委員会報告～学術国際貢献のための新たなシステムについて～」及び「死と医療特別委員会報告～尊厳死について～」の4件の対外報告について討論が行われ，それぞれ承認されました。

総会3日目（27日）は，午前は各常置委員会及び国際対応委員会が，午後は各特別委員会がそれぞれ開催されました。

新しい方式の国際研究所の設立について（勧告）（抄）

近年，学術の国際交流がますます盛んになるとともに，新しい方式の研究所が世界の国々に設立されている。それらの新しさは，固有の研究員をほとんどもたず，国内外から招請した客員研究員による共同研究を企画し実行する点にある。この方式にふさわしい分野としては，自然科学のみならず，人文科学，社会科学を含め様々な領域が考えられるが，理論構築を主眼とする研究領域においては，研究テーマを学際的、機動的に選択する上で特に有効である。これは，また国を異にする若手研究者が相集い，生活と研究ないし研修を共にする場としても大きな効果を生むであろう。実際，世界的には，この意味で成果をあげている新研究所も少なくない。

さらに，いま国際貢献が基礎科学においても強く求められているが，それは，学術研究の推進と相互に強め合うべきものであって，このためにも新しい方式は最適である。

こうした観点から，新しい方式の国際研究所の設立が必要であり有用であるとの結論に達したので，ここにその設立を勧告する。

公的機関の保有する情報の学術的利用について（要望）（抄）

研究者が学術研究のために必要とする情報には、極めて広範囲なものが含まれており，その内容は，学問分野によっても多種多様である。学問分野によっては，公的機関の保有する情報が学術研究にとって極めて重要ないしは不可欠な意味をもつことになる場合も少なくないが，多くの場合に，かかる公的機関の保有する情報を学術情報として利用することには困難が伴っている。それは，公的機関の保有する情報の少なくない部分が公開されておらず，学術情報としての利用についてもその開示を求めることができないからである。

このような公的機関の保有する情報の学術的な利用のためにも，まず基本となるのは，国民の基本的な権利に基づく公的機関の保有する情報の公開制度である。この制度の確立によって，公的機関の保有する情報の学術情報としての利用も同時に保障されることになるからである。公的機関としては，国家機関及び地方公共団体機関を挙げることができるが，国家機関の保有する情報についての公開制度が設けられていないことは，学術研究にとっても特に重大な障害となっている。国民の「知る権利」を中心とする基本的権利を保障するための国家機関の保有する情報の公開制度は、学術研究にとっても極めて重要な意味をもっているということができる。国民の基本的な権利を保障するために，また学術研究の推進のためにも，原則公開を基本とし的確な内容を持つ国の情報公開制度の確立が不可欠であると考えられるので，ここに情報公開法の制定を要望する。

なお，公的機関の保有する情報の学術的利用については，情報の保存及び研究者による非公開情報の利用についての検討が必要である。

女性科学研究者の環境改善の緊急性についての提言（声明）（抄）

女性の社会的地位の向上を目指す取組が，国際的にも国内的にも種々行われているが，日本学術会議においても第10期及び第12期に女性科学研究者の地位の向上に関する「要望」を決議した。今期，すなわち第15期の発足に当たり，日本学術会議は「女性研究者の地位の向上」に留意することを再確認し，今期の活動計画の一つにこの課題を取り上げ審議してきた。その結果，女性科学研究者の地位の向上の必要性は理念的には一般化したものの，科学者全体の対応の遅れもあって，その地位は実質的に余り改善されていないことが明らかになった。

このため，特に基礎科学分野における科学研究者不足の事態が目前に迫っている現在，我が国における科学の調和のある発展のために，第10期，第12期での男女平等の視点を前提としつつ，日本学術会議は，改めて女性科学研究者の環境改善の緊急性を指摘するとともに，関係方面に環境改善の促進を強く訴えるものである。

「日本学術会議だより」について御意見，お問い合わせ等がありましたら，下記までお寄せください。
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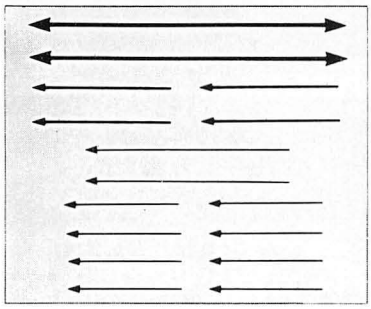

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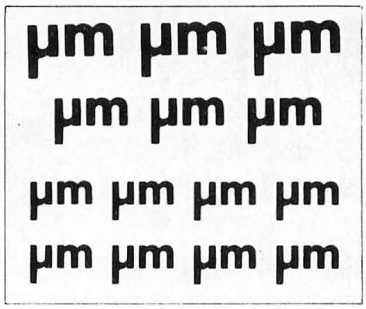

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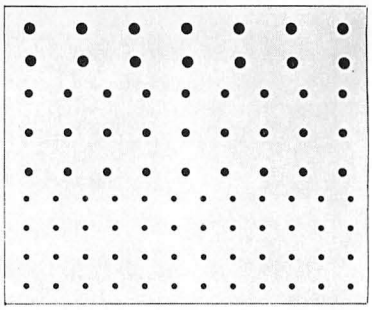

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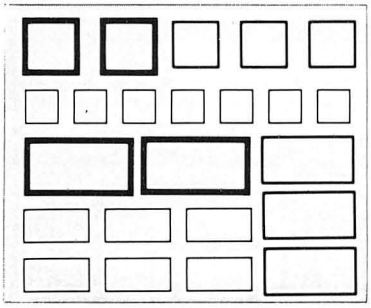

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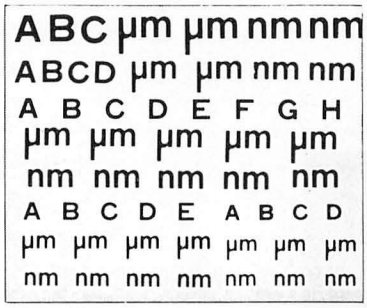

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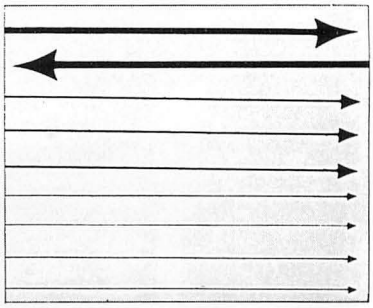

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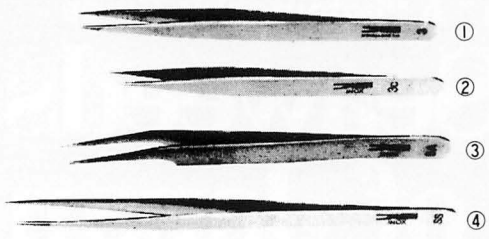

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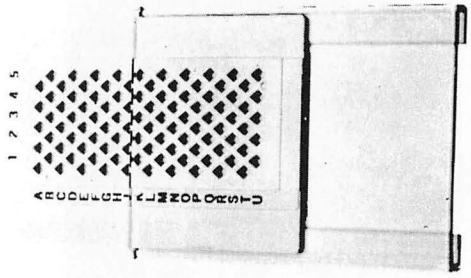

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3. 山田幸男先生追悼号　藻類25巻増補．1977．A5版，xxviii＋418頁．山田先生の遺影・経歴・業績一覧・追悼文及び内外の藻類学者より寄稿された論文50編（英文26，和文24）を掲載，価格7,000円。

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2. **Index of the Bulletin of Japanese Society of Phycology.** Vol. 1 (1953)–Vol. 10 (1962), Price 2,000 Yen for member, or 2,500 Yen for nonmember; Vol. 11 (1963)–Vol. 20 (1972), Price 3,000 Yen for member, or 4,000 Yen for nonmember. Vol. 1 (1953)–Vol. 30 (1982), Price 4,000 Yen for member, or 5,000 Yen for nonmember (incl. postage, surface mail).

3. **A Memorial Issue Honouring the late Professor Yukio Yamada** (Supplement to Volume 25, the Bulletin of Japanese Society of Phycology). 1977. xxviii + 418 pages. This issue includes 50 articles (26 in English, 24 in Japanese with English summary) on phycology, with photographs and list of publications of the late Professor Yukio YAMADA. 8,500 Yen (incl. postage, surface mail).

4. **Contribution to the Systematics of the Benthic Marine Algae of the North Pacific.** Edited by I. A. ABBOTT and M. KUROGI, 1972. xiv + 280 pages, 6 plates. Twenty papers followed by discussions are included, which were presented in the U.S.-Japan Seminar on the North Pacific Benthic Marine Algae, held in Sapporo, Japan, August 13–16, 1971. 5,000 Yen (incl. postage, surface mail).

5. **Recent Studies on the Cultivation of *Laminaria* in Hokkaido** (in Japanese). 1977. 65 pages. Four papers followed by discussion are included, which were presented in a symposium on *Laminaria,* sponsored by the Society, held in Sapporo, September 1977. 1,200 Yen (incl. postage, surface mail).

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