

The Japanese Journal of PHYCOLOGY

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日本藻類学会

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昭和62年度日本藻類学会第11回大会を下記の要領で開催します。藻類に関係のあるあらゆる分野の研究についての発表を広く歓迎します。所属機関長への出張要請等の文書などご入用の方は宛先を明記して大会準備委員会までご遠慮なくお申し込みください。

大会終了後には日本藻類学会主催で若狭湾における海藻採集会を企画しています(裏面参照)。奮ってご参加下さい。

- (1) 期 日 昭和62年 3月30日(月)～3月31日(火)
- (2) 会 場 京都大学楽友会館 京都市左京区吉田近衛町 TEL. 075-751-1100〔国鉄京都駅北口より市バスA2のりば206番, 京阪四条駅より市バス(南座向かいのりば), または 阪急四条河原町駅より市バス(北側のりば)201番または31番で, 近衛通り下車(京都駅から約30分, 四条から約20分, 料金は160円)〕なお会場付近に駐車場はありません。
- (3) 研究発表 発表形式は口頭発表と展示発表とします。口頭発表は1演題につき討論を含めて15分を予定しています。展示発表は原則として大会期間中とし, 演者はポスターの前で決められた時間に説明と質疑応答を行うこととなります。
- (4) 参加申し込み 講演の有無にかかわらず, 大会に参加を希望される方は, 同封の振替用紙にてお申し込み下さい。参加費は2,500円です。ただし学生は2,000円とします。懇親会(3月30日夜開催)に出席希望の方はさらに会費2,500円を添えてお送り下さい。
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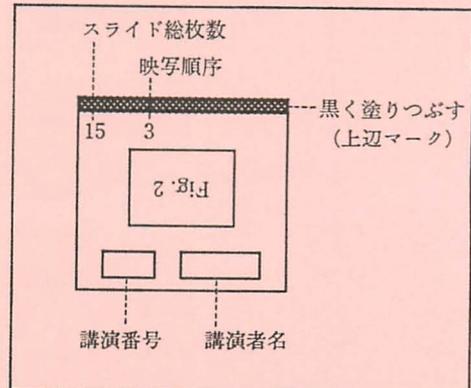
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— 日本藻類学会主催海藻採集会のお知らせ —

下記の要領により若狭湾での海藻採集会を開催します。参加者を募集します。

- (1)期日 昭和62年3月31日(火)午後5時(第11回大会終了後)～4月2日(木)正午
- (2)日程と内容(予定)
3月31日(火), 大会終了後集合, 京都祇園から京都バス(路線バス)にて舞鶴まで移動後水産実験所に宿泊。4月1日(水), 9時～12時, 若狭湾(高浜)での磯採集, 13時～17時, 室内観察・分類同定。4月2日(木), 9時～12時, 室内観察のつづき, 昼食後解散。
- (3)会場 京都大学農学部附属水産実験所 舞鶴市長浜
TEL. 0773-62-5512
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しくは後日参加者にお知らせいたします。

(3月31日の京都～舞鶴間の移動バス代は団体割引とする予定ですが, 参加費とは別途に当日徴収いたします。)

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Field, culture and cytological studies of *Porphyra carolinensis* COLL et COX (Bangiales, Rhodophyta) from North Carolina

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FRESHWATER, D. W. and KAPRAUN, D. F. 1986. Field, culture and cytological studies of *Porphyra carolinensis* COLL et COX (Bangiales, Rhodophyta) from North Carolina. Jap. J. Phycol. 34: 251-262.

The morphological life history of *Porphyra carolinensis* has been studied in the field and laboratory culture. Cross-gradient light-temperature culture in 10:14 and 14:10 LD cycles was utilized to investigate the effects of photon flux, temperature and daylength on growth and reproduction. Conchospore release appeared to be controlled by a requirement for a combination of short photoperiod and low temperature. The blade phase was found to grow and reproduce itself by monospores throughout the year. Four chromosomes occur in conchocelis, conchospores, carpospores, spermatia, and vegetative cells of the foliose phase.

Key Index Words: Bangiophyceae; cytology; North Carolina; Porphyra; reproductive seasonality; Rhodophyta.

The life history of *Porphyra* species typically includes a conspicuous blade phase which alternates with a microscopic filamentous conchocelis phase (COLE and CONWAY 1980). The blade phase is usually reported to be an annual with a summer maximum of growth and reproduction at higher latitudes (MUMFORD 1975) and a winter-spring maximum in lower latitude temperate waters (EDWARDS 1969, BIRD *et al.* 1972, KAPRAUN and LUSTER 1980, HAWKES 1981).

Previous field studies in coastal North Carolina (34°N lat.) indicated that *Porphyra carolinensis* (COLL and COX 1977) seems to have a phenology unique for warm temperate species, with the blade phase growing and reproducing throughout the year (KAPRAUN 1980).

This communication presents the results of field, culture and cytological studies conducted to determine the life history of *Porphyra carolinensis* and its responses to photon flux, temperature and daylength

which are responsible for the phenology observed in nature.

Materials and Methods

Monthly observations on the growth and phenology of *Porphyra carolinensis* were made on a rock jetty at Masonboro Inlet, Wrightsville Beach, North Carolina from November 1983 to May 1985. Blades were examined microscopically in the laboratory for the presence of reproductive cells. Blade areas with monospores and carpospores were excised and kept in culture to determine germination pattern. Unialgal cultures were grown in an enriched seawater medium (salinity 34-36‰) modified after Von STOSCH (KAPRAUN 1970). GeO₂ was used to control diatom growth (LEWIN 1966). Blue-green algal contaminants were treated with 100 units Penicillin G per ml of medium (PAGE 1973).

Two sets of apparatus were utilized for the culture studies. Photon flux, photoperiod

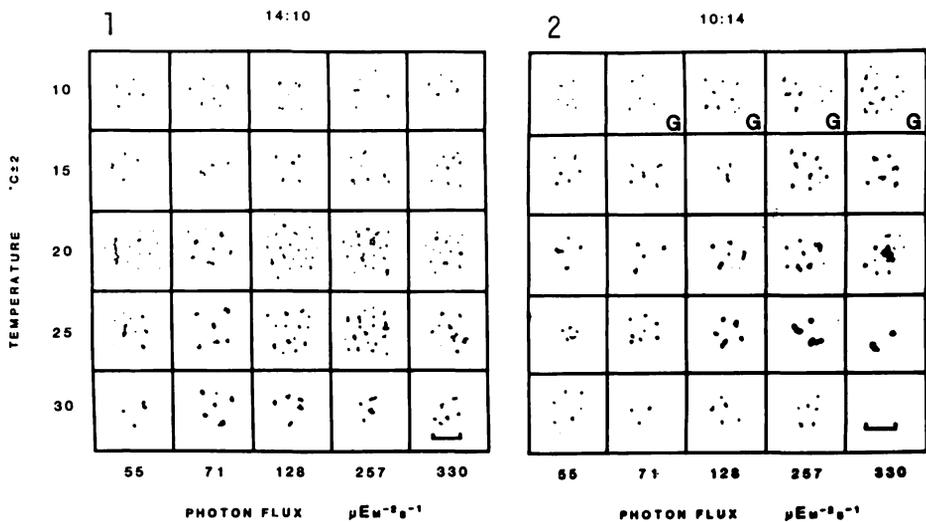
and temperature effects on growth and reproduction were studied using a cross-gradient light-temperature apparatus (EDWARDS and VAN BAALEN 1970) which permitted the simultaneous culture of the isolates in 25 combinations of the two parameters (Fig. 1). Photoperiods used were 14:10 and 10:14 LD. Culture vessels were 15×60 mm, and contained 25 ml medium.

Conchocelis for culture experiments came from subcultured spores of blades collected in nature January 18, 1983 and maintained at 18:6 LD, 20°C and 55 $\mu\text{Em}^{-2}\text{s}^{-1}$ photon flux. In the first experiment, ten tufts of conchocelis were put in each vessel and cultured for 21 days. The medium was changed every 6–8 days. These cultures were then examined microscopically to determine their relative growth and degree of conchosporangial production. In the replicate experiment, five tufts of conchocelis were put in each vessel and cultured for 55 days (Figs. 1 and 2). The medium was changed every 3–4 days. These cultures were studied to determine the effects of photon flux, photoperiod, and temperature on conchospore release and development.

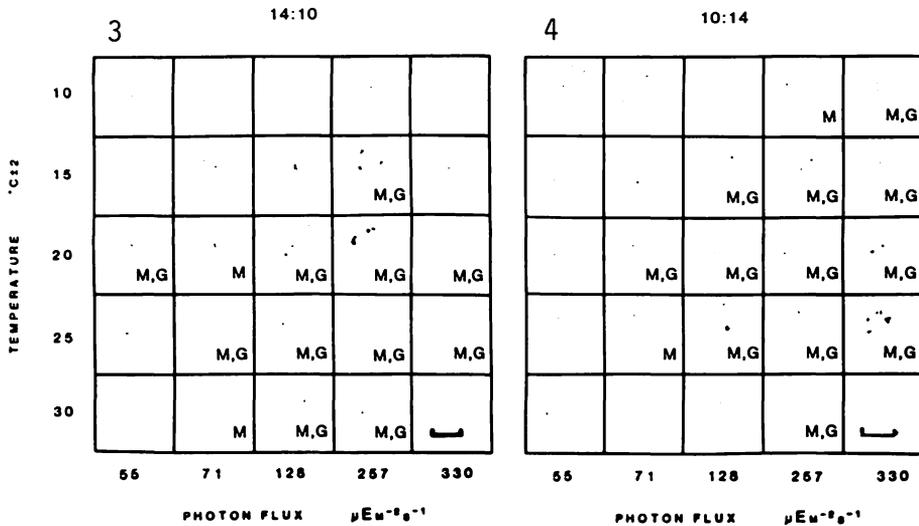
Germlings were grown from monospores of blades collected on November 20, 1983 and maintained at 12:12 LD, 15°C and 45 $\mu\text{Em}^{-2}\text{s}^{-1}$. Three to five germlings were put in each vessel and cultured 24 days in the initial experiment and 39 days in the replicate. These cultures were then examined to determine growth and sporulation patterns (Figs. 3 and 4). Illumination was provided by Phillips TL 34 cool white fluorescent tubes. Photon flux ranged from 55–330 $\mu\text{Em}^{-2}\text{s}^{-1}$ and was measured with a Lambda I. Cor. PAR (Photosynthetic Active Radiation) quanta meter.

Incubators with light sources as described above were used to maintain isolates and to study the life history under varying temperature, photoperiod, and quantum flux combinations (Tables 2 and 3).

Chromosome counts were made using a procedure modified after AUSTIN (1959) in vegetative and sporulating sections of mature blades, germlings, conchocelis and conchosporangia. Conchocelis from culture and blades collected in nature were fixed at 1 h intervals beginning 1 h before sunset (or dark cycle) and continuing for five h,



Figs. 1 and 2. Growth and reproductive responses of *Porphyra carolinensis* conchocelis phase to photon flux densities and temperature regimes after 55 days. Fig. 1. 14:10 LD. Fig. 2. 10:14 LD. (Photon flux densities, temperature gradient, and scale in Fig. 1 apply to Figs. 2–4, Scale=1 cm). G=germling development.



Figs. 3 and 4. Reproductive response of *Porphyra carolinensis* blade phase to photon flux densities and temperature regimes after 32 days. Fig. 3. 14 : 10 LD. Fig. 4. 10 : 14 LD. G=germling development, M=monospores.

and again beginning at sunrise (or light cycle) and continuing for four h. Material was fixed in 3 : 1 absolute ethanol-glacial acetic acid and left overnight. Fixed material was stored in 70% ethanol, hydrolized in 1 N HCl for 10 min at room temperature, rinsed in distilled water, and stained in 2% acetocarmine or aceto-orcein for 2-3 h prior to squash preparation. Documentation was made by both microphotographs and camera lucida drawings using an Olympus BH 2-RFK microscope.

The geographical range of *Porphyra carolinensis* was investigated by examining herbarium specimens from the following herbaria : University of South Florida-Tampa (USF), University of Michigan-Ann Arbor (MICH), and the University of North Carolina-Wilmington (WNC).

Daylength was calculated from sunrise and sunset data for 34°N lat. (US DEPT. COMM. 1984). Water temperature data for Wrightsville Beach for the period November 1983 to May 1985 were made available by the Laque Center for Corrosion Technology.

Results

Field observations: *Porphyra carolinensis* was found on upper eulittoral and lower supralittoral rocks every month of the study. Maximum abundance and blade development were observed from November to April (Fig. 5). Monospore production from blade

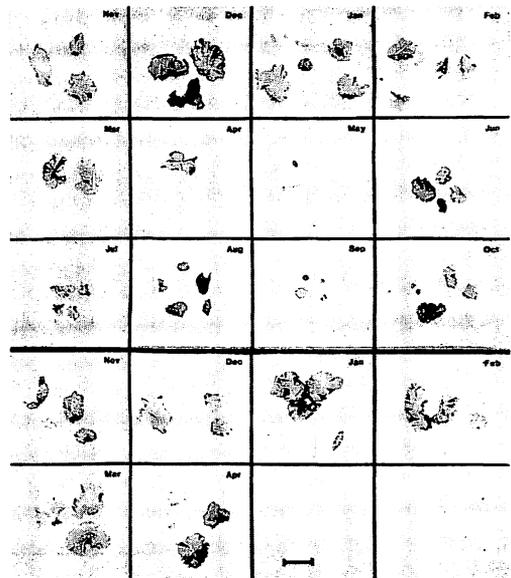


Fig. 5. Seasonal variation in the blade phase (herbarium specimens) of *Porphyra carolinensis* from Masonboro Inlet, November 1983-March 1985. Scale=2 cm.

margins occurred continuously while carpospore and spermatium formation coincided with the November-April period of maximum vegetative growth (Table 1, Fig. 6). Subsequent development of monospores followed in the laboratory revealed that all surviving

monospores germinated in a bipolar manner to produce blades except in the collections of 12 June and 16 July, 1984 when fewer than 1% of the monospores germinated to produce conchocelis. Unipolar germination was observed for all surviving carpospores.

Table 1. Sporulation of *Porphyra carolinensis* blades collected in nature (November 1983-March 1985).

Date	Water Temperature °C	Daylength (hr : min)	Carpospores	Spermatia	Monospores
Nov. 20	16	10 : 15	+	+	+
Dec. 19	14	9 : 48	+	+	+
Jan. 14	9	10 : 04		+	+
18	7	10 : 08	+	+	+
Feb. 02	9	10 : 30	+	+	+
17	12	10 : 59	+	+	+
Mar. 16	12	12 : 01	+	+	+
31	16	12 : 34	+		+
Apr. 26	18	13 : 25			+
May 10	21	13 : 49			+
16	20	13 : 58			+
June 12	26	14 : 25			+
July 16	27	14 : 13			+
Aug. 08	28	13 : 40			+
Sept. 23	21	12 : 07			+
Oct. 25	24	11 : 01			+
Nov. 24	18	10 : 10	+	+	+
Dec. 19	15	9 : 52	+	+	+
Jan. 19	8	10 : 12	+	+	+
Feb. 07	9	10 : 42	+	+	+
Mar. 08	17	10 : 46	+		+
20	13	12 : 07	+		+

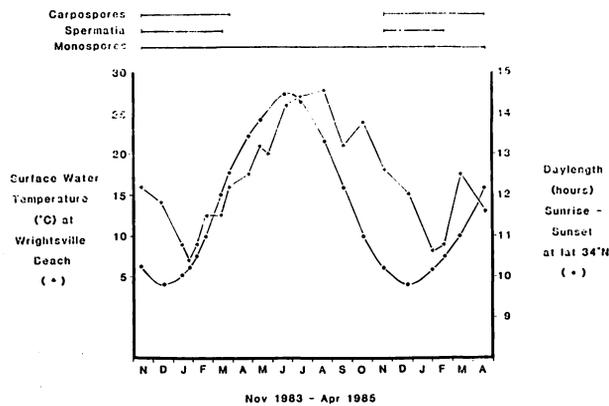


Fig. 6. Phenology of *Porphyra carolinensis* correlated to monthly water temperature and daylength (November 1983-April 1985).

Cross-gradient culture: In both cross-gradient conchocelis experiments, growth and conchosporangial production occurred in all photon flux-temperature combinations under both 10 and 14 h days. In the second experiment, which was initiated with a smaller amount of inoculum, reproduction by fragmentation was especially pronounced at 20°C in all flux densities. After 55 days, conchospore release and subsequent blade germling development were observed only in 10 h days at 10°C and photon flux densities of 71–330 $\mu\text{Em}^{-2}\text{s}^{-1}$ (Figs. 1 and 2).

In both cross-gradient blade experiments, growth and reproductive responses were similar in 10 and 14 h days. Germlings survived in all photon flux and temperature combinations except at 30°C. After 32 days, monospore production and blade germling development appeared to increase with increasing temperature in 14 h days (Fig. 3), and was observed in only one culture dish at temperatures below 20°C. In contrast, monospore production and blade germling development appeared to increase with photon flux in 10 h days (Fig. 4), and was observed through all temperatures tested (10–30°C).

The relationship of sporulation in cultured conchocelis and subsequent spore development to irradiance in both cross-gradient photoperiods is summarized in Fig. 7. Although conchospore release and blade development were observed through a wide range of irradiance (quantum doses of 2.56–12.9 $\text{Em}^{-2}\text{day}^{-1}$), both phenomena occurred only

at 10°C in 10 h days. A combined photoperiodic and temperature requirement is implicated.

Incubator experiments: Additional tests to determine the effect of temperature and photoperiod on conchospore release confirmed the results of the cross-gradient experiment: only a combination of 10°C and 10 h days among the parameters tested produced conchospore release (Table 2).

Additional tests were conducted to induce both uni- and bipolar germination of blade monospores in cultured material as had been observed in nature. In the parameters tested only bipolar germination was observed (Table 3).

Blade morphology: *Porphyra carolinensis* was recently distinguished from the other *Porphyra* species on the North American Atlantic coast and recognized as a new species (COLL and COX 1977). The reported diagnostic features include: blades monostromatic with 1 plastid per cell, microscopically dentate margins, marginal monospores, carpospores and spermatia formed in adjacent marginal patches on the same blade, carpospores in packets of 16 in two tiers, spermatia in packets of 32 in four tiers.

In general, blades examined in this study show the same morphological features (Figs. 8–10) previously reported for this species (COLL and COX 1977, KAPRAUN 1980). However, we found the division sequence and final number of cells in mature carposporangia and spermatangia to differ from

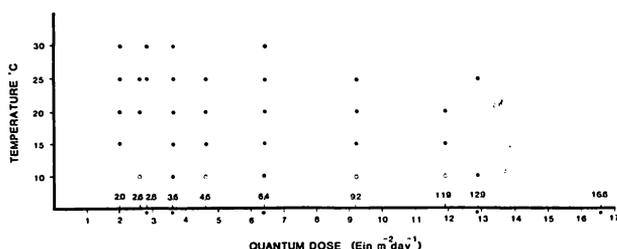


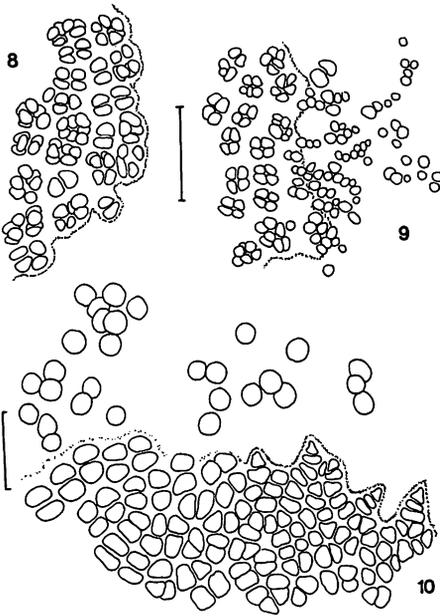
Fig. 7. Maximum developmental stage reached by conchocelis at various quantum dose rates in 14:10 (*) and 10:14 (other): ● = conchosporangial development in <50% of inoculum; ○ = conchospore release and blade germling development.

Table 2. Release of conchospores under various conditions of photoperiod and temperature after 28 days.

L : D	Temperature (°C)	Photon flux ($\mu\text{Em}^{-2} \text{s}^{-1}$)	Conchospore release	Development
18 : 6	20	52	—	
12 : 12	15	30	—	
10 : 14	26	130	—	
10 : 14	10	43	+	Bipolar

Table 3. Development of monospores released from germlings under various photoperiods and temperatures after 14 days.

L : D	Temperature (°C)	Photon flux ($\mu\text{Em}^{-2} \text{s}^{-1}$)	Germling development	
			Bipolar	Unipolar
18 : 6	20	52	+	—
12 : 12	15	30	+	—
10 : 14	25	130	+	—
10 : 14	10	43	+	—



Figs. 8-10. Formation of reproductive cells on blade margin. Scale=50 μm . Fig. 8. Carpospore formation. Fig. 9. Spermatia formation. Fig. 10. Monospore formation. Note dentate margin.

the accounts given by COLL and COX (1977). The division sequence in a mature carposporangium results in the formation of eight carpospores in two tiers (Fig. 11) instead of

16 as previously reported. Apparent cases of 16 carpospores we observed are assumed to be artifacts of recent vegetative divisions producing small daughter cells in close proximity. The carposporangial division sequence begins with a planar division (Fig. 11). In contrast, at least two vertical divisions occur before the first planar division in spermatangia (Fig. 12). The division sequence in a mature spermatangium results in the formation of 32 spermatia in two tiers (Fig. 12) instead of four as previously described.

Carposporangia and spermatia typically occur on the same blade, and though generally in different areas, they have been observed in close association. Even in these cases, they are easily distinguished since carposporangia gain pigment and become darker than the surrounding vegetative cells, while spermatia lose pigment and are almost clear.

Using the criteria designated by KUROGI (1972) as having taxonomic significance, a comparison was made of *P. carolinensis* with the descriptions of other *Porphyra* species reported for the North and South Atlantic coasts (ROSENVINGE 1909, TAYLOR 1957, 1960, GAYRAL 1958, 1966, CONWAY 1964a,

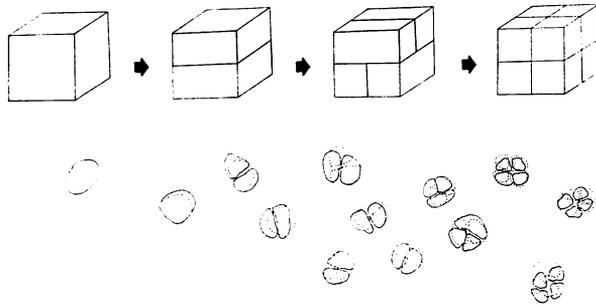


Fig. 11. Division sequence in the formation of a mature carposporangium of eight carpospores.

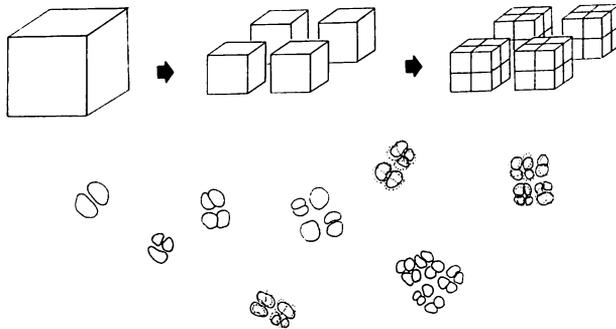


Fig. 12. Division sequence in the formation of a mature spermatangium of thirty-two spermatia.

1964b, ARDRÉ 1970, OLIVEIRA FILHO and COX 1975, COLL and OLIVEIRA FILHO 1976, COLL and COX 1977, KORNMANN and SAHLING 1977, JOHN *et al.* 1979). Despite the minor differences between the observations in our study and the original description by COLL and COX (1977), we are in agreement with their conclusion that *Porphyra carolinensis* is distinct from other Atlantic species.

Geographical distribution: The known distribution of *Porphyra carolinensis* includes coastal, stenohaline habitats in North and South Carolina, and northern Florida. It is possible that the range of this species could include suitable habitats in Virginia and Bermuda, but we were unable to confirm this with the herbarium specimens available.

Representative specimens: FLORIDA. Marine Land, coquina rock, 31 March 1978, R. McINTOSH and C. DAWES (as *Porphyra leuco-*

sticta), USF 131070. NORTH CAROLINA. Kure Beach, coquina rock, 2 Sept. 1971, D. KAPRAUN, WNC 9537; Wrightsville Beach, jetty rocks, 18 Dec. 1971, D. KAPRAUN, WNC 7907. SOUTH CAROLINA. Myrtle Beach, pilings, 20 July 1985, W. FRESHWATER, WNC 16557.

Life history: Culture studies have produced a functional life history for *Porphyra carolinensis* from filamentous conchocelis to macroscopic blade and back to conchocelis (Fig. 13). Monospores from blades develop in bipolar fashion to produce the blade phase (Fig. 14). Carpospores from blades develop in unipolar fashion to produce conchocelis (Fig. 15a-d). Conchocelis filaments from conchosporangia (Fig. 15e) under all environmental conditions tested, but conchospore release occurs only in cold temperatures under short day conditions. Conchospores

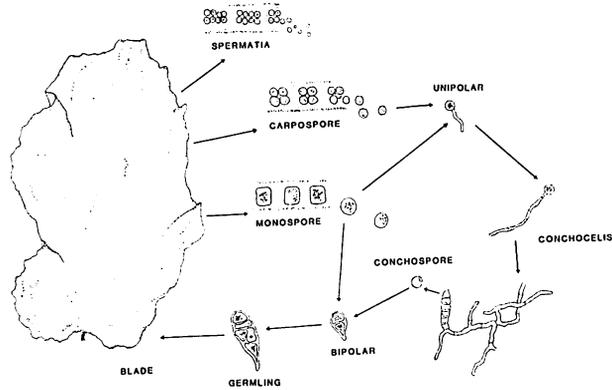


Fig. 13. Life history of *Porphyra carolinensis*.

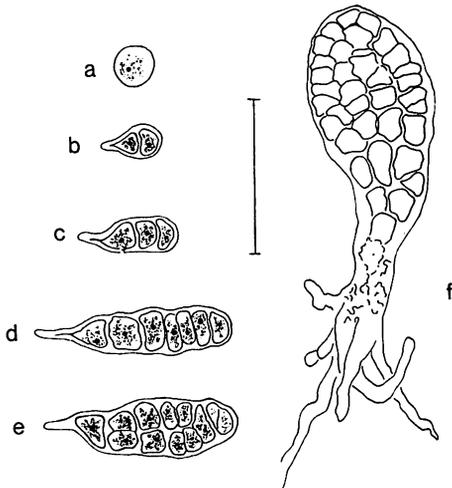


Fig. 14. Bipolar development of monospores and blade germling formation. Scale=50 μ m.

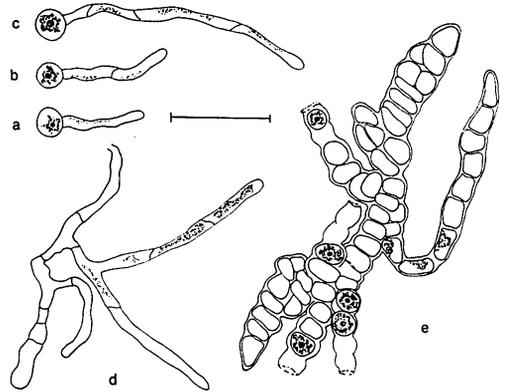


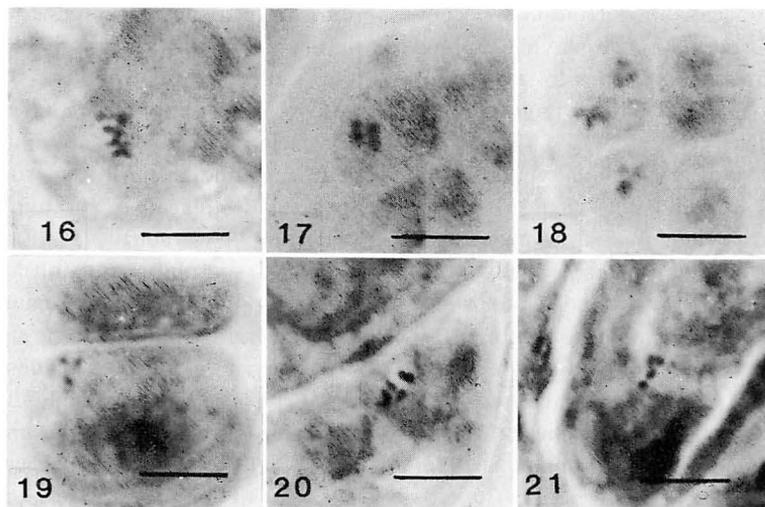
Fig. 15. Unipolar development of carpospores and conchocelis formation. Scale=50 μ m.

develop in a bipolar fashion to produce blades, thus completing the life cycle. Spermata are apparently vestigial.

Cytological observations: Four chromosomes were found in mitotic prophase cell divisions in conchocelis, conchospores, carpospores, spermata, and vegetative cells of the blade phase (Figs. 16-21). In general, adequate mitotic figures were found in actively growing material from all fixation periods. Aceto-orcein was found to be superior to acetocarmine as it was less likely than the latter to stain cytoplasm and obscure chromosomes.

Discussion

Conchocelis phase: Individually or in combination, temperature, photon flux and photoperiod have been implicated in the control of conchospore formation and release in *Porphyra* species (KUROGI and AKIYAMA 1966, DRING 1967, RENTSCHLER 1967, KAPRAUN and LUSTER 1980). In this study, conchospore formation did not appear to be dependent on photon flux density. However, a temperature effect was apparent with maximum conchospore formation at 20 and 25°C in both 10 and 14 h days. Conchospore release and subsequent blade germling de-



Figs. 16-21. Chromosomes of *Porphyra carolinensis*. Scale = 5 μm . All chromosomes are mitotic. Fig. 16. Vegetative blade cell anaphase with four pairs of chromosomes. Figs. 17 and 18. Four prophase chromosomes in spermatia. Fig. 19. Carposporangium with three visible chromosomes. The fourth is below the plane of focus. Figs. 20 and 21. Conchosporangia with four chromosomes (Fig. 20. Late metaphase. Fig. 21. Prophase).

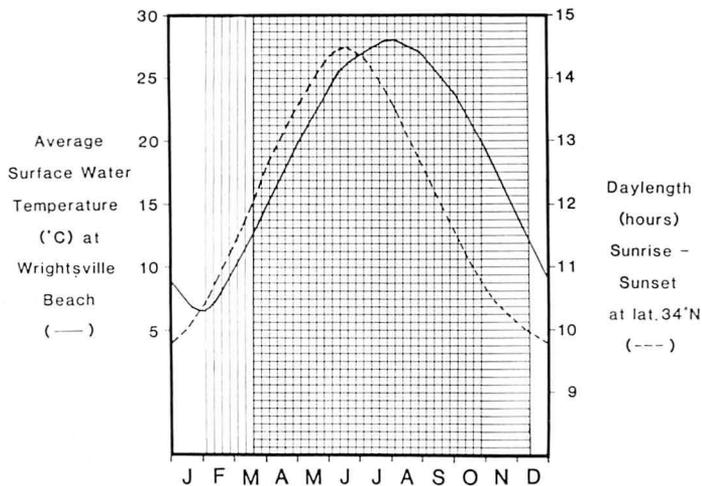


Fig. 22. Relationship between conchospore release and daylength or seawater temperature at Wrightsville Beach. Vertical lines indicate inhibition by daylength, horizontal lines by temperature.

velopment were controlled by a combination of low temperature (10°C) and short days (10 h). Previous studies of other *Porphyra* species have demonstrated a similar disparity between environmental parameters which promote conchospore induction and release

(KUROGI and HIRANO 1956, KUROGI and AKIYAMA 1966, LÜNING 1980).

In *P. carolinensis*, the pathway leading to conchospore release is opened in short days only within a rather narrow temperature interval, around 10°C, with complete inhi-

bition at 15°C or less. Only from mid-December to early February are daylength and temperature in the appropriate range for the process of blade formation from conchospores to occur (Fig. 22). Thus, the "window" for blade reseeding via conchocelis is rather small, and would be even smaller in years when water temperatures remain above normal through the winter. Since blade formation via blade monospore production does not seem to be inhibited by any ambient combination of temperature and photoperiod, it can be surmised that this accessory means of reproduction is of critical importance to the continued survival of this species in local waters.

Blade phase: Investigations of the importance of environmental parameters on sporulation in the blade phase of *Porphyra* species have demonstrated considerable variation among the species investigated. IWASAKI (1961) found *P. tenera* blades remained vegetative in 8 h days, but formed carpospores in 13 h light. In contrast, several species have been found to produce both carpospores and spermatia through a wide range of temperatures and daylengths (BIRD *et al.* 1972, EDWARDS 1969, KAPRAUN and LUSTER 1980). Apparently, in these cases a maturation sequence or "ripening" rather than an environmental stimulus controls the initiation of sporogenesis.

In this study, both carpospore and spermatium formation showed a distinct seasonality in field collected material (Fig. 6). Comparison of sporulation patterns with water temperature and photoperiod data suggests a threshold of 16°C and 10.5 h days is required to initiate both carpospore and spermatium formation. Sporogenesis is subsequently inhibited as temperatures rise above 16°C, but continues in daylengths approaching 12.5 h. This strongly suggests that vegetative cells, once induced by photoperiod, may continue to undergo sporogenesis under inappropriate (non-inducing) daylengths. Unfortunately, there are few experimental data to correlate with these field observations. We have been successful

only once in our attempts to induce sporulation in laboratory grown blades in any of our experimental conditions. Usually the rapid erosion resulting from monospore formation seems to prevent tissue from maturing and initiating sporogenesis. However, blades placed in aerated flasks at 16°C, 100 $\mu\text{Em}^{-2}\text{s}^{-1}$, and 10 : 14 LD after 14 days produced spermatia and initiated carpospore divisions. These environmental parameters coincide with the values predicted above.

Porphyra carolinensis blades produce two distinct spore types capable of germination: 1) monospores from single undivided vegetative cells, and 2) carpospores arising in packets of eight. Carpospores invariably develop in unipolar fashion to produce the conchocelis phase. This developmental sequence is typical of most *Porphyra* species (CHEN *et al.* 1970, BIRD *et al.* 1972, HAWKES 1977, KAPRAUN and LUSTER 1980).

In contrast, *P. carolinensis* monospores usually, but not invariably, develop in bipolar fashion to produce the blade phase. Of the *Porphyra* species which produce monospores from large blades (CONWAY and WYLIE 1972, HAWKES 1977, OGAWA and LEWMANOMONT 1978), only the two species investigated in North Carolina have been shown to have the flexibility of both uni- and bipolar monospore development (KAPRAUN and LUSTER 1980).

Cytology: Four chromosomes (N=4) were found in all phases of the life history of *P. carolineensis* confirming the absence of sexuality and meiosis in this species. Interestingly, the other two local *Porphyra* species, *P. rosengurtii* (KAPRAUN and LUSTER 1980) and *P. leucosticta* (unpublished data), also lack an alternation of ploidy levels. Elsewhere, the presence of both haploid and diploid nuclear phases has been shown to be a common occurrence. YABU (1975) reported haploid and diploid numbers for most of the 19 species investigated in Japan. On the west coast of North America, MUMFORD and COLE (1977) found haploid and diploid numbers in three of seven species studied. All three species of *Por-*

phyra in the North Atlantic which have been examined cytologically possess haploid and diploid phases (MAGNE 1952, GIRAUD and MAGNE 1968, KITO *et al.* 1971).

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フレッシュウォーター, D. W.・カプラウン, D. F.: ノースカロライナ産 *Porphyra carolinensis*
COLL et COX (紅藻ウシケノリ目) の野外, 培養および細胞学的研究

北米ノースカロライナ産の *Porphyra carolinensis* の生活史について, 野外と室内培養で研究した。光周期 10L:14D および 14L:10D のもとで種々の光強度と温度を組合せ, 光強度, 温度および日長が生長と生殖に及ぼす影響を調べた。殻胞子の放出は, 短日条件と低温の組合せを必要とすることにより御制されていること, 葉状体の生長と単胞子による増殖が年間を通して行われていることが明らかになった。また, 糸状体, 殻胞子, 果胞子, 精子, 葉状体の栄養細胞の染色体数は, いずれも 4 であった。(米国ノースカロライナ大学生物科学部)

Studies of the green alga *Kornmannia* (Kornmanniaceae fam. nov., Ulotrichales) in British Columbia

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GOLDEN, L. and COLE, K. M. 1986. Studies of the green alga *Kornmannia* (Kornmanniaceae fam. nov., Ulotrichales) in British Columbia. Jap. J. Phycol. 34: 263-274.

Studies were made on field and cultured material of *Kornmannia* collected at Triple Island and southern Vancouver Island in British Columbia in order to test the taxonomic reliability of morphological characters. While two distinct entities were readily distinguished according to morphology and apparent ontogenies of field material as well as host preference, under controlled culture conditions the differences were negligible. Both had similar ontogenies, morphologies and cytology. Culture data for the British Columbia material resembled that reported from Japan, Norway and Germany. Consequently, it is concluded that only one circumboreal species, *K. leptoderma*, deserves recognition. *Monostroma areolatum* and *K. zostericola* have been synonymized as *K. leptoderma* (KJELLM.) BLIDING and the description of the genus has been emended. In addition, a new family, Kornmanniaceae, has been erected based on unique life history and cytology.

Key Index Words: Algal systematics; British Columbia; Chlorophyta; culture; Kornmannia; life history; ultrastructure.

Northern British Columbia has a rich and varied algal flora that is only recently becoming better known (HAWKES *et al.* 1978, GARBARY *et al.* 1980). Much of this richness may be attributed to the subarctic water temperatures of 5° to 10°C during the colder half of the year, coupled with a mild maritime climate that leaves the shore ice free year round. Green algae with heteromorphic life histories are particularly abundant. Species that may be only insignificant winter ephemerals in phycologically better known areas to the south often dominate the intertidal region during luxuriant spring blooms in northern British Columbia. *Monostroma* and *Kornmannia* are two such monostromatic genera. GOLDEN and GARBARY (1984) studied *Monostroma* in this area, reducing the profusion of reported entities to three circumboreal species. However, *Kornmannia* has

not yet been treated.

Members of the genus *Kornmannia* have distinctively thin, small-celled blades, but the relationship of the different geographic entities is not clear. In Europe KORNMANN and SAHLING (1962) and BLIDING (1968) reported an asexual life history for *K. leptoderma* (KJELLM.) BLIDING, but in Japan YAMADA and TATEWAKI (1965) and TATEWAKI (1969, 1972) found a heteromorphic alternation of generations between a macroscopic bladed sporophyte and a microscopic gametophyte of *Monostroma zostericola* TILDEN. To date the North America taxa have not been studied in culture so that the relationship between the Pacific and Atlantic taxa remains unclear. For example, BLIDING (1968) considered the European and Japanese entities to be separate genera on cytological and life history grounds and the Pacific

American one to be cytologically similar to the European. However, contrasted to this was the opinion of KORNMAN and SAHLING (1962) that the European and Japanese taxa are closely related, if not identical.

A field and culture study has now been completed on *Kornmannia* in British Columbia. In contrast to this genus in California which is only 1-2 cm, in northern British Columbia it reaches 10 cm and may cover much of the winter-spring intertidal region. At the primary study site, Triple Island, *Kornmannia* is represented by two entities. *K. zostericola* (TILD.) BLIDING (KZ), the often reported epiphyte on seagrasses referred to as *Monostroma zostericola* in the west coast North American literature (e.g. SCAGEL 1966, ABBOTT and HOLLENBERG 1976), reaches its maximum size and cover in late spring. It has readily observable disc and saccate stages, and usually a single, often funnel-shaped juvenile blade (SCAGEL 1966). The other entity (KH), which grows luxuriantly on the intertidal algae *Halosaccion glandiforme* (GMEL.) RUPRECHT and *Fucus gardneri* SILVA, has not been previously noted in eastern Pacific literature, although it is represented by numerous collections under the name *K. zostericola* in the University of British Columbia Herbarium (UBC). It reaches its maximum size and cover in late winter, never has a saccate stage, and appears to arise directly from an endophytic basal system to produce a cluster of collar-like upright blades.

In this current study field observations of *Kornmannia* were documented at the primary study site and, to test the taxonomic reliability of the characters, plants from Triple Island were cultured in 1984 and 1985 and plants from southern Vancouver Island, in 1985. These data were used to evaluate the characters employed in diagnosing *Kornmannia* at the species, generic, and family levels.

Material and Methods

Specimens of *Kornmannia* were collected in northern British Columbia at Triple Island

(54°17'N 130°53'W) and from southern Vancouver Island at Sooke (48°25'N 123°43'W). Triple Island, the primary study site, was described in a recent publication (GOLDEN and GARBARY 1984). Field material from this area was sampled and examined irregularly through the growing season (December to June) on a daily, weekly, or monthly basis. Cultures were set up from March to June in 1984 and 1985 using specimens from Triple Island, and in April and May 1985 using material from southern Vancouver Island. Relevant herbarium material at the University of British Columbia, including Phycoteca Boreali-America (PBA) (COLLINS *et al.* 1905), was also examined.

Cultured material was initiated as follows: 1) freshly collected moist blades, singly or in clusters, were examined with a dissecting microscope; 2) when releasing areas were seen and confirmed, either motile spores were pipetted drop by drop onto a 20×20 mm cover slip, or clean, small fragments of releasing material were transferred to a coverslip and floated in a drop of filtered seawater; 3) after 5 to 30 min fresh seawater was pipetted over the coverslip to remove everything but settled spores; if release was judged insufficient, the hanging drop method described in WYNNE (1969) was used from 1 to 24 h; 4) coverslips were either cultured individually or broken and the fragments of the clonal juveniles were cultured under different conditions; 5) isolates were replicated using three to ten different blades per host; 6) most isolates were kept through one complete life cycle and then discarded in three to twelve weeks.

Cultures initiated at Triple Island were kept in a growth chamber at about 8°C and 12 h light: 12 h dark. After several weeks, they were transferred to growth chambers in the Department of Botany at the University of British Columbia and replicates were maintained under the following conditions: 5°C 8 h light: 16 h dark, 10°C 8 h light: 16 h dark, 10°C 16 h light: 8 h dark, exposed to approximately 210 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ intensity. Cultures set up from southern

Vancouver Island material were placed immediately into culture chambers at the University of British Columbia under the foregoing conditions. PES medium (PROVASOLI 1968) was used, supplemented with GeO_2 and/or antibiotics when needed (GOLDEN and GARBARY 1984). Cultured material was observed and photographed periodically using the dissecting and compound microscopes.

For light microscopy, whole mounts and freezing microtome sections of blades were viewed unstained and following staining with IKI. In preparation for transmission electron microscopy (TEM), field collected plants were fixed in 2.5% glutaraldehyde-seawater at 4°C overnight, postfixed in 2% osmium tetroxide-seawater for 2 h and then dehydrated using a graded series of methanol-propylene oxide. Materials were embedded in Spurr's low viscosity resin (SPURR 1969). Sections were cut on a Reichert ultramicrotome OMU3 using glass knives. They were stained with a saturated solution of uranyl acetate, followed by lead citrate (REYNOLDS 1963), and viewed in a Zeiss EM10 electron microscope.

Results

Field material:

I. At Triple Island *Kornmannia* Z grew epiphytically on leaf margins of the vascular plant *Phyllospadix*, colonizing the tips of only a few plants in intertidal pools (Fig. 1). Size and habit varied with the season. Early in March many small (approx. 1 cm) cuneate blades were observed arising directly (without apparent saccate stages) from a few scattered, minute crust stages. As the season progressed to its peak in May, plants were more conspicuous; usually there was a single blade per basal crust, and saccate stages were readily observable (Fig. 2). With larger blades (to 10 cm), the crust was often no longer distinguishable from the lacinated, plate-like base of the plant. All blades disappeared by late June; a new crust phase was found occasionally during the summer and autumn.

The basal and vegetative regions of typi-

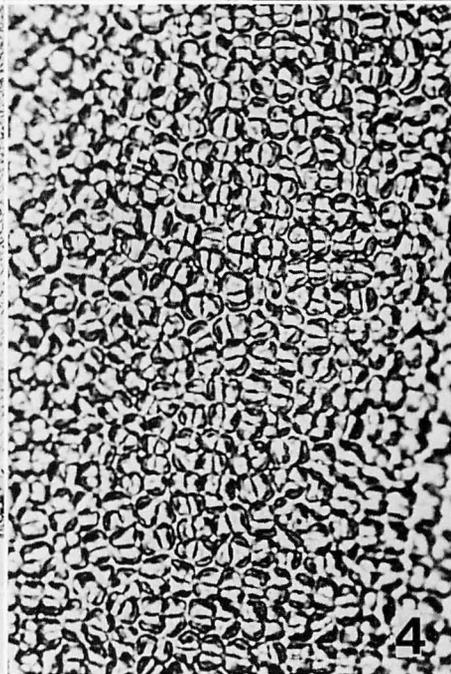
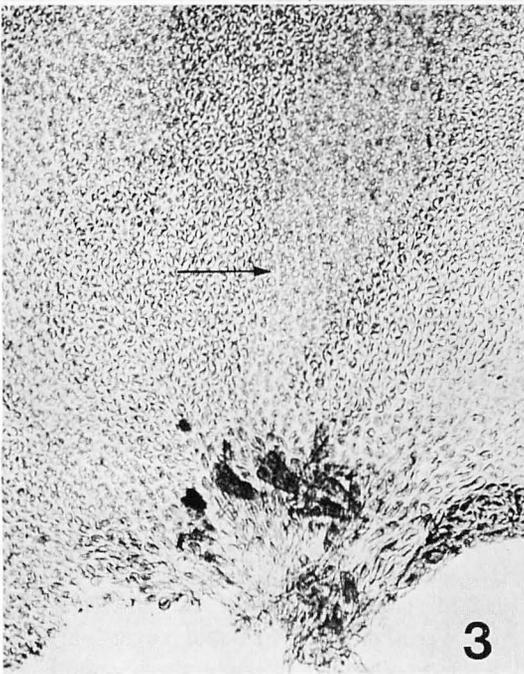
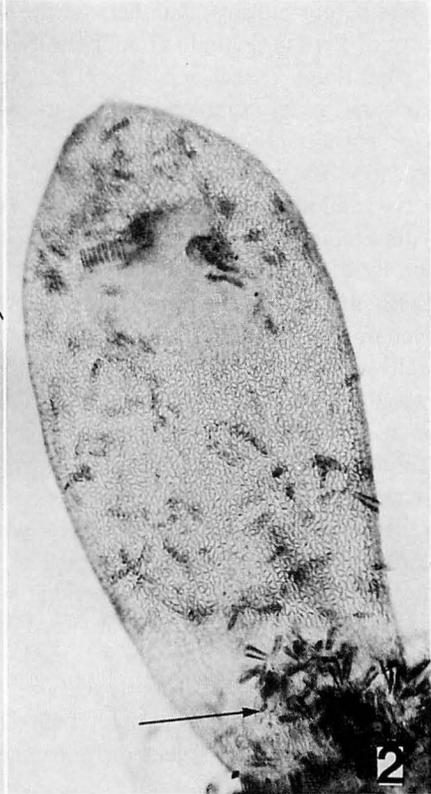
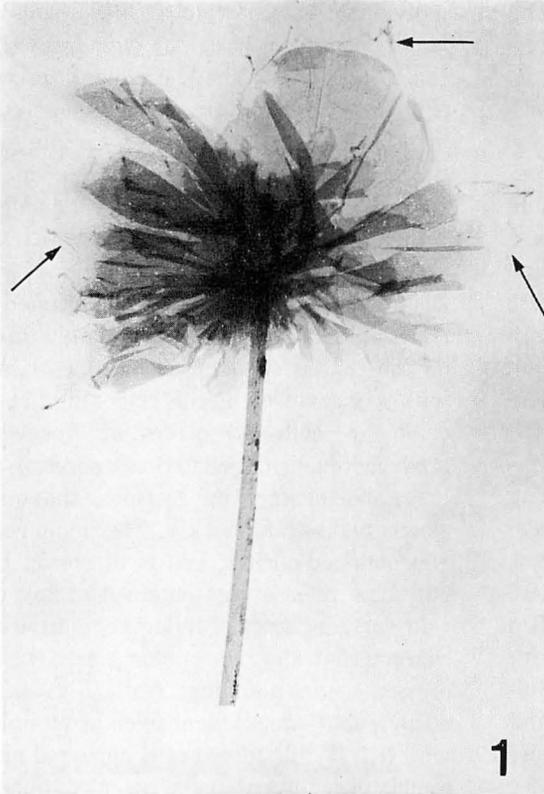
cal thalli showed little differentiation, though individuals varied widely. Basal cells often lengthened into irregular, quadrate shapes that occasionally had rhizoidal processes (Fig. 3). Distally, the cells became equidimensional ($5\ \mu\text{m} \times 5\ \mu\text{m}$). In saccate stages they organized in linear files but, in later stages, became increasingly randomly arranged. A "vein-like" (TATEWAKI 1969) arrangement was often apparent (Fig. 3). Distally, vegetative cells differentiated into *Ulva*-like sporangia. These usually remained on the thallus following spore release, along with a margin of sterile cells (Fig. 1).

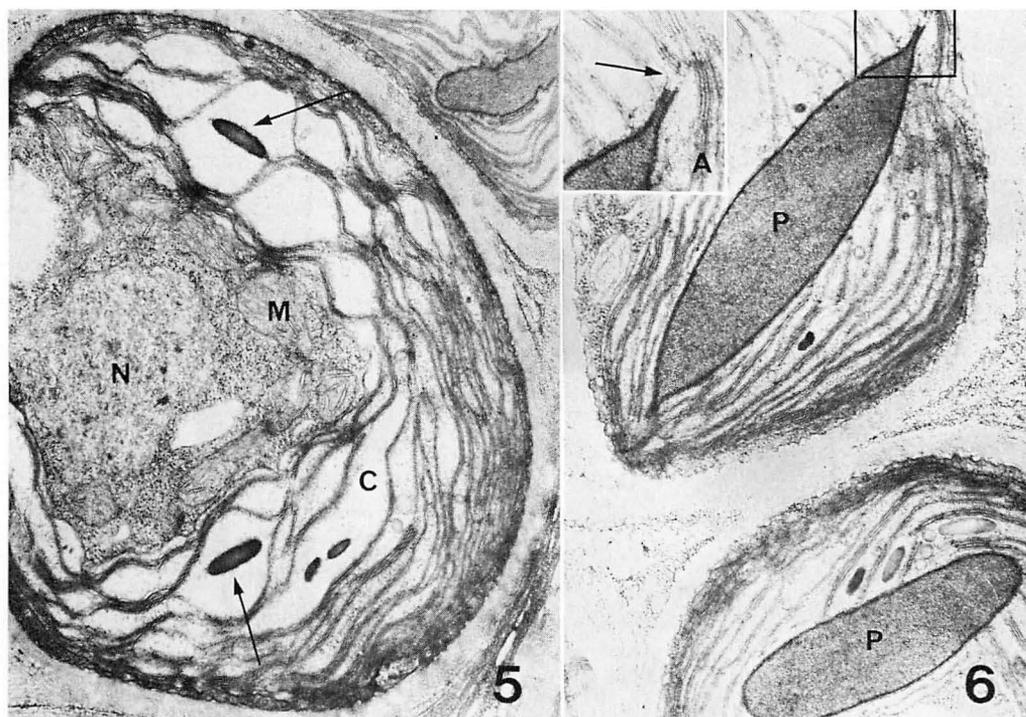
All field collected blades of *Kornmannia* produced quadriflagellated zoospores, 4–5 μm long and lacking an eyespot, that moved slowly and settled quickly. Maximum release was obtained during periods of spring tides, but some release was obtained at any time.

In surface views of living vegetative cells, characteristically the chloroplast was appressed to an anticlinal wall (Fig. 4), and no pyrenoid was evident even after staining with IKI. While turgid cells appeared almost round, plasmolysed ones revealed quadrate cell walls. Distinctive areolate patterns of cells were usually evident in unfixed dried material.

Ultrastructurally, vegetative cells contained a large, parietal chloroplast with an internal, long, ellipsoid pyrenoid which lacked associated starch plates (Figs 5, 6). The pyrenoid matrix was bound by thylakoid membranes (Fig. 6A) and small starch grains were randomly arranged within the stroma. Mitochondria with long, wide cristae were closely associated with the inner side of the chloroplast, concentrated in the region between the chloroplast and the large nucleus.

II. *Kornmannia* H epiphytized all available overwintering *Halosaccion*, and some *Fucus* was also infected. In good growing years all substrates in the mid intertidal region were covered; size and cover varied with the season. In December, minute sterile blades were seen on a few *Halosaccion* plants, arising endophytically (Fig. 7). By spring





Figs. 5, 6. *Kornmannia* Z: electron micrographs of sections through vegetative cells. 5. Whole cell showing large, parietal chloroplast (C) and starch (arrows) within the stroma. Note many mitochondria (M) with long, wide cristae concentrated in the region between the chloroplast and nucleus (N). $\times 20,000$. 6. Long, ellipsoid pyrenoid (P) lacking associated starch plates within each chloroplast. The dense matrix is bound by thylakoid membranes. $\times 20,000$. Inset A is an enlargement of the tip of the pyrenoid showing the thylakoid association (arrow). $\times 35,000$.

most hosts were covered with 1-3 cm blades (Fig. 8) which appeared to arise directly from uniseriate or multiseriate endophytic filaments. Saccate stages were never found. Individual blades were broader apically, narrowing to a funnel-like stipe which appeared closed but was actually open (Fig. 9). Most of the host plants from the previous year had disappeared by late May. Few-celled *Kornmannia* crusts were common on lower parts of the current year hosts throughout the summer and autumn.

Typical thalli were differentiated into basal and vegetative regions. The cells in the

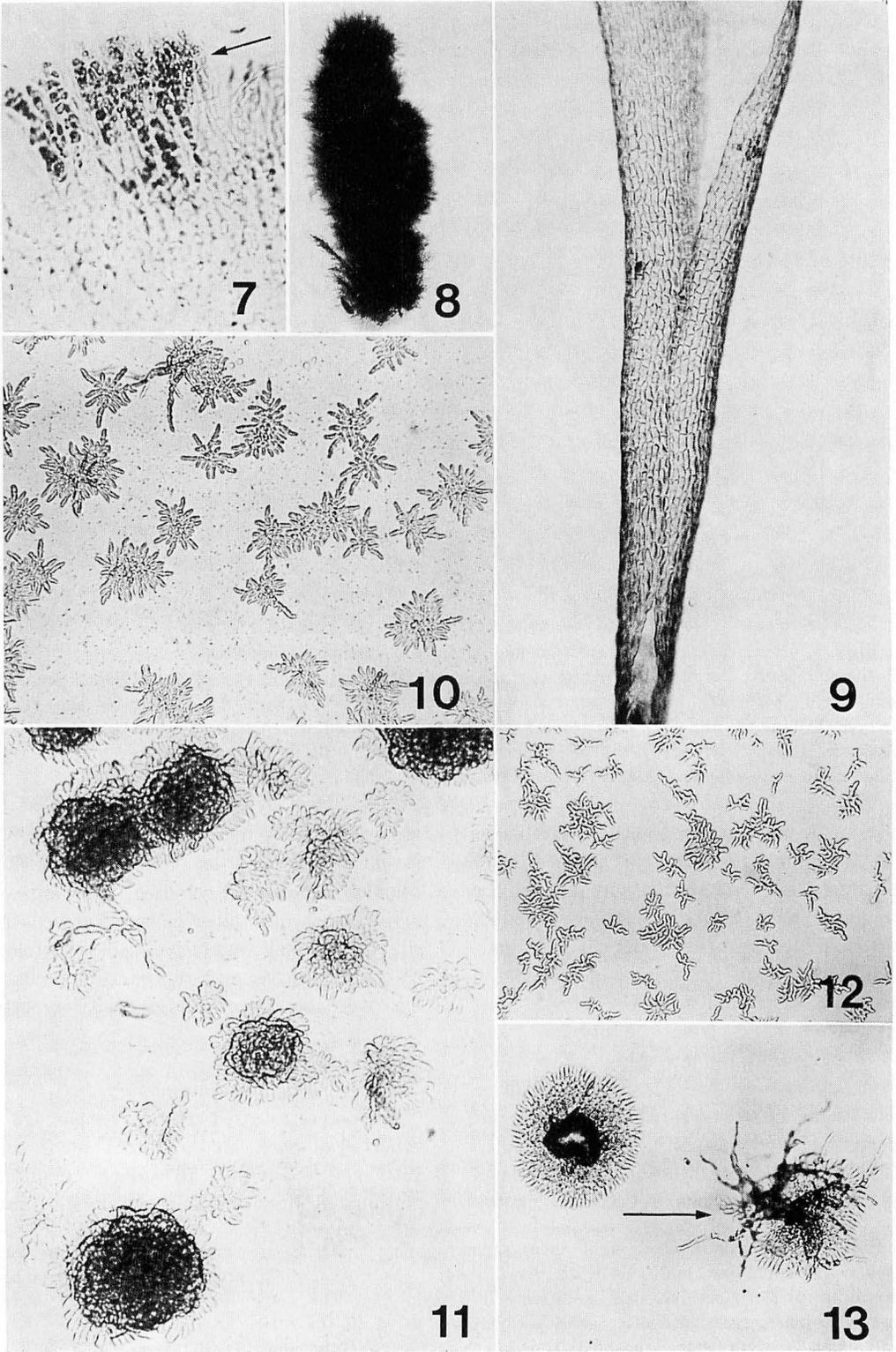
stipe were long, narrow and quadrate (Fig. 9), measuring $25+ \mu\text{m} \times \text{approx. } 6 \mu\text{m}$. Rhizoidal processes were common, occurring even in juveniles. Distally, cells developed into equidimensional vegetative cells. Cytologically, vegetative and reproductive cells of KH were similar to those of KZ reported above.

Cultured material:

Gametophyte generation—

Zoospores released from *Kornmannia* Z collected at Sooke and cultured at 5° and 10°C and 8 h light; 16 h dark conditions germinated directly into prostrate filaments.

Figs. 1-4. *Kornmannia* Z: light micrographs of living material growing epiphytically on *Phyllospadix*. 1. Blade-like thallus on tip of *Phyllospadix*. Note clear distal areas where spores have been released (arrows). Some sterile vegetative cells remain along the outer margins. $\times 1.5$. 2. Saccate stage with unistratose basal disc (arrow) which was lifted off the cuticle of *Phyllospadix*. $\times 110$. 3. Basal region of a long lacinated blade showing "vein-like" arrangement of cells (arrow) and rhizoids. $\times 180$. 4. Surface view of vegetative cells showing the chloroplast appressed to the walls. $\times 650$.



At the three- to five-celled stage branching commenced and four or more files of cells soon radiated outwards. Distal cells were usually longer and unbranched (Fig. 10). This produced a small, irregular, pseudo-parenchymatous disc which then began to thicken centrally as the lateral growth slowed or ceased (Fig. 11). The plants became reproductive in three to four weeks; gametangia covered the surface of a crust. The onset of release was signalled by the rapid movement of gametes inside the gametangia. All the gametes were released within a short time, rising in a cloud that remained just above the disc. This swarm was composed of conjugating, biflagellated isogametes that were about 4 μm long and fast moving. The crusts released randomly and no mixing of gametes between neighboring crusts was observed.

Culture data from KZ and KH collected at Triple Island differed in that the zoospores had an empty spore germination type. Gametophytes of KH were also more regular in outline and indistinguishable from young sporophytes (see below).

Gametophytes cultured at 10°C under long day conditions had an isomorphic life history. Instead of developing into paranchymatous crusts, they usually became dense tufts of uniseriate, branched filaments (see Fig. 13 arrow for a similar early stage in the sporophyte). Monoecious isogametes were produced which recycled similar irregular tufts or crusts, some of which produced zoospores when mature.

Sporophyte generation:

All cultured zygotes grown at 5° and 10°C under short day conditions germinated di-

rectly into prostrate filaments which often began branching at the second two-celled stage (Fig. 12). Cells at the end of filaments often had a bifurcating form of division not seen in the gametophytic stages. A small, circular disc was soon formed which then began to thicken and upheave centrally (Fig. 13). The resulting saccate stages either opened at the apex immediately, or grew into a long narrow tube.

Sporophytic growth in the 1984 KH (Triple Island) cultures was atypical in that saccate stages were not formed. Instead, a blade was produced by a "horse shoe"-shaped upheaval (BLIDING 1968), or else by irregular upright filaments that developed directly into blades. The 1985 KH cultures had normal disc-sac ontogeny.

Cultured material from zygotes grown at 10°C short day conditions showed some abnormal growth forms which were not present in material grown at 5°C short day conditions (Fig. 13). In addition, some sporophytic cultures that became overgrown with germlings developed blades on the water's surface without an intervening disc stage. Sporophytes normally became reproductive at sizes of 2-3 mm when grown under 10°C short day conditions; those under 10°C long day conditions grew vegetatively indefinitely, reaching lengths of 2-3 cm in four weeks.

Asexual plants:

Kornmannia H from Sooke was asexual. Under all conditions germinating zoospores had a disc-sac ontogeny similar to that of the sporophytic phase described above. However, growth was less affected by the 10°C long day conditions, and some clones showed no abnormalities at this temperature.

Figs. 7-9. *Kornmannia H*: living material growing epiphytically on *Halosaccion*. 7. Minute endophytic germlings (arrow) growing out from *Halosaccion* tissue in December. $\times 300$. 8. *Halosaccion* plant in the spring covered with blades arising from uniseriate and multiseriate endophytic filaments. $\times 0.5$. 9. Portion of an individual blade showing the open, collar-like, tubular stipe. $\times 120$. Figs. 10, 11. *Kornmannia Z*. epiphytic on *Phyllospadix*: developing gametophytes. 10. Early stages following germination. Note longer unbranched distal cells. $\times 160$. 11. Later stages showing polystromatic gametophytes. Note centrally thickened pseudo-parenchymatous discs. $\times 220$. Figs. 12, 13. *Kornmannia H*. epiphytic on *Halosaccion*: developing sporophytes. 12. Early stages following germination. Note branching commencing at two-celled stage. $\times 100$. 13. Later stages showing a circular disc with thickened central upheaval and an abnormal form (arrow) with irregular filament growth. $\times 380$.

Discussion

Species:

Historically, putative differences in blade morphology, habit and size have been used to differentiate taxa in the *Kornmannia* complex, i.e. thin (approx. 10 μm), small-celled (approx. 5 \times 5 μm) blades lacking pyrenoids. This group included *Monostroma leptodermum*, *M. zostericola*, and *M. areolatum* (UBC #A114, "co-type"). Small cell sizes were sufficient to separate *M. leptodermum* from previously described *Monostromas*. KJELLMAN (1877) based his description upon fragments of drift found along the shores of Novaya Zemlya in the Russian Arctic. Working in Greenland, ROSENINGE (1893) and JÓNSSON (1904) found large (to 10 cm) plants, attached to the substrate by long tubular stipes, which they equated to KJELLMAN's stipeless fragments. TILDEN (1900) erected *Monostroma zostericola* for the small, sessile blades epiphytic on the seagrass *Zostera* in the Puget Sound area of Washington State. But, as COLLINS (1909) pointed out, the Pacific plants are identical to those epiphytic on *Zostera* along the New England coast (PBA #1272), and neither is incompatible with KJELLMAN's description. COLLINS also questioned the conspecificity of the Greenland and North American material. SETCHELL and GARDNER (1920a) agreed with TILDEN's designation of *M. zostericola* from Puget Sound. However, they erected *M. areolatum* S & G for a similar but much larger (20-35 cm) *Zostera* epiphyte from Sitka, Alaska, which they further believed had a distinct areolate cellular pattern and more ephemeral saccate stage. Northwestern Pacific workers have identified their seagrass epiphyte as *M. zostericola* (TOKIDA 1954, VINOGRADOVA 1979), although SCAGEL (1966) suggested that the entity described by YAMADA and TATEWAKI (1965) differs significantly in zoospore and vegetative cell size from that in the type locality. Despite the above reservations, in practice the Atlantic plants have been referred to *K. leptoderma* even when only present as *Zostera* epiphytes (SOUTH

and HOOPER 1980), or quite small (PEDERSEN 1976), and Pacific plants to *K. zostericola*, regardless of size (VINOGRADOVA 1979) or host (NAGAI 1940).

The differences in field collected KH and KZ at Triple Island are comparable to those previously used to distinguish species. These differences may be summarized as a single large, irregular blade with an ephemeral tubular stipe and a distinct saccate stage (KZ), contrasted with a cluster of small, collar-like blades differentiated into a stipe and a blade which develops directly without saccate stages (KH). However, under controlled culture conditions, the differences in blade morphology between the two entities became negligible. Whatever the variations between and among isolates, basically both KH and KZ had a disc-sac ontogeny. Size, stipe morphology, number of blades per crust, etc. varied with culture conditions, particularly crowding. It is concluded that the field differences noted for the sporophytic blades were phenotypic and taxonomically unreliable.

Kornmannia culture data from Japan, Germany and Norway were indistinguishable from those obtained from British Columbia in the current study. In Europe, cultures grown at temperatures less than 10°C and unstated daylengths produced blades which recycled asexually by means of a disc-sac ontogeny (KORNMANN and SAHLING 1962). BLIDING (1968) further reported that in some plants the disc's central upheaval was incomplete, producing a collar rather than a sac, the "horseshoe" ontogeny. At 15°C and unspecified photoperiod, irregular thalli ("tufts", this paper) developed which produced zoospores (KORNMANN and SAHLING 1962). In Japan, YAMADA and KANDA (1941), using cultures grown in windows, found the macroscopic blade recycles itself by the disc-sac ontogeny, the disc being present all summer and autumn and the upheaval commencing with winter conditions. Later, YAMADA and TATEWAKI (1965), using controlled temperatures and photoperiods, reported a heteromorphic life cycle at 5°C and

short day conditions. While the zygotes usually followed a disc-sac ontogeny, there were variations including uniseriate filaments arising from the disc as precursors of the blade. At 13°C and a 14 h light: 10 h dark photoperiod, there was an isomorphic alternation of generations with the blade phase suppressed.

Cytologically, the Japanese, European and British Columbia taxa are indistinguishable at the light microscope level. All lack apparent pyrenoids, even when stained with IKI, contrary to some earlier reports [SCAGEL 1966, BLIDING 1968-interpretation of YAMADA and TATEWAKI (1965) figures]. At the TEM level, HORI (1972) dealt incidently with the pyrenoid of *Kornmannia* in a comparative study. He pointed out that this pyrenoid is unique among green algae, both in shape and the lack of a starch sheath, and so is practically invisible in the light microscope. The results of the current study confirm HORI's data.

Summarizing, it has been demonstrated in the present investigation that using field material the two *Kornmannia* epiphytes, KZ and KH, at Triple Island are more clearly distinguished morphologically than are the Atlantic *K. leptoderma* and the Pacific *K. zostericola*. However, it has also been shown that these differences are not evident in cultured material and are phenotypic. As the culture data of *Kornmannia* in Japan, Norway, and Germany were similar to those obtained for British Columbia, it is concluded that only one circumboreal species, *K. leptoderma*, deserves recognition at this time.

The small, consistent differences noted between the two epiphytes, KZ and KH, in British Columbia suggest that the two separate and independent populations of *Kornmannia* may be in the process of speciating. The development of KZ and KH gametophytes and sporophytes cultured from Triple Island material differed slightly and, at Sooke, field material of KH was asexual and grew adjacent to that of KZ which was sexual. In addition, the distribution of KZ is more southerly, into California. The

application of modern techniques such as electrophoresis may reveal a greater genotypic distance between these populations than that shown by morphology and ontogeny.

Genus:

As BLIDING (1968) did not consider the Japanese material to be congeneric with the European, his generic description of *Kornmannia* included only the monophasic, asexual life history, and his diagnosis relied upon anatomical features such as the blades, small cells, the absence of pyrenoids and rhizoids. In light of the present study, the generic diagnosis requires emendation, which is done formally at the end of this paper. The diagnostic characters of the genus are considered to be the heteromorphic life history of a macroscopic sporophytic blade alternating with a gametophytic microthallus and the unique cytology.

Family:

Ulvalean algae are usually separated into two families based upon life histories; this dichotomy is supported ultrastructurally (O'KELLY *et al.* 1984). KUNIEDA (1934) erected the Monostromaceae to include those taxa with a heteromorphic life history in which a macroscopic gametophytic blade alternates with a single-celled *Codiolum* sporophyte, in contrast to the isomorphic life history in the Ulvaceae. Considering the life history and unique cytology, *Kornmannia* does not fit into either family. Therefore, it is necessary to erect a new family, the Kornmanniaceae. This is done formally at the end of this paper.

Many authorities consider *Blidingia* and *Kornmannia* to be closely related because of their similar blade development and more recently, a report of heteromorphic life history in the former (TATEWAKI and IMA 1984). However, ontogeny is not a good indicator of taxonomic relationship. For example, GOLDEN and GARBARY (1984) using spore release characters and O'KELLY *et al.* (1984) using flagellar apparatus ultrastructure showed that *Ulvaria obscura* (KÜTZ.) GAYRAL var. *blyttii* (ARESCH.) BLID. is not conge-

neric with *Monostroma oxyspermum* (KÜTZ.) DOTY as BLIDING (1968) had held based upon their similar ontogenies. Regarding TATEWAKI and IMA's (1984) interpretation of heteromorphy in the life history of *Blidingia*, GOLDEN and COLE (unpublished data) have observed that some slow growing *Enteromorpha*s which form prostrate basal systems may become reproductive before the upright is produced. This was a culture artifact in an essentially isomorphic life history.

Although *Blidingia* and *Kornmannia* have similar cell sizes, ultrastructurally their vegetative cells are not alike. It appears that *Blidingia* exhibits typical ulvacean cytology while *Kornmannia* does not. The pyrenoid of *Blidingia* is a type common to all ulvacean genera: *Ulva*, *Enteromorpha*, *Percursaria*, *Ulvaria* (HORI 1972, SWANSON and FLOYD 1978); in contrast, that of *Kornmannia* is unique. The organelle arrangement within *Blidingia* cells is also similar to that in *Ulva* (LØVLIE and BRÅTEN 1968, MICALÉF and GAYRAL 1972, SWANSON and FLOYD 1978). The characteristic placement of mitochondria as a layer between the chloroplast and nucleus in *Kornmannia* has not been observed in any other Ulvaceae examined to date.

Ordinal:

Wide-cristaed mitochondria similar to those observed in *Kornmannia* are evident in electron micrographs included in several other ultrastructural studies on most algae in the orders Ulvales, Ulotrichales, and Acrosiphonales (e.g. MATTOX and STEWART 1973, LOKHORST and TRASK 1981, SLUIMAN *et al.* 1983), but not in the Cladophorales or siphonaceous algae (e.g. HIRAYAMA and HORI 1984, ROBERTS *et al.* 1984). MATTOX and STEWART (1973) suggested the transfer of *Pseudendoclonium* to the Ulvales based on several characters including its ulvacean pyrenoid and the appearance of its mitochondria. They were aware of the "folly" of comparing algae on the basis of mitochondrial ultrastructure, but there may now be some merit in considering all available EM data on ulvacean, ulotrichalean and

acrosiphonalean algae to determine if they have sufficiently similar cytological features to form a more natural single group (Ulotrichales).

Kornmanniaceae fam. nov.

Sporophyton macroscopicum, laminaris, monostromatica et pertenuis. Cellulae parvae, pyrenoides sine vaginis amyli. Gametophyton minutum, pulvinatus, monoicum.

Sporophyte macroscopic, blade-like, monostromatic and thin. Cells small, pyrenoids without starch sheath. Gametophyte minute, cushion-shaped, monoecious.

GENUS TYP I: *Kornmannia* BLIDING 1968, p. 610.

Accepted species: *K. leptoderma* (KJELLMAN) BLIDING, 1968.

Synonyms: *Monostroma zostericola* TILDEN Amer. Algae 1900, #388.

Kornmannia zostericola (TILDEN) BLIDING 1968. p. 620.

Monostroma areolatum S & G 1920b.

Emended description of genus *Kornmannia*: Plants with thin, monostromatic blades; stipes tube-like, collar-like or absent; cells small; rhizoids present or not; pyrenoids lacking starch sheath. Heteromorphic alternation of generations or asexual; macroscopic bladed sporophyte usually product of a disc-sac ontogeny alternates with a microscopic crust-like monoecious gametophyte. Reproductive cells 3-5 μm long, without eyespot.

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ゴールドン, L.・コール, K. M.: プリチッシュ コロンビア産の紅藻モツキヒトエ
(モツキヒトエグサ科〔新称〕ヒビミドロ目)の研究

本研究は、プリチッシュ コロンビア北部のトリプル島と南部のバンクーバー島産モツキヒトエの野生及び培養材料について、形態的特徴の分類学的信頼度を確めるために行われた。異った二種類のものが、野生での形態や個体発生、並びに宿主選好によって容易に区別されたが、培養では差異は認められなかった。両者は個体発生、形態及び細胞学からみて同種であった。プリチッシュ コロンビア産の培養結果は日本、ノルウェーとドイツ産での報告と共通した。従って、*K. leptoderma* が唯一の北方域種であると結論され、*Monostroma areolatum* と *K. zostericola* は *K. leptoderma* (KJELLM.) BLIDING のシノニウムとし、属記載が修正された。さらに、新しい科として Kornmanniaceae が、独特の生活史と細胞学に基づいて創設された。

Studies on morphological variations in *Sargassum cristaeifolium* C. AGARDH (Phaeophyta, Fucales)

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SOE-HTUN, U and YOSHIDA, T. 1986. Studies on morphological variations in *Sargassum cristaeifolium* C. AGARDH (Phaeophyta, Fucales). Jap. J. Phycol. 34: 275-281.

The developmental process of *Sargassum cristaeifolium* C. AGARDH is described to study morphological variations in vegetative and reproductive features. Morphological variations of branches, leaves and vesicles depend on ages and habitats of the plants. Gradual changes in morphology of these three features are numbered arbitrarily to know the lowest and highest limits of development in the plants growing in shallow and deep water at different ages. Receptacles of shallow and deep water plants are nearly uniform in morphology.

Key Index Words: Fucales; morphology; Phaeophyta; Sargassaceae; Sargassum; *S. cristaeifolium*; variations.

A wide range of phenotypic morphological variations shown by many species of *Sargassum* caused much difficulties in identifying the plants as to species or understanding of variability in the same species. Our observations on development of the thallus in several species occurring in the Indo-Pacific regions suggest that there is certain regularity in morphological changes of branches, leaves and vesicles according to ages or developmental stages and habitats of the plants. We present here, as an example, our observations on *Sargassum cristaeifolium*, first described by C. AGARDH in 1820 based on the specimen from Ceylon (Sri Lanka), and known from tropical Pacific areas as well as Indian Ocean regions. Similar observations on each taxon are indispensable to go further in understanding the taxonomy of this genus of Phaeophyta.

Materials and Methods

The materials were collected from various localities, such as Guam Island, Micronesia

and Kagoshima Prefecture, Japan at ecologically different habitats throughout the growing season. Specimens were preserved in 10% formalin in seawater and also mounted on herbarium sheets. Herbarium sheets examined were deposited in the herbarium of Faculty of Science, Hokkaido University (SAP). Liquid-preserved specimens of whole plants were used for observations of external morphology and habits of vegetative and reproductive features. The terms used here were in accordance with those of YOSHIDA (1983). Stems, branches, leaves, vesicles and receptacles were studied from lower to upper parts according to their positions on plants. Sections were made by hand using a double-edge razor blade for the study of reproductive organs.

Observations

S. cristaeifolium (Fig. 1) is normally an annual plant. Plants attach to rocks and coral reefs by a discoidal holdfast from the lower intertidal zone in shallow rock and tidal

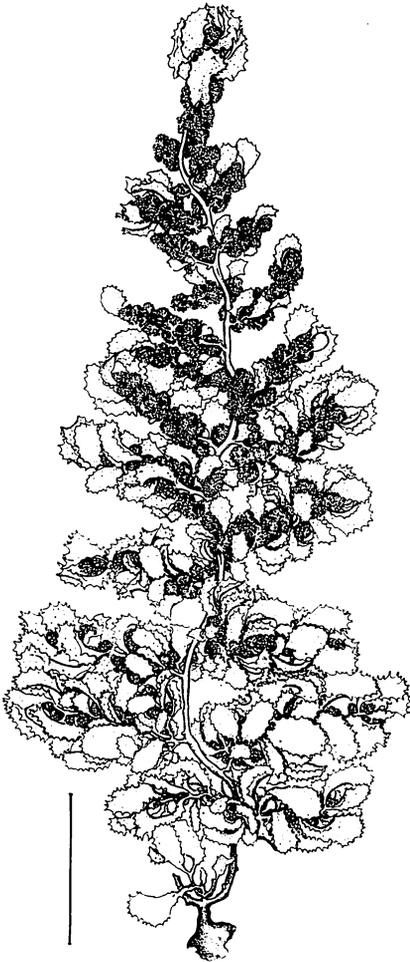


Fig. 1. *Sargassum cristaefolium* C. AGARDH. Pago Bay, Guam I. June 18, 1984. leg. T. YOSHIDA. Scale, 5 cm.

pools to the subtidal zone, about 2 m deep. Young plants appear in autumn and become mature in next spring to summer. The stem is less than 1 cm in length and 2–4 mm in diameter, usually without branching. The length of main branches of shallow water plants, measuring 10–20 cm, is shorter than that of deep water plants, measuring 20–40 cm. In some cases, the shortest length of main branches, measuring 5–10 cm is found in plants which are exposed to air during the ebb tide.

The developmental process of *S. cristaefolium* is schematically shown in Fig. 2. In

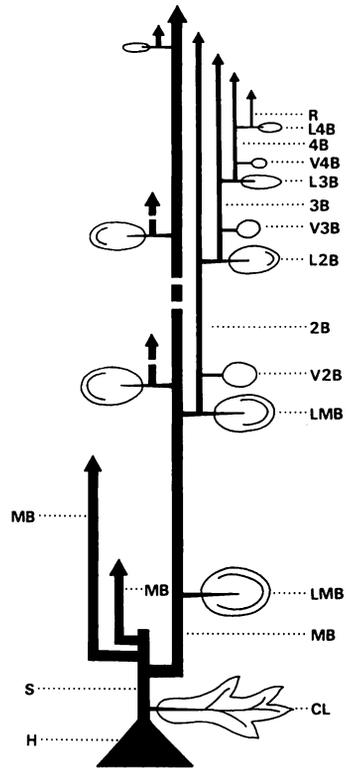


Fig. 2. Developmental process in *Sargassum cristaefolium*. H, holdfast; CL, cauline leaf; S, stem; MB, main branch; LMB, leaf of main branch; 2B, second branch; L2B, leaf of secondary branch; V2B, vesicle of secondary branch; 3B, tertiary branch; L3B, leaf of tertiary branch; V3B, vesicle of tertiary branch; 4B, fourth order branch; L4B, leaf of fourth order branch; V4B, vesicle of fourth order branch; R, receptacle.

younger stages, several furcate cauline leaves without marginal duplications are formed in the early season of growth. Subsequently, main branches are issued in spiral order from lower to upper parts of the stem. After the development of main branches, cauline leaves fall off. Main branches on the stem become longer, although those on the upper part of the stem remain short in length. One to five leaves in the proximal parts of the branches do not issue the branches of next order. From lower middle to middle parts of main branches, secondary branches are issued in the axils

of leaves of main branches with vesicles and leaves of secondary branches, then tertiary branches, vesicles and leaves of tertiary branches, branches of fourth order, vesicles and leaves of fourth order and receptacles successively. However, in the upper parts of main branches, younger secondary branches with its small vesicles and leaves are formed, usually without further development of next order branches. Vesicles are totally absent on main branches. Vesicles are also absent on secondary branches arising from lower parts of main branches. One or two vesicles replace the leaves formed at the proximal parts of secondary and higher order branches. As far as we have examined, well grown individuals have branches of fourth order in deep water habitats. These plants denude leaves of main branches from lower to middle parts of main branches after initiation of axillary branches. However, leaves of main branches mostly remain in the distal parts.

Width of main branches is always two times larger than that of secondary branches according to their positions on plants. The same relations are found between secondary and tertiary branches, and so on. Likewise, size diminution occurs in leaves and vesicles of branches concerned. At the end of growing season, fifth order branches in the lower parts of fourth order branches and fourth order branches in the lower parts of tertiary branches are normally transformed into receptacles in deep water plants, but fourth order and tertiary branches can be changed into receptacles in shallow water and exposed plants. Receptacles are nearly uniform as for size and furcation even in the plants growing in different habitats. These are always androgynous irrespective of plant size and habitats.

Grades of development of branches, leaves and vesicles are arbitrarily classified into five steps (Fig. 3). Grade 4 means the highest limit of variations or maximum state of development and grade 0 represents the lowest limit of variations or minimum

state of development for these three parts of the plants. Between grades 4 and 0, grades 3, 2 and 1 indicate gradation of morphological development. Whole range of variations is found along main branch (grades 4-0), while on secondary branch lesser range is seen (grades 3-0). Similarly, tertiary (grade 2-0) and fourth order (grades 1-0) branches have narrower range of variations according to their positions on plants. Such a tendency in gradual changes of morphological characters also occurs in leaves and vesicles depending on ages of plant and its habitats.

The highest limit of variations or maximum developmental grade of main branch development is always observed at the proximal parts of early formed main branches from younger to older stages of the plants collected from every habitat. However, as for leaves and vesicles, developmental grade 3 is firstly formed in younger stages of plants. Later, as the plants are getting older, these grades 3 in leaves and vesicles gradually develop into the highest grade of variations (i.e. grade 4). These gradual developmental changes normally occur in individual leaf and vesicle as affected by ages and ecological conditions. The extent of these changes in each leaf and vesicle are more eminently observed than in the proximal parts of main branches.

As shown in Fig. 3A, proximal parts of main branches, which are issued from the lower parts of the stem, are ancipital (i.e. grade 4) but lower middle to upper part of main branches are usually compressed to terete without ridges (i.e. grades 3-0). However, according to the relative position on the stem, proximal parts of later issued main branches become compressed without ridges (i.e. grades 3-0). Simultaneously, gradual changes of morphology (i.e. grades 3-0) are also found on secondary, tertiary and fourth order branches from lower to upper parts of plants. In this case, secondary and tertiary branches are mostly compressed but fourth order branches are usually terete. Issuing of secondary, ter-

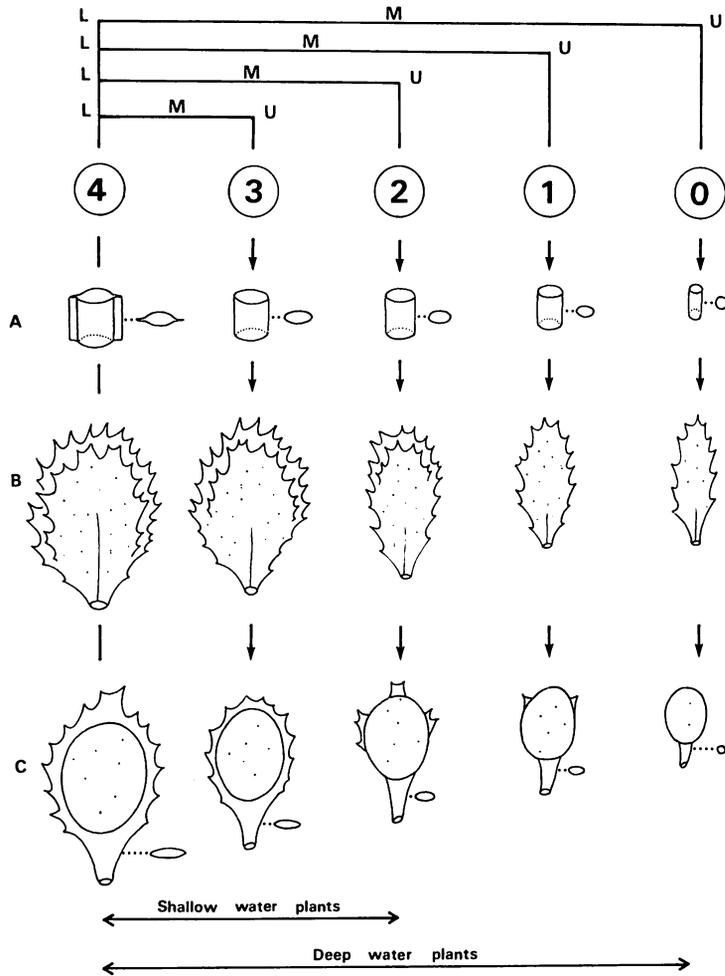


Fig. 3. Gradual changes of morphology in *Sargassum cristaeifolium*. Grades (4-0). L, lower; M, middle; U, upper.

tiary and fourth order branches are affected by their life time and environmental factors. Moreover, even in a single plant, fewer branches of higher order are produced on main branches which are issued later than those formed in earlier season.

Heterophylly observed is shown in Fig. 3B. Leaves in the lower parts of main branches are thick, concave at the surface and strongly curved upwards, bifariously dentate and spatulate to oblong in shape with marginal duplications starting from lower middle portions of blades on each side. This state is called here as grade 4 while those on the upper parts of main

branches become smaller and thinner, irregularly serrate and oblong to lanceolate in shape without marginal duplications (i.e. grades 1-0). Gradual changes of leaf morphology (grades 3-0) are also found on leaves of secondary, tertiary and fourth order branches. Morphological variations of leaves in shallow water plants (i.e. grades 4-2) have lesser range than those of deep water plants (i.e. grades 4-0).

Interval of leaf formation or the length of internode depends on depths where the plants grow. The length of the internode is usually shorter in plants of shallow water or exposed habitats while relatively longer

in deep water plants. Distinction of midrib in leaves depends on ages of plants. The midrib reaches to the middle portion of blade in older leaves but only to the lower part of blade in younger leaves.

Fig. 3C represents the morphological range of vesicles. Vesicles of secondary branches formed in the lower middle parts of main branches are bigger and usually have small lateral appendages (i. e. grade 4) but those of secondary branches disposed in the upper parts of main branches become smaller in size and have no lateral appendage (i. e. grade 0). Apices of well grown vesicles are slightly mucronate but vesicles of grade 0 are always mutic at the apex. And also, stipes of the higher grade vesicles are mostly flattened but those of the lower grades are normally compressed to terete. Similar gradual changes of morphology (i. e. grades 3-0) occur on vesicles of tertiary and fourth order branches.

The main characteristics of *S. cristae-folium* can be summarized as follows:

- (1) Main branches are slightly flattened to compressed with or without ridges at the basal parts, 10-40 cm in length and 2-4 mm in width.
- (2) Leaves are spatulate, oblong to lanceolate in shape, 10-20 mm in length, 10-20 mm in width, mostly concave at the surface and strongly curved upwards, duplicate to simple, shortly stipitate with symmetrical base, evanescent midrib vanishing at the middle way to the apex, bifariously dentate to irregularly serrate margins and obtuse to acute apex.
- (3) Vesicles are mostly elliptical in shape with or without small appendages, 3-10 mm in diameter with slightly mucronate or rounded tips and flattened, compressed to terete stipes of 1/2-1/3 length of vesicles.
- (4) Receptacles are androgynous, cymosely arranged, compressed, loosely twisted with small spines, irregularly forked, 5-10 mm in length and 0.5-1.0 mm in width with a short sterile stipe.

Discussion

The developmental process of the plant body (thallus) in *S. cristae-folium* is fundamentally similar to that of *S. piluliferum* (TURNER) C. AGARDH, *S. patens* C. AGARDH, *S. duplicatum* J. AGARDH, *S. cristipifolium* YAMADA and *S. asymmetricum* YAMADA reported by TERAWAKI *et al.* (1982, 1983a, b, c, 1984). At early stages of development of germlings, simple cauline leaves are formed and then furcate cauline leaves appear in all these species. Later, main branches replace the cauline leaves at certain stage of development. The phenomenon of apical dominance, as mentioned by CHAMBERLAIN *et al.* (1979) for *S. muticum* (YENDO) FENSHOLT, may control the development of next order branches. In other words, the upper limits of morphological development of branches, leaves and vesicles are closely related with the position of each part of the plants. Growth in length of branches, also depends on habitat conditions.

In shallow or rough water habitats, the plants have shorter main branches, giving rise to poorly developed short secondary and tertiary branches. Maximum to minimum grades of development of each part cannot be easily seen in these plants. In deep or calm water habitats, main branches grow generally longer and give rise to longer secondary and tertiary branches often provided with short fourth order branches. Leaves of the lower parts of main branches are quite different from those of the upper parts in morphology. All grades of gradual changes in leaf morphology are observed. That is to say, heterophylly is more conspicuous. On the other hand, leaves of fourth order branches are quite similar in shape to leaves of fifth order branches. A narrower range of leaf morphology is noticed on the branches of higher orders. The same phenomena are also found in branch and vesicle characteristics.

Based on these observations, ranges of gradual changes of morphology in branches, leaves and vesicles are diagrammatically

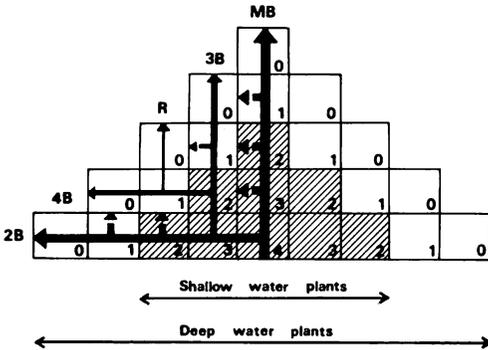


Fig. 4. Scheme of gradual changes of morphology in *Sargassum cristaefolium*. Hatched area shows shallow water plants. Grades in numerals 4-0. MB, main branch; 2B, secondary branch; 3B, tertiary branch; 4B, fourth order branch; R, receptacle.

expressed in Fig. 4. For instance, in well grown deep water plants, highest limit of variations or maximum developmental grade (i. e. grade 4) can be seen in the proximal parts of main branches which are issued earlier in growth season. The lowest limit of variation or minimum developmental grade (i. e. grade 0) is found in the distal parts of main, secondary, tertiary and fourth order branches. Grade 3 is formed in the lower middle of main and lower parts of secondary branches. Intermediate grade 2 occurs in the middle parts of main, lower middle parts of secondary and lower parts of tertiary branches. Similarly, grade 1 can be found in the upper parts of main, secondary, middle portions of tertiary and lower parts of fourth order branches. However, in plants grown in shallow water, range of developmental grades (i. e. grades 4-2) is less than that (i. e. grades 4-0) of deep water plants. In general, variation of deep water plants with older main branches exhibits widest range of developmental grades.

In some cases, it is very difficult to obtain complete specimens. And also, maximum developmental grade cannot be observed at the end of growing season because the first formed leaves on main branches have fallen off during the growth. The gradation of

developmental stages from grades 0 to 4 must be clearly recognized as for branches, leaves and vesicles as well as their relation with habitats. For each species, the whole range of morphological variations must be known and recorded from various geographical areas of its distribution in understanding a species limit. Without this process, circumscription of taxa remains always insufficient and comparison of population from different geographical areas would be incomplete. Hence, the advance of taxonomic knowledge cannot be expected.

Acknowledgements

The first author (U. S. H.) is indebted to the Ministry of Education of the Socialist Republic of the Union of Burma for making this study possible at Hokkaido University under UNDP BUR/74/017. He wishes to express his heartiest thanks to Dr. U MIN-THEIN for his helpful suggestion and criticism in the studies of *Sargassum*.

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ウ スートン*・吉田忠生**： 褐藻トサカモク *Sargassum cristaefolium* の形態変異について

トサカモク *Sargassum cristaefolium* C. AGARDH の個体発生の過程を栄養体と生殖器官の発達について記述した。枝，葉，気胞の形態的な変異の範囲は個体の齡と生育場所によって定まる。これら体の3部分のそれぞれについて形態の単純なものからよく発達したものまで5段階に分け，生育場所や発育段階によってどの段階の形質を示すかを明らかにした。生殖器床は比較的変異が少ない。（* Department of Marine Sciences, Moulmein University, Moulmein, Burma ** 060 札幌市北区北十条西8丁目 北海道大学理学部植物学教室）

Change of Office and Editor

The new Editor of the Japanese Journal of Phycology for 1987-1988 is Yoshihiro Tsubo of Kobe University. Starting in January 1987, manuscripts for publication should be submitted directly to the Editor, **Prof. Y. Tsubo, Department of Biology, College of Liberal Arts, Kobe University, Nada, Kobe, 657 Japan.**

Membership dues should be sent to **The Business Center for Academic Societies Japan, 4-16, Yayoi 2-chome, Bunkyo-ku, Tokyo, 113 Japan** and all other inquiries should be made to **The Japanese Society of Phycology, c/o. Division of Tropical Agriculture, Faculty of Agriculture, Kyoto University, Kyoto, 606 Japan.**

Tylopus (Gigartinales, Rhodophyceae), a genus known in Australia and Japan, newly recorded in South Africa

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NORRIS, R. E. 1986. *Tylopus* (Gigartinales, Rhodophyceae), a genus known in Australia and Japan, newly recorded in South Africa. Jap. J. Phycol. 34: 282-286.

Recent studies on *Tylopus* have shown that all species except the type and one from Japan have been transferred to *Gracilaria*. Plants found in Natal, which are gametophytic, have characters similar to the type species, *T. obtusatus*. Distribution of this species was restricted to southern Australia but the discovery of it in Natal has extended its distribution across the Indian Ocean. This is the first record for any species of the Dicranemaceae in Africa.

Key Index Words: Dicranemaceae; Gigartinales; red algae; Rhodophyceae; South African algae; *Tylopus*.

Coriaceous blade-like thalli characterize the genus *Tylopus* J. AGARDH (1876), the irregularly divided blades, usually repent, arising from a basal prostrate section that is attached by peg-like outgrowths from the lower surface. These outgrowths give the thallus an essentially dorsi-ventral habit that is also reflected in the reproductive structures on the monoecious gametophytes that have male structures only on the upper surface and female reproductive structures on the lower side (KRAFT 1977a). The thallus medulla is comprised of large thick-walled, angular cells and the cortex of smaller cells growing in short filaments perpendicular to the thallus surface. Characteristics of the female reproductive system have been studied by KRAFT (1977a) for the type species, *T. obtusatus*, revealing that its structure is different from the Gracilariaceae, where it had been placed by KYLIN (1932, 1956), and that it has characteristics similar to the Dicranemaceae of the Gigartinales. The production of zonate tetrasporangia in *Tylopus obtusatus* also reinforces the removal of *Tylopus* from the Gracilariaceae, a family in which cruciately divided

tetrasporangia are always produced. KRAFT (1977b) reviewed the present status of *Tylopus*' systematics revealing that besides the type species only one other species, *T. lichenoides* OKAMURA (1921), from Japan, remains in the genus.

Tylopus obtusatus is found on Australia's southern coast but has not been previously discovered outside that region. A few specimens of this species have been found amongst Dr. M.A. POCOCK's Natal collections of marine algae, thereby extending the range of the species across the Indian Ocean to the shores of Africa. Furthermore, the family, Dicranemaceae, has not been previously recorded on the African shores.

Materials and Methods

Three specimens of *Tylopus obtusatus* are in Dr. POCOCK's herbarium at the Albany Museum in Grahamstown (GRA). One specimen (Pocock no. 9675) was collected in the drift at Richard's Bay (17 Oct. 1951) and the other two are from an intertidal collection at Crayfish Point, St. Lucia Rocks (20 Oct. 1951, Pocock nos 9800 & 9860).

Dr. POCKOCK made a drawing of one specimen before it was mounted on the herbarium sheet, clearly depicting the prostrate proximal part of the thallus and the peg-like outgrowths that attach the plant. Because only herbarium specimens are available of this species all side preparations were prepared by sectioning fragments of dried thalli, soaking the sections in water and then staining in a 1% aniline blue, 20% Karo mounting medium.

Results and Discussion

The thalli of the Natalian *Tylopus* are subdichotomously branched, up to eight centimeters long and the branches are up to approximately one centimeter broad except in distal regions where some of them expand to two centimeters (Fig. 1). The thallus margins are irregularly crenate and thickened in distal regions but are entire and unthickened in proximal parts (Fig. 1).

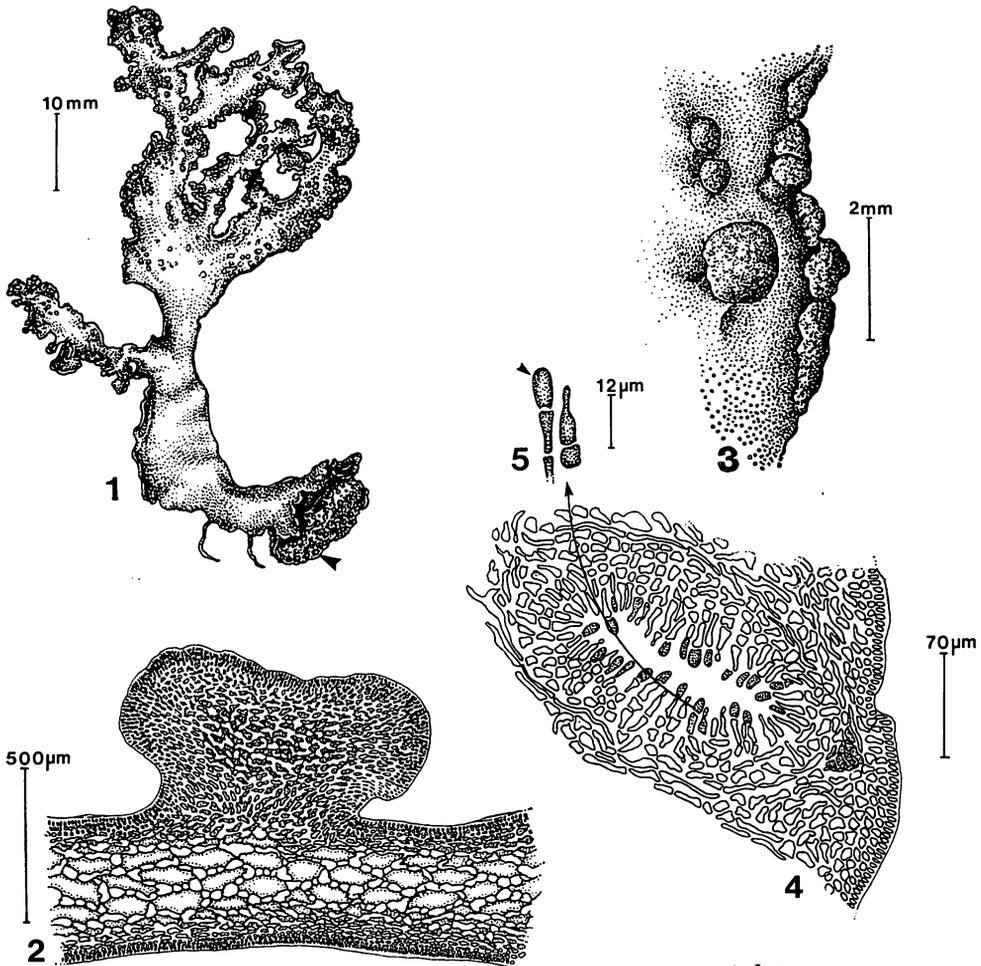


Fig. 1. Habit of *Tylopus obtusatus* from Natal (GRA, Pocock No. 9800). Note rhizomatous and peg-like outgrowths (large arrow-head) from the lower side of the thallus. Fig. 2. Section of thallus showing a surface protuberance on which are borne carpogonial branches (not shown). Fig. 3. Surface view of thallus showing surface protuberances, the largest contains a cystocarp. Fig. 4. Cellular details of a single locule in a cystocarp in which short gonimoblast filaments terminate in single carposporangia. Fig. 5. Detail of the terminal part of two adjacent gonimoblast filaments from Fig. 4 (arrow) showing a young carposporangium (small arrow-head).

In section the thalli are up to 500 μm thick and comprised of large pseudoparenchymatous medullary cells that measure up to $50 \times 125 \mu\text{m}$ and smaller cortical pseudoparenchyma cells that are covered by an outer cortex of small cells, 5 μm in diameter (Figs. 1 and 2). Cell walls of medullary and inner cortical cells in mature parts of thalli are very broad in section, measuring up to 15 μm thick (Fig. 2).

The vegetative structure and form of the South African plants is similar to the type species of *Tylopus*, *T. obtusatus* (SONDER) J. AGARDH (1876). The only other species of *Tylopus*, *T. lichenoides* OKAMURA (1921) has not been studied from the point of view of KRAFT's recent analysis of *Tylopus*, but if the Japanese plant is a *Tylopus*, its shorter, somewhat broader branches indicate that it may be a species separate from *T. obtusatus*. KRAFT (1977a), however, noted that some Australian plants sometimes are similar to the form described for *T. lichenoides*.

All of the plants in the Natal collection are gametophytes, two of them producing cystocarps. KRAFT (1977a) noticed a dorso-ventral arrangement of male and female reproductive cells in the Australian thalli, the males being produced on the 'upper' surface and female reproductive structures on the 'lower' side of the thallus. Natalian plants produce carpogonial branches in protuberances (Figs. 2 and 3) on the thallus upper surface and clusters of male reproductive organs, as illustrated by KRAFT (1977a), have not been found. Instead, in the Natalian thalli, what appear to be male reproductive cells are borne singly on outer cortical cells in scattered irregular positions on either surface of the thalli. Many carpogonial branches are formed in the large protuberances each having three cells that are laterally attached to a subcortical cell, the supporting cell. All of these cells have a denser protoplasmic material than the surrounding cells of the cortex giving a slightly darker stain in the sections. KRAFT (1977a) gave convincing evidence that the reproductive system is procarpic, the sup-

porting cells functioning as auxiliary cells, and my observations support his conclusion. Sometimes several fusion cells in a protuberance were found in the Natal plants indicating, presumably, that multiple fertilizations or possibly diploidizations have taken place. A section through cystocarps shows a highly convoluted gonimoblast causing an eruption above the protuberance surface but in some cases it seems that adjacent cystocarps have fused into one on the protuberance. Gonimoblast filaments form a thin layer of tissue lining the cavities of the cystocarp (Fig. 4), producing upright short filaments that terminate in single carposporangia (Fig. 5). The cavities in the cystocarps are narrow and it could not be determined whether or not they form a continuous system. A definite ostiole has not been observed on cystocarps of the Natal plants although they were observed in those from Australia. Cystocarps often become eroded thereby releasing the carpospores.

Tetrasporophytes have not been found in South Africa.

KRAFT (1977a, b) characterized *Tylopus* as the only pseudoparenchymatous and procarpic member of the Dicranemaceae. KRAFT placed the genus in this family, removing it from the Gracilariaceae where KYLIN (1956) had placed it, because of early stages in growth of the gonimoblast as well as tetrasporangial and male reproductive characteristics. He also noted that the single terminal carposporangia and the hemispherical-shaped cystocarps are characteristic of Dicranemaceae. Cystocarps on Natal specimens have the hemispherical-shaped structure with a continuous narrow lumen above the gonimoblast in early stages of development. Older cystocarps become more protuberant, sometimes being almost spheroidal, and the gonimoblast becomes highly convoluted forming narrow cavities that probably are continuous throughout the cystocarp but this could not be determined with certainty. KRAFT showed a convoluted gonimoblast in his figures of *Tylopus obtu-*

satus but the configuration is far more extensive and complex in the South African specimens. The presence of carpogonial branches on protuberances in the Natal specimens is different from KRAFT's description of *Tylotus obtusus* from Australia. In addition, there may be a difference in male reproductive structures but this needs to be confirmed with more extensive collections in Natal. Neither of these differences seems to be reason, at the present time, to establish a new species for the South African plants, especially because the general structure of the thalli is similar to the Australian type species.

Comparison of *Tylotus obtusatus* with species in the genus *Curdiea* are of interest because of the strong similarity between the two genera in vegetative structure and in form of cystocarps. Both genera have thickly coriaceous subdichotomously branched thalli. I have compared the Natalian specimens of *Tylotus* with the numerous specimens of several species belonging to *Curdiea* that I collected in Australia, specimens that are now in the Herbarium of the University of Natal. *Curdiea* is not a well-known genus but seems to belong in the Gracilariaceae, probably quite closely related to *Gracilaria* (*sensu* FREDERICQ and NORRIS 1985). My examination of specimens has shown that the two genera can be separated on the following characters: 1) thalli of *Tylotus* attach by specialized peg-like outgrowths whereas *Curdiea* attaches by a tightly adherant discoid holdfast; 2) the large medullary cells of *Curdiea* have moderately thick walls, not clearly discrete for each cell, that often have calcite granules between them as well as many secondary pit connections with adjacent cells, but these large cells in *Tylotus* have fewer pit connections and thicker discrete walls that never seem to have calcite granules between them; 3) the cortex of *Curdiea* has many small cells in rows perpendicular to the thallus surface but in *Tylotus* the cortex is relatively thin, consisting of only a few (1-4) cells in a series; 4) cystocarps of

Curdiea are spheroidal, the gonimoblast radiating from a basal mass of pseudoparenchyma and carposporangia occurring in long chains; in *Tylotus* cystocarps are hemispherical to spheroidal the gonimoblast forming an invasive core of pseudoparenchyma (branched in older cystocarps and perhaps with vegetative tissue) into the center of the cystocarp, the tissue becoming convoluted and the cavities lined with short gonimoblast filaments that terminate in single carposporangia. In addition, tetrasporophytes of the two genera can be distinguished by the zonately divided sporangia in *Tylotus* contrasted with the cruciately divided sporangia in *Curdiea*.

Acknowledgements

The staff of Albany Museum Herbarium, particularly Mrs. E. BRINK and Dr. A. JACOT-GUILLERMOD, kindly allowed me to examine and borrow some of Dr. MARY AGARDH POCOCK's extensive algal collections which has resulted in the discovery of many interesting species. I am grateful to them for their assistance. Funding for this research is from the CSIR, Pretoria, which is gratefully acknowledged. My thanks are also extended to Professor R.N. PIENAAR for his support of these studies as well as to the Botany Department, University of Natal, Pietermaritzburg, for the excellent facilities provided. I am also grateful to Dr. M.E. AKEN for technical assistance in the study of the POCOCK specimens and to Mrs. OLIVE ANDERSON for her artistic expertise.

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ノリス, R. E.: ナミイワタケ属 (紅藻スギノリ目) 藻類 南アフリカに産す

ナミイワタケ属 *Tylopus* に関する近年の研究により, 本属のタイプと日本産の1種を除き, 本属にいれられていた種は全てオゴノリ属 *Gracilaria* に移された。南アフリカのナタル産の標本(配偶体)を調べたところ, この藻体はタイプ標本 (*T. obtusatus*) と同じ特徴を備えていることが明らかになった。本種の分布は南部オーストラリアに限られるとされていたが, 本研究の結果, その分布域はインド洋を越えて南アフリカにまで及ぶことになる。これは, また, アフリカにおける Dicranemaceae 藻類の最初の記録である。(南アフリカ ナタル大学 植物学教室)

The taxonomy of *Protectocarpus speciosus* (BØRGESEN) KORNMANN (Myrionemataceae, Phaeophyceae)

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TANAKA, J. 1986. The taxonomy of *Protectocarpus speciosus* (BØRGESEN) KORNMANN. Jap. J. Phycol. 34: 287-292.

Protectocarpus speciosus collected from Pacific coasts of northern Honshu was fully described and illustrated. This alga is characterized mainly by the unilaterally branched plurilocular reproductive organs and heterotrichous thallus. *Protectocarpus speciosus* was designated as the lectotype of this genus for the first time. Taxonomic relationship of the genus *Protectocarpus* in the Ectocarpaceae *sensu lato* was discussed. This is the first report for the occurrence of this genus and species in Japanese waters.

Key Index Words: Ectocarpaceae; Myrionemataceae; Phaeophyceae; *Protectocarpus speciosus*; taxonomy.

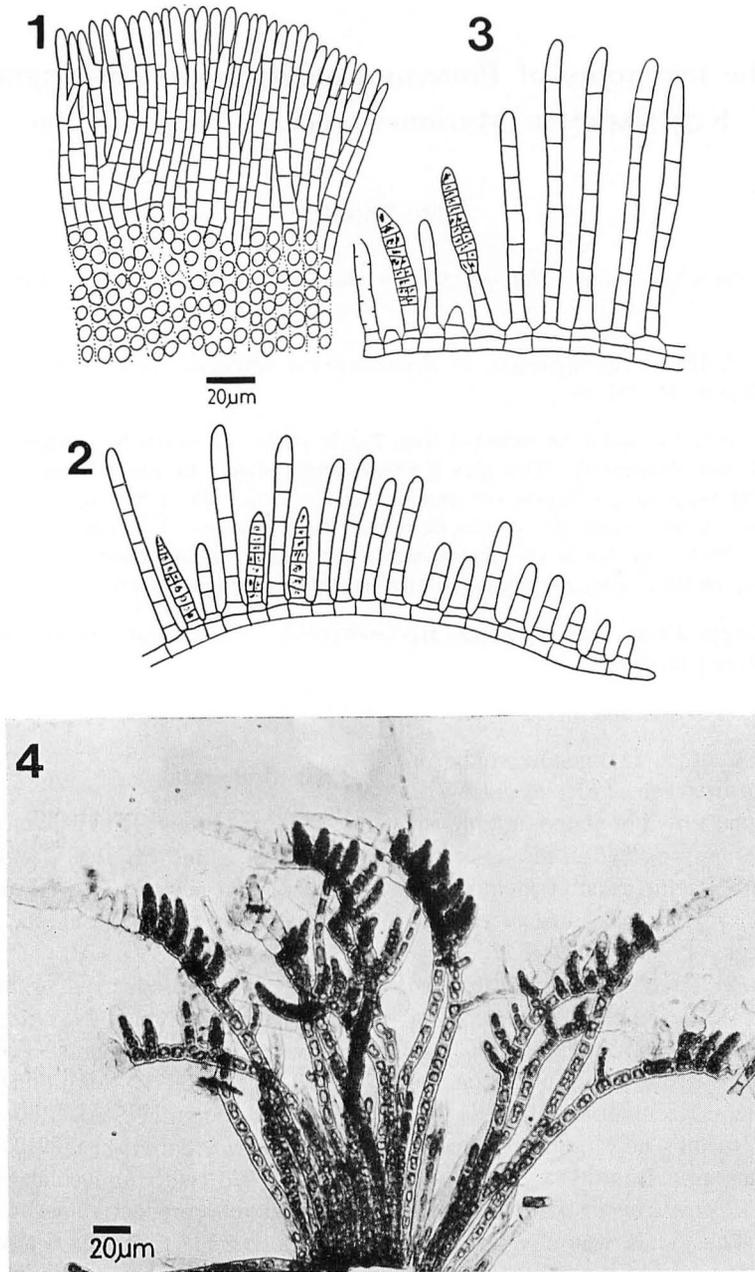
In the course of a taxonomic study on Japanese Ectocarpaceae, *Protectocarpus speciosus* was found growing abundantly on the marine spermatophyte *Phyllospadix iwatensis* along the north Pacific coast of Japan. The genus has not previously been reported from Japanese waters.

The genus *Protectocarpus* was established by KORNMANN (1955), chiefly on the basis of *Myrionema speciosum* BØRGESEN (1902), a species described from the Faeroes in the North Atlantic. Kornmann referred two other species to his new genus, namely, *Myrionema faeroense* BØRGESEN (1902) and a new species, *Protectocarpus hecatonemoides* KORNMANN. The genus was characterized as having heterotrichous thalli with unilaterally branched plurilocular reproductive organs.

The present paper describes in detail the morphological features of *Protectocarpus speciosus* collected in Japan, compares them with those of *P. speciosus* from Europe and the other species in the genus, and discusses the systematic position of the genus.

Collection Data

1. Cape Shioya, Fukushima-ken (37°00'N, 140°58'E), June 14, 1983 (with plurilocular reproductive organs) TNS-AL-5020 (in liquid).
2. Togawa, Choshi-shi, Chiba-ken (35°42'N, 140°52'E), May 2, 1981 (with plurilocular reproductive organs) TNS-AL-5166 (in liquid); June 14, 1980 (with plurilocular reproductive organs) TNS-AL-5167 (in liquid); June 5, 1977 (with plurilocular reproductive organs) TNS-AL-5166 (in liquid).
3. Ooarai, Ibaraki-ken (36°20'N, 140°38'E), Apr. 4, 1976 (with unilocular sporangia and plurilocular reproductive organs, mixed with *Giffordia sandriana* and *Ectocarpus confervoides*) TNS-AL-5173 (in liquid).
4. Akahama, Ootsuchi-cho, Iwate-ken (39°21'N, 141°55'E), March 19, 1985 (with plurilocular reproductive organs) TNS-AL-5235, 5240 (in liquid); March 1, 1986 (with plurilocular reproductive organs, mixed with *Rhodophysema* sp.) TNS-AL-5337.
5. Tanohama, Yamada-cho, Iwate-ken (39°24'N, 141°59'E), May 17, 1985 (with plurilocular reproductive organs) TNS-AL-



Figs. 1-4. *Protectocarpus speciosus*. Fig. 1. Surface view at the margin. Fig. 2. Vertical view, showing basal disc with one cell-layer and plurilocular reproductive organs directly upon basal filaments. Fig. 3. Vertical view, showing basal disc with two cell-layers. Fig. 4. Vertical view of thallus with mature and empty plurilocular reproductive organs.

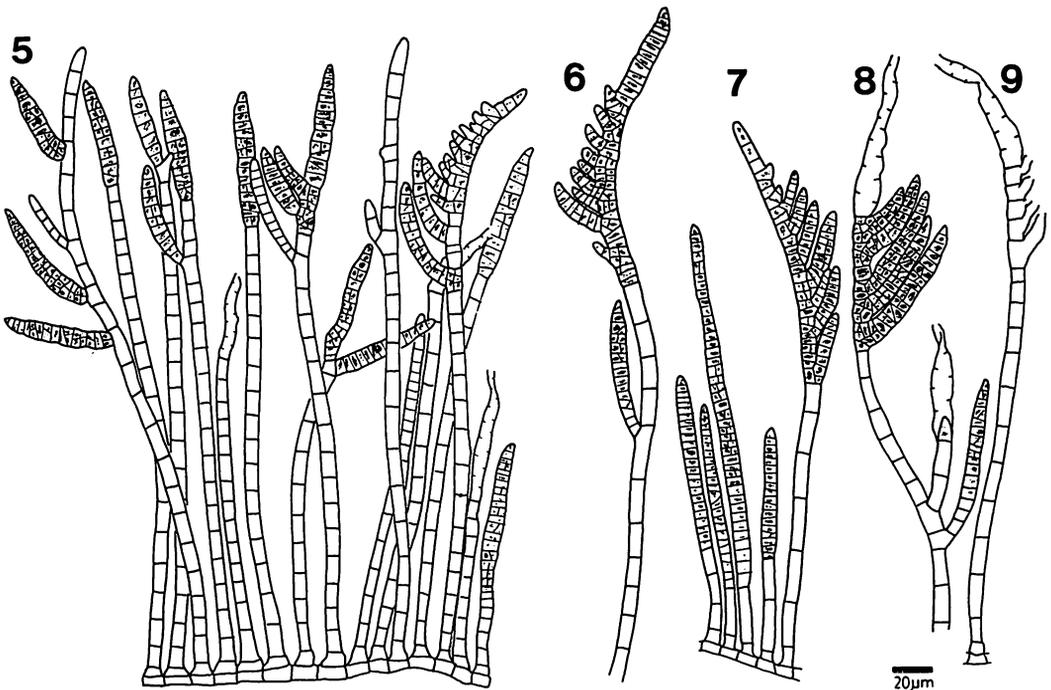
5267, 5271 (in liquid).

Description of *Protectocarpus speciosus* as found in Japan

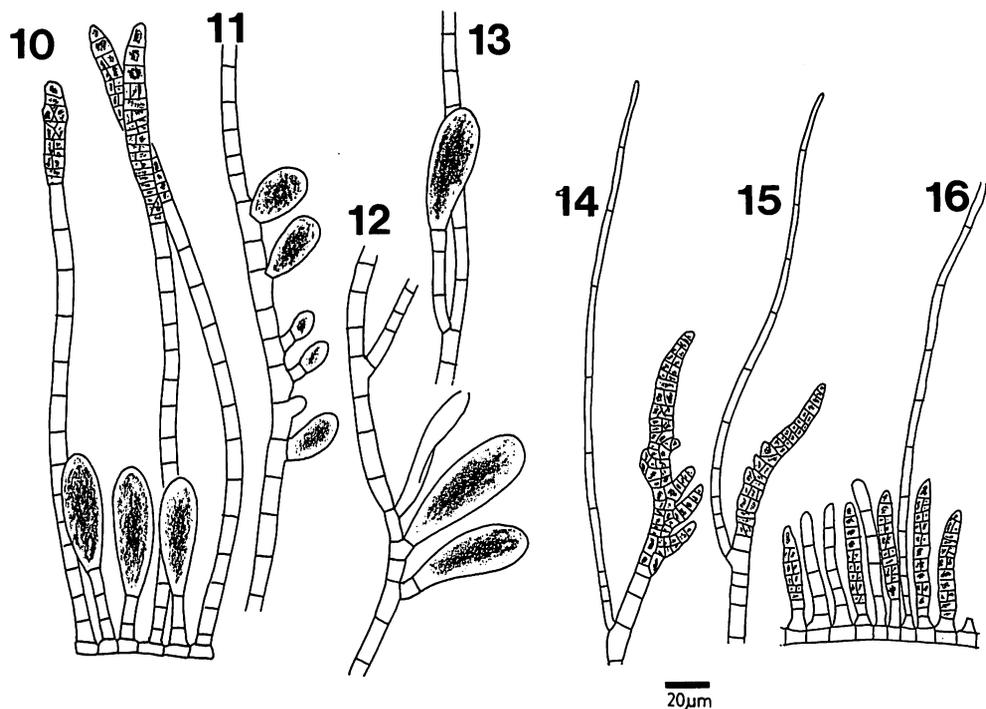
Thalli epiphytic on *Phyllospadix iwatensis*, dark brown, forming rounded patches 2–4 mm in diameter, sometimes overlying one another and becoming irregular in outline, showing marginal growth with a distinct marginal line, heterotrichous, consisting of a basal disc and erect filaments (Fig. 1); basal disc expanding over the surface of the substrate usually monostromatic but sometimes distromatic in the central part, composed of basal filaments (Figs. 2 and 3); basal filaments dichotomously branched, radiating from the center, sticking to one another to form a pseudoparenchymatous tissue; cells of basal filaments 5–10 μm high and 10–18 μm wide, apical cells at margin 15–20 μm long (Fig. 1).

Erect filaments 300–800 μm high, developed from center of basal disc and gradually decreasing in height to the margin, free from one another, usually unbranched but sometimes sparsely branched near the apex, each composed of 15–28 cells, the basal cell flattened, other cells 7.5–9 μm in diameter and 1–2.5 times as high as broad (Figs. 4 and 5).

Plurilocular reproductive organs and unilocular sporangia often borne on the same thallus of the materials from Ibaraki-ken. Plurilocular organs formed in four patterns: (1) directly upon basal filaments (Fig. 2); (2) terminally on short erect filaments (Figs. 3 and 7); (3) laterally from the upper portion of erect filaments (Figs. 6 and 8); and (4) terminally on upper part of erect filaments (Figs. 6 and 7). In the first to third cases, the organs cylindrical, 100–220 μm long and 10–12 μm in diameter, and in the fourth case, second with unilateral upwardly curved



Figs. 5–9. Vertical view of *Protectocarpus speciosus*. Fig. 5. Thallus with plurilocular reproductive organs. Fig. 6. A unilaterally branched plurilocular reproductive organ terminally on upper part of erect filaments, also showing laterally produced one. Fig. 7. Plurilocular reproductive organs terminally on short erect filaments and a unilaterally branched organ terminally on upper part of erect filament. Figs. 8 and 9. Empty plurilocular reproductive organs, showing apical pores.



Figs. 10-16. Vertical view of *Protectocarpus speciosus*. Fig. 10. Unilocular sporangioborne terminally on short erect filaments associated with plurilocular reproductive organs. Fig. 11. Unilocular sporangia borne laterally on erect filament. Fig. 12. Unilocular sporangia with and without stalk, borne laterally on erect filament, also showing empty one with an apical pore. Fig. 13. Unilocular sporangium with stalk. Figs. 14 and 15. Hairs arising just below the plurilocular reproductive organs. Fig. 16. Hair arising on basal disc.

branches, 50-160 μm long and 40-60 μm wide (Figs. 6 and 7); swarmers releasing from a few apical pores in each organ (Figs. 4, 8-9).

Unilocular sporangia formed in several positions: (1) directly upon prostrate filaments; (2) terminally on short erect filaments (Fig. 10); (3) laterally on erect filaments with or without short stalk cells (Figs. 11-13), ellipsoidal, 17-23 $\mu\text{m} \times$ 50-75 μm ; swarmers releasing from an apical pore (Fig. 12).

Hairs arising from thallus in two positions: (1) laterally on erect filaments always just below plurilocular reproductive organs (Figs. 14 and 15); (2) directly upon the basal disc (Fig. 16), with or without a basal collar, 5-8 μm wide and 500-800 μm long, gradually attenuated to the apex, meristematic zone of hair situated just above the basal cell (Figs. 14-16).

Chloroplast plate-like, one or a few per cell, scant in hairs.

The present alga grows abundantly on old and often colorless leaves on *Phyllospadix iwatensis* in the lower tidal zones. It is distributed along the Pacific coast of northern Honshu (Chiba-ken, Ibaraki-ken, Fukushima-ken and Iwate-ken). The thallus is often mixed with many other algae; with Ectocarpaceae (*Giffordia sandriana* and *Ectocarpus confervoides*) in Ibaraki-ken and Fukushima-ken; with Myrionematæceae (*Myrionema* sp. and *Halothrix ambigua*), *Papenfusiella kuromo*, *Punctaria* sp. and crustose red algae (*Rhodophyseta* sp. and Corallinaceae) in Iwate-ken. Thalli from Iwate-ken are smaller than those from the other localities listed above and produce no unilocular sporangia, but produce many more hairs.

Discussion

BØRGESSEN (1902) described two new species, *Myrionema speciosum* and *M. faeroense*, from the Faeroes in the North Atlantic. Subsequently, these species were assigned to other genera in the Ectocarpaceae or the Myrionemataceae, namely, *Ectocarpus*, *Comptonema* and *Hecatonema*. In his handwritten manuscript, KUCKUCK (1955, published posthumously under the editorship of KORNMANN) recognized that these two species could form a particular group (which he called "Sectio X") of the Ectocarpaceae *sensu lato* because of their peculiarly shaped plurilocular reproductive organs. He added his new (but unpublished) species *Ecotcarpus hecatonemoides* to this group. KORNMANN, when publishing KUCKUCK's manuscript, established a new genus *Protectocarpus* for KUCKUCK's "Sectio X", including in it the three species mentioned above. (Kornmann incorrectly attributed the generic and specific names to Kuckuck, but they should be attributed directly to KORNMANN.) When Kornmann established this genus *Protectocarpus*, he did not indicate any of three species as the type. Now it is reasonable to designate *P. speciosus* as the lectotype of *Protectocarpus* because the generic definition of *Protectocarpus* had been made mostly by the characteristics of *P. speciosus*, as follows:

[*Protectocarpus* KORNMANN 1955, HELGOL.

wiss. Meeresunters. 29: 119. Lectotype: *P. speciosus*]

The present alga has the unilaterally branched plurilocular reproductive organs and heterotrichous habit characteristic of the genus *Protectocarpus*. In Table 1, morphological characteristics of plants from Japan are compared with those of *P. speciosus* from Europe and the other two species of the genus (*P. faeroensis* and *P. hecatonemoides*). This table shows that the Japanese alga is almost identical to *P. speciosus* as described from Europe, the slightly smaller diameter of the erect filaments in Japanese alga being considered a minor difference.

KUCKUCK (1955) did not mention the occurrence of a distromatic basal disc, but one of his illustrations (fig. 4B on p. 126) and my observation of Japanese material made clear that the center of the disc is partly distromatic in this species.

With regard to the systematic position of *Protectocarpus*, there remains still some uncertainty. CARDINAL (1964) included the genus in his monograph of the Ectocarpaceae. PARKE and DIXON (1976) stated that its systematic position was uncertain, but tentatively placed it in the Myrionemataceae. On the basis of presently observed features, it is concluded that *Protectocarpus* is more closely related to the Myrionemataceae than to the Ectocarpaceae *sensu stricto*. These features include (1) a heterotrichous thallus

Table 1. Morphological comparison among the present alga and three taxa of *Protectocarpus*.

	<i>P. speciosus</i> (BORG.) KORNM.	<i>P. faeroensis</i> (BORG.) KORNM.	<i>P. hecatonemoides</i> KORNM.	Present alga
Type locality	Faeroes, Denmark	Faeroes, Denmark	Helgoland, West Germany	
Height of thallus	600-800 μm	-500 μm	300-400 μm	300-800 μm
Diameter of erect filament	8-10 μm	9 μm	7-10 μm	7.5-9 μm
Plurilocular reproductive organs (width \times length)	much ramified 11 \times 40 μm max. 200 μm long	rarely ramified 11-15 \times 40-80 μm max. 150 μm long	rarely ramified 8-10 \times 50-80 μm	much ramified 10-12 \times 100-220 μm
Unilocular sporangia (width \times length)	20-25 \times 30-75 μm lateral & terminal	18 \times 50 μm lateral, rare		17-23 \times 50-75 μm lateral & terminal
Hairs	6-7 μm diam. lateral, rarely terminal		7-9 μm diam. terminal, rarely lateral	7-9 μm diam. lateral & terminal

with the prostrate system and the erect system developing to an equal degree; (2) slender erect filaments (7.5–9 μm in diameter); (3) plurilocular reproductive organs developing not only on erect filaments but also on prostrate filaments; (4) plurilocular reproductive organs in one or two rows; and (5) phaeophycean hairs arising abundantly on both prostrate filaments and erect filaments.

Protectocarpus speciosus occurs on the Pacific coast of Honshu north of Cape Inuboh, Chiba-ken. *Phyllospadix* occurs abundantly on the coast of the Izu Peninsula, which is influenced by the Kuroshio warm current, but *Protectocarpus* could not be found there. Judging from these Japanese distributional data and other data published for this species (CARDINAL 1964, JAASUND 1965, PARKE and DIXON 1976, KORNMANN and SAHLING 1977, YONESHIGUE and OLIVEIRA FIGUEIREDO 1984), *P. speciosus* may be considered a cool-temperate species.

NODA (1969) reported *Compsonea ramulosa* SENCHELL et GARDNER growing on *Pachydictyon coriaceum* or *Padina arborescens* from Sado Island off the middle part of the Japan Sea coast of Honshu. Judging from his description and illustration, his specimen is considered to be the same as the present material of *Protectocarpus speciosus*.

Acknowledgement

The author would like to express special thanks to Prof. P. SILVA for his critical reading of the manuscript and his valuable advice.

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田中次郎：日本産プロテクトカルプス属の1種（ミリオネマ科，褐藻類）の分類

本邦太平洋沿岸の親潮海域（関東—東北地方）より採集されたプロテクトカルプス属の1種 [*Protectocarpus speciosus* (BØRGESEN) KUCKUCK] について記載および分類学的考察を行った。現在までこの属にはタイプが指定されていない。この属に含まれるすべての種を形態的に比較した結果、本種は属の形質を最もよく表していることから、属のタイプとして指定した。本属、種は日本新産である。（160 東京都新宿区百人町 3-23-1 国立科学博物館植物研究部）

A taxonomic study of *Polysiphonia japonica* HARVEY and *P. akkeshiensis* SEGI (Rhodophyta)

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KUDO, T. and MASUDA, M. 1986. A taxonomic study of *Polysiphonia japonica* HARVEY and *P. akkeshiensis* SEGI (Rhodophyta). Jap. J. Phycol. 34: 293-310.

Polysiphonia japonica HARVEY and *P. akkeshiensis* SEGI were studied through their life history stages in laboratory culture. These two species are similar in morphology, growth and reproductive responses to varying temperatures (10-20°C) and photoregimes (16:8LD and 8:16LD). Cultured plants of the two species possessed segments similar in length, which strongly suggests that the taxonomic criteria show phenotypic plasticity; alternative criteria have not been found. It may be concluded that employing morphological features, these two algae are referable to the same taxonomic species. However, artificial hybridization experiments reveal that two virtually non-interbreeding groups separated by various isolating mechanisms exist among ten local populations studied. *Polysiphonia novae-angliae* auct. japon. is included in the species complex studied.

Key Index Words: Life history; *Polysiphonia akkeshiensis*; *Polysiphonia japonica*; *Polysiphonia novae-angliae*; reproductive isolation; Rhodomelaceae; Rhodophyta; taxonomy.

Polysiphonia japonica HARVEY (1856) is one of common species of the genus in Japan (SEGI 1951). This alga is characterized principally by having four pericentral cells, trichoblast-unconnecting branches and cortical cells (SEGI 1951). In a laborious monograph SEGI (1951) reported the following six species sharing these features with *P. japonica*: *Polysiphonia spinosa* (C. AGARDH) J. AGARDH (1842), *P. harlandii* HARVEY (1859), *P. decumbens* SEGI (1951), *P. nipponica* SEGI (1951), *P. novae-angliae* W.R. TAYLOR (1937) and *P. akkeshiensis* SEGI (1951). Except for *P. harlandii* these species have been reported from either a single locality or only a few localities included in the geographical range of *P. japonica*. *P. harlandii* has a more southerly distribution: Taiwan, Hong Kong and Hainan Island (SEGI 1951, TSENG

1983). It is difficult to distinguish these species from each other despite SEGI's (1951) detailed descriptions. Later, NODA described *Polysiphonia grateloupeoides* NODA (1970) and *P. echigoensis* NODA (1975) from single localities, Iwagasaki and Kakumi-hama respectively. These localities are also included in the range of *P. japonica*. These two species are distinguished from *P. decumbens* and *P. harlandii* by only a few features (NODA 1970, 1975). This may require a critical study to elucidate the taxonomic relationship between *P. japonica* and related species.

Polysiphonia japonica and related species have densely ramified, numerous branches and give a bushlike habit. For the *P. japonica* species complex a comparative study through life history stages may be useful to evaluate their taxonomic features as pointed out by DIXON (1963) and exemplified for *Neorhodomela* (Rhodomelaceae) by MASUDA (1982). Little information is

Abbreviations used in the figures. a, apical cell; ab, adventitious branch; cc, cortical cell; ob, ordinary branch; pr, primary rhizoid; sr, secondary rhizoid; tb, trichoblast.

available concerning the vegetative ontogeny of the genus, although life history studies have been reported for several taxa: *Polysiphonia hemisphaerica* var. *boldii* (WYNNE et EDWARDS) RUENESS (as *P. denudata*) (EDWARDS 1968), *P. denudata* (DILLWYN) KÜTZING (EDWARDS 1970, KAPRAUN 1978a), *P. hemisphaerica* ARESCHOUG (RUENESS 1971), *P. ferulacea* SUHR (KAPRAUN 1977), and *P. urceolata* (DILLWYN) GREVILLE (KAPRAUN 1978a). In this paper we present the pattern of morphological development for *Polysiphonia japonica* and *P. akkeshiensis* and the results of hybridization experiments among their cultured strains.

Materials and Methods

Plants were collected at the localities shown in Fig. 1. Date of collection and culture numbers for cultured plants are given in Table 1, although additional samples for morphological study were obtained in each collection, which were fixed and preserved in 10% formalin in seawater. Plants for culture study were transported to the laboratory in sterile seawater in an



Fig. 1. Outline map of Japan indicating collection sites.

insulated chest on ice. Unialgal cultures were established from carpospores, tetraspores or excised branch apices according to the methods described earlier (MASUDA 1982). Spores or apices from individual plants were cultured separately from each other. Thus each strain represents a single individual plant. These were cultured in plant growth chambers illuminated with cool-white fluorescent lamps (2500-3000 lux). The temperatures and photoperiods were regulated in the following combinations: 10°C, 16:8 LD (light and dark cycle); 10°C, 8:16 LD; 15°C, 16:8 LD; 15°C, 8:16 LD; 20°C, 16:8 LD and 20°C, 8:16 LD. The cultures were chiefly maintained at 15°C, 16:8 LD and transferred to other conditions in order to test growth and reproductive responses to varying temperatures and photoregimes.

All cultures were changed to fresh medium every 2 weeks and maintained in glass dishes (71×61 mm or 65×80 mm) containing one-half strength PES. They were not agitated except when female and male crosses were being attempted; these were placed on a Taiyo R-II Rotary Shaker at 90-100 rpm. Clonally cultured fertile female and male plants were crossed to determine interfertility among the strains. Excised small pieces (2-3 cm long) of fertile female and male branches were introduced into single dishes (71×61 mm) and placed on a Taiyo R-II Rotary Shaker at 90-100 rpm in 15°C, 16:8 LD. Crosses were considered positive if cystocarps developed and carpospores were released from the cystocarps. Plants from resulting carpospores were cultured to test their viability and fertility. Crosses in which no carpospores were released were treated as negative and negative crosses were repeated once.

Microscopic examination was carried out on living and liquid-preserved materials. Sections were made by hand using a razor blade and pith stick. Voucher specimens are deposited in the Herbarium of Faculty of Science, Hokkaido University, Sapporo (SAP 047547-047568).

Table 1. Collection data and culture numbers.

Species	Locality	Date	Plants sampled	Reproductive state	Isolation material	Culture number	
<i>P. japonica</i>	Oshoro	4 Feb 84	2	⊕	BA	2373, 2375	
		5 Nov 84	2	⊕	TS	2711, 2712	
			2	♀	CS	2713, 2714	
	Abashiri	2 Jul 83	1	♂	BA	1995	
	Erimo	19 Sep 83		2	♀	BA	2144, 2145
				2	♂	BA	2146, 2147
	Samani	30 Jul 84	1	⊕	TS	2590	
	Kannonzaki	9 Mar 84		2	⊕	BA	2425, 2426
				2	♀	BA	2423, 2424
				2	♂	BA	2422, 2427
	Enoshima	30 May 84	1	♂	BA	2499	
	Shiaku	27 Sep 84		2	⊕	BA	2627, 2633
				1	♀	BA	2628
				2	♂	BA	2631, 2632
	Iwagasaki	8 Oct 83		1	⊕	BA	2203
				2	♀	BA	2204, 2206
				1	♂	BA	2201
<i>P. akkeshiensis</i>	Utoro	1 Jul 83	1	⊕	BA	1993	
		1 Jul 84	3	♀	BA	2571-2573	
			1	♂	BA	2574	
	Akkeshi	28 Jun 83		2	⊕	BA	1978, 1979
				2	♀	BA	1980, 1981
				2	♂	BA	1976, 1977
		30 Jun 84	3	♀	BA	2567-2569	
			1	♂	BA	2570	
		6 Jul 85	1	⊕	TS	2990	
		1	♀	CS	2991		

⊕, plants with tetrasporangia; ♀, plants with cystocarps; ♂, plants with spermatangia; BA, branch apices; CS, carpospores; TS, tetraspores.

Results

Examination of voucher specimens

The specimens identified as *Polysiphonia japonica* and those as *P. akkeshiensis* fit the descriptions for these species given by SEGI (1951). The following features are common to all the specimens examined. The thallus arises from a tuft of densely aggregated rhizoids which are cut off from pericentral cells and cortical cells as separate cells. It has a main axis which bears deciduous

trichoblasts or ordinary branches* of the first order in a spiral manner running in a counterclockwise direction toward the apex from every segment except the lower ones. The ordinary branches are exogenous, replacing the trichoblasts in development, and grow in a manner similar to the main axis. They are divided into progressively

* We use the term 'ordinary branch' for a branch arising from a subapical segment and the term 'adventitious branch' for a branch arising secondarily from another position.

shorter branches and so give a bushlike habit. Each segment has four pericentral cells and is corticated in the older parts. In addition to ordinary branches, two kinds of adventitious branches arise either from axial cells of lower segments of the main axis or from scar cells (basal cells of fallen trichoblasts). The latter branches are known as cicatrigenous branches (HOLLENBERG 1942). Tetrasporangia are spirally arranged in swollen segments of branches. Cystocarps are ovate and have a stalk consisting of a segment. Spermatangial branchlets arise from a primary branch of the trichoblasts, and are nearly cylindrical and have one or two-celled sterile tips. The dimensions of some vegetative and reproductive structures

of the fertile specimens examined are given in Table 2.

The diameters of main axes and length/diameter ratios of segments vary correlatively with thallus length within each species: smaller specimens have more slender axes with shorter segments and larger specimens possess thicker axes with longer segments. Utoro and Akkeshi populations belonging to *Polysiphonia akkeshiensis*, however, have much longer segments than the others: the length/diameter ratios of Utoro and Akkeshi populations range between 2.6 and 4.7, whereas those of other populations vary between 0.4 and 2.6 (Table 2). This difference does not correlate with thallus length: smaller plants of these two populations have

Table 2. The dimensions of vegetative and reproductive structures of ten local populations examined.

Locality	Number of specimens	Thallus length (mm)	Diameter of main axes (μm) ¹⁾	Length/diameter of segment ²⁾	Diameter of tetrasporangia (μm)	Cystocarps Length \times Diam. (μm) (μm)	Spermatangial branchlets Length \times Diam. (μm) (μm)
Oshoro	14	21-57	350-825	1.1-2.3	70-93	300-530 \times 230-460	165-250 \times 50-83
	41	7-25	180-450	1.1-3.1	58-88	240-390 \times 250-490	125-300 \times 53-98
Abashiri	5	60-91	750-1125	1.4-2.1	70-90	280-490 \times 350-540	93-153 \times 40-68
	1	—	—	—	—	—	118-163 \times 53-78
Erimo	14	21-54	375-750	1.1-2.6	73-100	370-700 \times 420-630	115-195 \times 45-68
	1	—	—	—	—	—	115-165 \times 55-80
Samani	9	18-31	550-925	1.2-2.2	60-83	290-560 \times 300-510	90-160 \times 33-53
	5	11-16	460-600	0.9-1.3	55-73	250-360 \times 290-430	145-185 \times 70-90
Kannonzaki	17	7-28	250-775	0.7-1.1	68-93	330-500 \times 390-580	—
	4	7-12	330-600	0.7-1.1	70-103	250-500 \times 260-550	95-253 \times 38-110
Enoshima	8	6-9	220-320	0.8-1.1	60-68	260-410 \times 260-400	—
	1	—	—	—	—	—	125-180 \times 68-90
Shiaku	9	3-15	150-360	0.6-1.2	63-75	—	80-160 \times 30-58
	5	15-19	350-460	1.0-1.2	65-88	250-420 \times 280-480	155-240 \times 63-75
Iwagasaki	28	4-12	170-430	0.4-1.4	65-103	210-430 \times 200-420	103-183 \times 30-63
	7	9-17	170-330	1.3-2.4	65-88	190-410 \times 230-470	123-283 \times 53-95
Utoro	5	40-56	600-700	2.7-4.6	75-100	270-510 \times 300-570	108-200 \times 50-83
	2	—	—	—	—	300-450 \times 300-430	145-253 \times 73-105
Akkeshi	8	25-107	500-750	2.6-4.7	70-105	310-520 \times 300-510	140-268 \times 50-75
	22	11-29	260-390	1.1-3.2	63-100	260-430 \times 250-440	165-283 \times 53-70

The data in the upper half are for field-collected plants and those in the lower half for cultured plants. Dashed line indicates no information. 1) The lowermost portions of main axes were measured. 2) Middle portions of main axes were measured.

longer segments than those of other populations. Two groups thus can be recognized by the length of segments among the local populations studied. The segment length affects gross morphological features. The specimens with longer segments are laxly expansive and give an impression that they are sparsely and distantly branched and have a flaccid texture. *P. akkeshiensis* is vegetatively characterized by these features (SEGI 1951). However, no significant differences in dimensions of reproductive organs were found among the populations studied.

Culture experiments

Polysiphonia japonica

The following account is based on observations of Oshoro 2713 and 2714 strains. Cultures were maintained at 15°C, 16:8 LD unless otherwise indicated. Liberated carpospores were globular and deep red in color. They averaged 60.3 μm (range 57.5–65.0 μm; 120 spores measured) in diameter (Fig. 2A). Isolated carpospores soon attached to the substrate and grew into bipolar sporelings of 6–7 segments, which, one day after inoculation, had differentiated into a

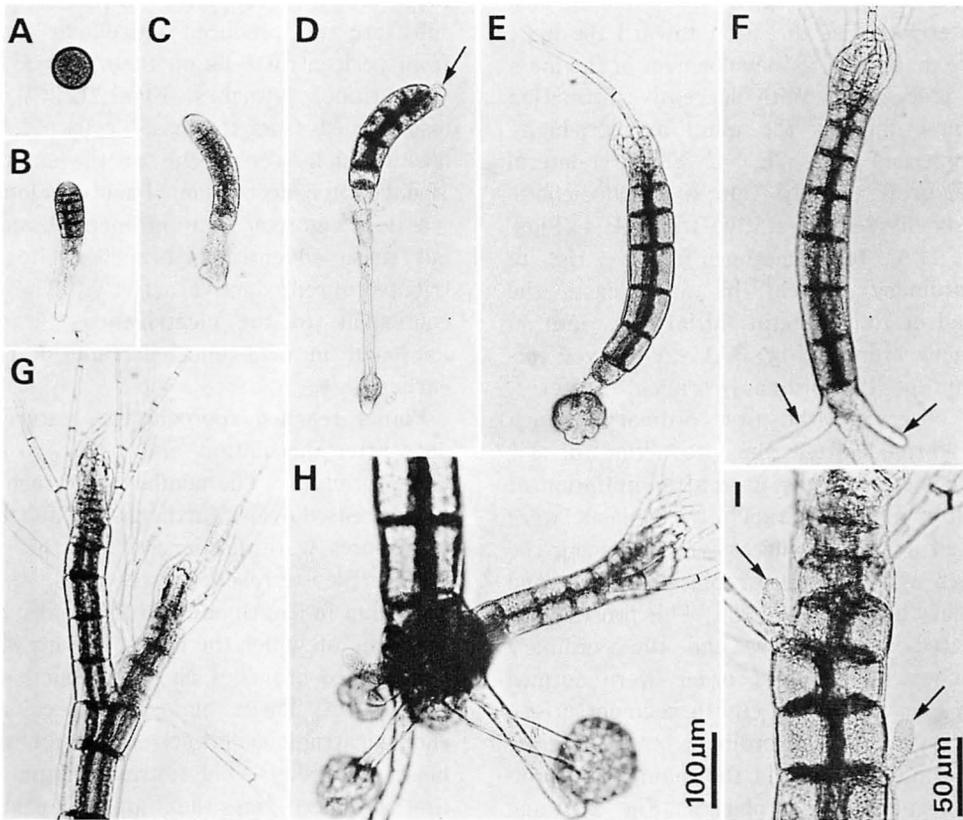


Fig. 2. Carpospore and its development of *Polysiphonia japonica* at 15°C, 16:8LD (Oshoro 2713 and 2714 strains). All photographs from living material. A. Liberated carpospore. B. One-day-old germling. C. Two-day-old germling; note the axis being recurved. D. Three-day-old germling forming a lateral initial (arrow) on the dorsal side. E. Five-day-old germling with spirally arranged laterals and an expanded disc-like rhizoid; note the main axis becoming straight. F. Seven-day-old germling with an almost straight main axis and two secondary rhizoids (arrows). G. Apical portion of a 10-day-old plant of which main axis and first order branch are forming vegetative trichoblasts. H. Basal portion of a 14-day-old plant forming an adventitious branch and five secondary rhizoids. I. Two adventitious branches (arrows) arising from the basal cells of trichoblasts before their shedding (17-day old). Scale in H applies also to A–G.

colorless rhizoid and a pigmented main axis (Fig. 2B). Each segment of the main axis was composed of an axial cell and four pericentral cells except apical, subapical, suprabasal and basal segments. The suprabasal segment had usually four pericentral cells but it sometimes possessed three or five pericentral cells. The basal segment was composed of a single cell. The main axis became recurved (Figs. 2C, D) and began to form lateral initials from a subapical segment, first on the dorsal side and second on the flank (Figs. 2D, 3A). Subsequently, lateral initials were formed from each segment in a spiral line running in a counterclockwise direction toward the apex of the main axis as development of the main axis proceeded. With successive formation of these laterals the main axis gradually straightened (Figs. 2E, F). The first lateral initial grew usually into a pseudodichotomously divided vegetative trichoblast (Figs. 2E, F, 3A), but sometimes it gave rise to an ordinary branch. In many cases the second or third lateral initial grew into an ordinary branch (Fig. 3A). A delayed formation of the ordinary branch, however, was observed: the first ordinary branch was formed after the production of 4-7 trichoblasts. In any case after initiation of the first ordinary branch trichoblasts were formed again, 2-7 successively replacing the branch and they were replaced by a second ordinary branch (Fig. 3C). This process was repeated continuously, and thus ordinary branches of the first order were formed from every third to eighth segment of the main axis. All the ordinary branches grew indeterminately as did the main axis, forming vegetative trichoblasts (Fig. 2G) and ordinary branches of the second order.

A primary rhizoid cut off from the basal segment became ramified at the growing tip (Fig. 3B), although it was not accompanied by the formation of a septum, and became an expanded disc-like holdfast (Fig. 2E). Primary rhizoids which were not ramified were also frequent and became elongated filamentous holdfasts (Figs. 2F, 3D). Some

of the latter rhizoids later became ramified as was the former. Secondary rhizoids were cut off from the basal segment (Figs. 3D, E) and from the pericentral cells of the suprabasal segment (Fig. 3F). Some of these secondary rhizoids became disc-like holdfasts (Fig. 2H).

One to three adventitious branches were formed from an axial cell of the suprabasal or third segment of the main axis 10 days after inoculation (Fig. 3E). These branches grew indeterminately (Fig. 3F). They developed first along the substrate (Fig. 2H) and later became upright. These adventitious branches sometimes attached to the substrate and produced unicellular rhizoids from pericentral cells on their ventral side. Adventitious branches (Figs. 2I, 3G) were also formed from the basal cells of trichoblasts which were borne on the main axis 17 days after inoculation. Their development was less vigorous than ordinary branches, but these adventitious branches later contributed to reproductive activity. These are equivalent to the cicatrigenous branches as found in field-collected plants described earlier.

Plants reached reproductive maturity 28 days after inoculation and began to form tetrasporangia. The number of tetrasporangia increased over a further week and many tetraspores were discharged. At this stage the fertile tetrasporophytes had reached 14-25 mm in length and had 14-26 first order branches of which the lowest one grew best and formed branches up to the fourth order (Fig. 4A). These plants produced many short cicatrigenous branches from the trichoblast scar cells. The tetrasporangia were first produced on the upper portion of ordinary branches (Fig. 4B) and later on cicatrigenous branches. Liberated tetraspores were slightly smaller than the parent carospores and averaged $51.0 \mu\text{m}$ (range $42.5-60.0 \mu\text{m}$; 120 spores measured) in diameter (Fig. 4C). The fertile plants produced a few cortical cells from pericentral cells of the lower segments (Fig. 5A). Cortical cells developed acropetally to the middle

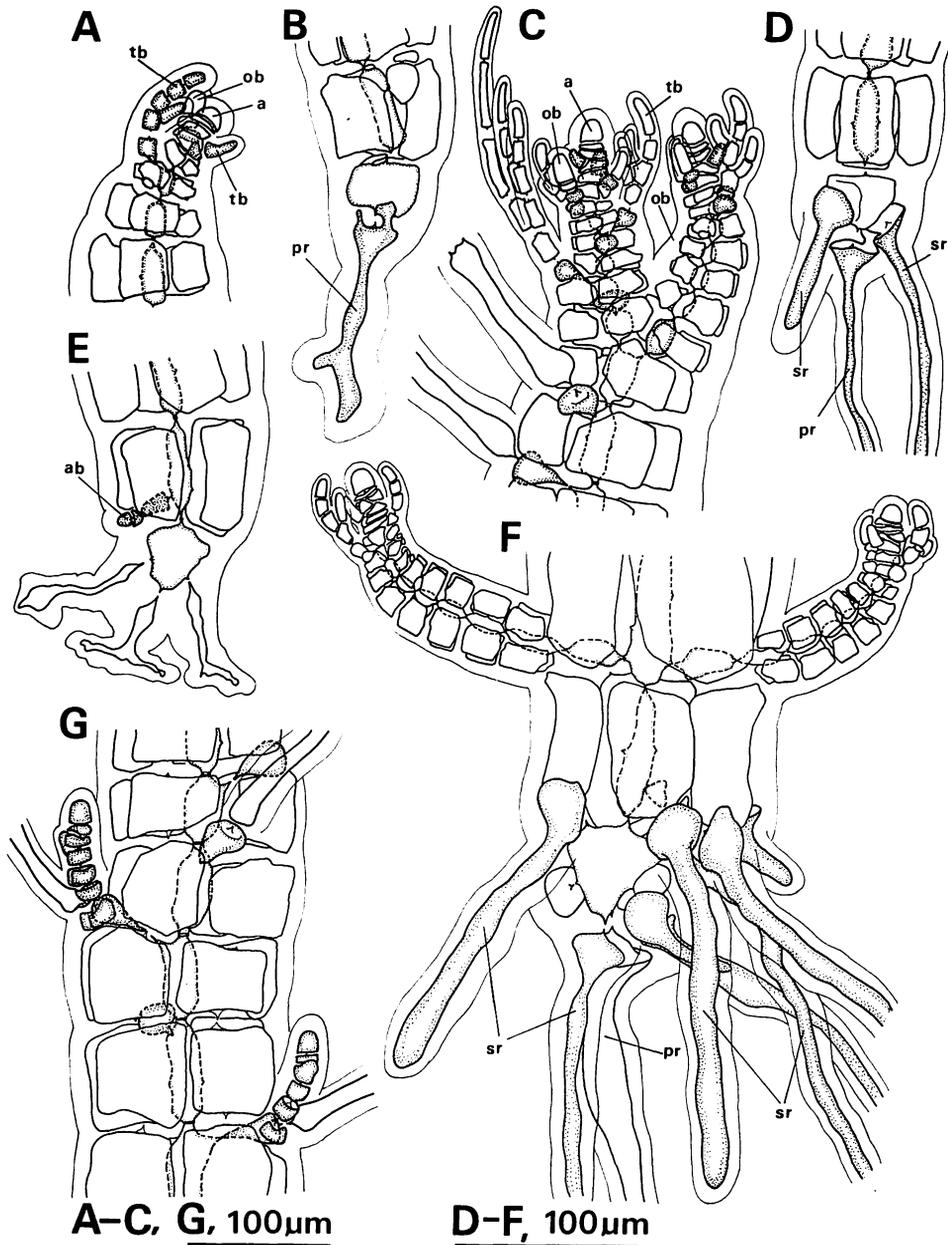


Fig. 3. Carposporelings of *Polysiphonia japonica* grown at 15°C, 16:8 LD (Oshoro 2713 and 2714 strains). A, B. Three-day-old germling (A, apical portion forming two trichoblasts and one ordinary branch; B, basal portion forming a primary rhizoid). C, D. Seven-day-old germling (C, apical portion forming spirally arranged trichoblasts and ordinary branches; D, basal portion with two secondary rhizoids cut off from the basal cell). E. Adventitious branch initial arising from an axial cell of the suprabasal segment of a 10-day-old germling. F. Basal portion of a 14-day-old sporeling issuing two adventitious branches and several secondary rhizoids (dotted) cut off from the pericentral cells of the suprabasal segment and from the basal cell. G. Adventitious branches formed from the basal cells of trichoblasts before their shedding (17-day old).

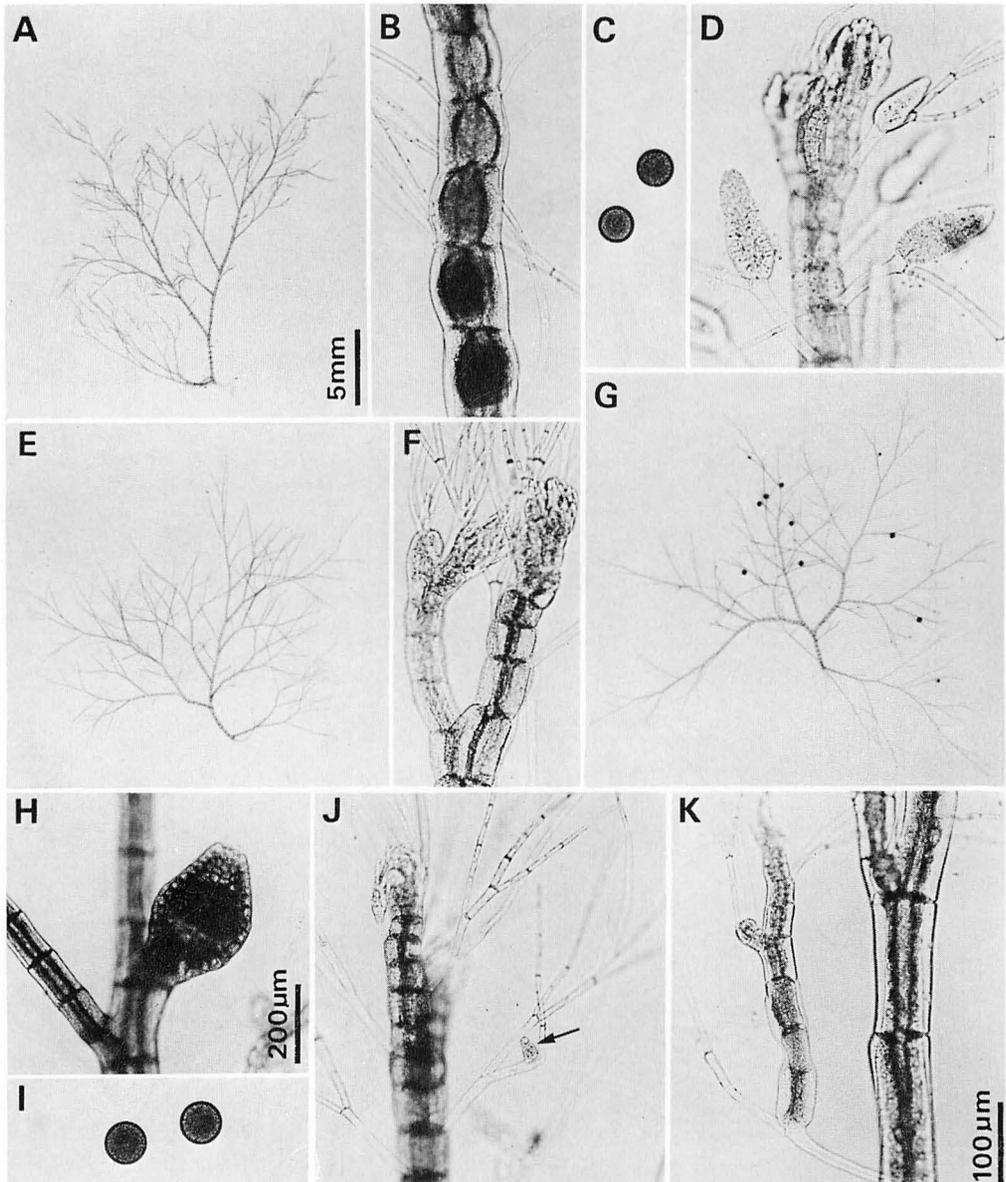


Fig. 4. *Polysiphonia japonica* cultured at 15°C, 16:8 LD (Oshoro 2713 and 2714 strains). All photographs from living material. A. Fertile tetrasporophyte (35-day old). B. Tetrasporangia formed on the upper portion of an ordinary branch. C. Liberated tetraspores. D. Spermatangial branchlets formed on the uppermost portion of the main axis (21-day old). E. Fertile male gametophyte cultured for 42 days. F. Procarps borne at the uppermost portion of the main axis and branch (21-day old). G. Fertile female gametophyte cultured stationarily for 24 days and then mixed with a male gametophyte for 18 days on a shaker. H. Mature cystocarp formed on the plant shown in G. I. Liberated carpospores. J. Propagule (arrow) formed on a trichoblast borne on a 28-day-old female gametophyte. K. Developing propagule on a supporting trichoblast before its shedding. Scale in A applies also to E and G; scale in K applies also to B-D, F, I and J.

portion of the main axis from pericentral cells (Fig. 5B) and from scar cells, but their increase was less vigorous than field-collected plants. The cortical cells produced on the lower segments cut off secondary rhizoids (Fig. 5A).

Tetraspores were inoculated onto glass slides. They germinated and grew into plants in a manner similar to that of the parent carpospores. These plants began to form spermatangial branchlets and procarps on separate individuals 14 days after inoculation. The spermatangial branchlets were formed as a first branch of the fertile trichoblasts (male trichoblasts) borne 2-6 successively at the uppermost portion of the main axis and branches (Fig. 4D). These male trichoblasts were replaced by ordinary branches or vegetative trichoblasts. Then, male trichoblasts were formed again, 2-6 successively. This process was repeated continuously as long as the plants continued to grow well (Fig. 4E). Male trichoblasts were also formed on short cicatrigenous branches. Mature spermatangial branchlets were nearly cylindrical and $125\text{--}300\ \mu\text{m}$ long \times $53\text{--}98\ \mu\text{m}$ wide. The procarps (Fig. 4F) were formed on the suprabaasal segments of fertile trichoblasts (female trichoblasts) borne on parts similar to those of male trichoblasts. The female trichoblasts were usually individually formed and rarely two successively. They were repeatedly replaced by ordinary branches and/or vegetative trichoblasts.

Fertile female gametophytes were mixed in single dishes with male gametophytes releasing spermatia and placed on a rotary shaker. All these female gametophytes (Fig. 4G) produced mature cystocarps which released viable carpospores 18 days after the initiation of mixed culture. The cystocarps were ovate and $240\text{--}390\ \mu\text{m}$ long \times $250\text{--}490\ \mu\text{m}$ wide (Fig. 4H). The resulting carpospores (Fig. 4I) were similar in every respect to those from field. Isolated female gametophytes did not produce cystocarps but continued to form procarps.

Propagules were often formed on trichoblasts borne on both female (Fig. 4J) and

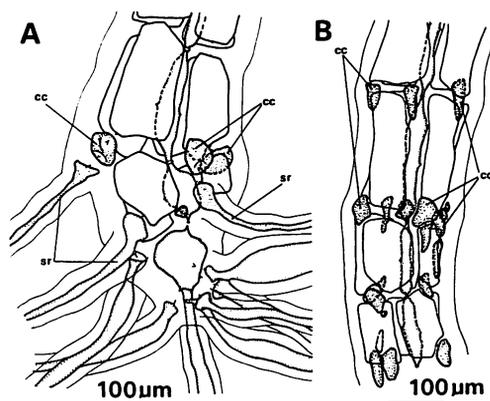


Fig. 5. Development of cortical cells of *Polysiphonia japonica* grown at 15°C , 16:8 LD (tetrasporophytes of Oshoro 2713 strain). A. Cortical cells cut off from pericentral cells of the lower portion of a 35-day-old plant; note two cortical cells issuing secondary rhizoids. B. Cortical cells cut off from pericentral cells of the middle portion of the main axis (3-month old).

male gametophytes. As the supporting trichoblasts were deciduous, these propagules became free from the parent plants, attached to the substrate, and bore rhizoidal filaments. They grew into fertile gametophytes bearing reproductive structures of their respective parents. The propagules sometimes grew rapidly on their supporting trichoblasts before release and formed gametangia (Fig. 4K).

Oshoro 2711 and 2712 strains and Samani 2590 strain, all of which were initiated from tetraspores of field-collected plants (Table 1), showed the same developmental pattern as did the above-described 2713 and 2714 strains.

All strains initiated from branch apices were cultured at 15°C , 16:8 LD and grew well, as did the sporelings of Oshoro and Samani strains. The apices grew into upright shoots and produced rhizoidal filaments from their lower segments. Secondary shoots sometimes developed from these rhizoidal filaments for Erimo 2147 male and Iwagasaki 2206 female strains. They reached reproductive maturity 1-2 months after inoculation. The gametophytic strains formed

the same gametangia as their parents. The morphological features of these strains were similar to those of their parent plants. Some of the strains were used for hybridization studies (Fig. 9). Tetraspores of the tetrasporophytic strains (Oshoro 2373, 2375; Utoro 1993; Kannonzaki 2425, 2426; Shiaku 2627, 2633 and Iwagasaki 2203) were cultured and their developmental patterns from sporelings to mature plants were traced at 15°C, 16:8 LD. These sporelings developed in a manner similar to that described for Oshoro 2713 and 2714 strains. No significant differences among the strains were observed. All the tetrasporelings gave rise to dioecious gametophytes at a ratio of 1:1 and formed procarps and spermatangia on separate individuals. Mature cystocarps were formed in mixed cultures of female and male plants of each strain. Some of these strains were clonally cultured from branch apices and used for hybridization experiments (Fig. 9).

In addition to analysis of morphological development, variations in growth and reproduction were observed at 10°C, 16:8 LD; 10°C, 8:16 LD; 15°C, 16:8 LD; 15°C, 8:16 LD; 20°C, 16:8 LD and 20°C, 8:16

LD, using the second generations of Oshoro 2711 and 2714 strains (2711 tetrasporophytes and 2714 gametophytes) and the first (tetrasporophytes) and second (gametophytes) generations of Iwagasaki 2203 strain. The growth and reproductive responses of the tetrasporophytic and gametophytic phases to varying temperatures and photoregimes were similar. The plants grew most rapidly at 15°C, 16:8 LD and most slowly at 10°C, 8:16 LD. Tetrasporangia were formed first at 20°C, 16:8 LD and 20°C, 8:16 LD 21 days after inoculation and lastly at 10°C, 8:16 LD 77 days after inoculation. Spermatangia and procarps were formed first at 15°C, 16:8 LD, 20°C, 16:8 LD and 20°C, 8:16 LD 14 days after inoculation and lastly at 10°C, 8:16 LD 63 days after inoculation.

The dimensions of some vegetative and reproductive features of cultured fertile plants are given in Table 2. The diameters of main axes and length/diameter ratios of segments in cultured plants in general varied correlatively with thallus length as in field-collected plants. Some plants of Oshoro strains possessed slightly longer segments than field-collected plants. No

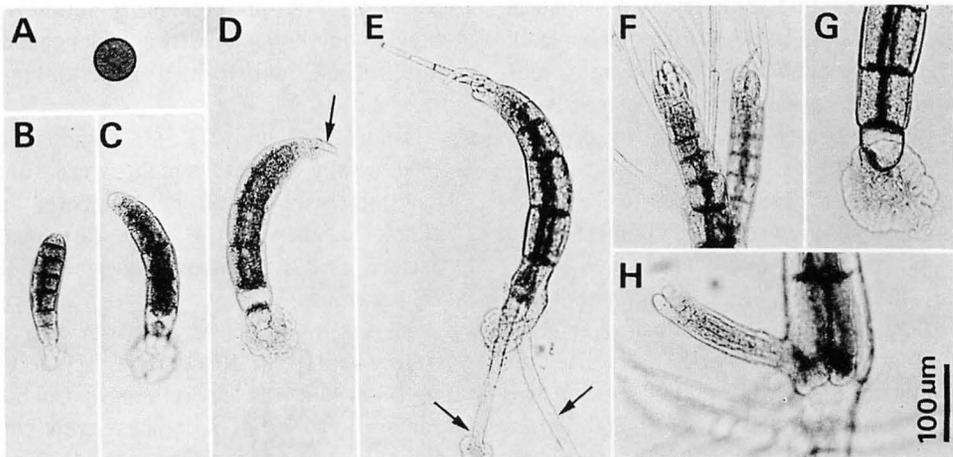


Fig. 6. Carpospore and its development of *Polysiphonia akkeshiensis* at 15°C, 16:8 LD (Akkeshi 2991 strain). All photographs from living material. A. Liberated carpospore. B. One-day-old germling. C. Two-day-old germling; note the axis being recurved. D. Three-day-old germling forming a vegetative trichoblast (arrow) on the dorsal side. E. Four-day-old germling with spirally arranged laterals and primary and secondary (arrows) rhizoids. F, G. Seven-day-old germling (F, apical portion; G, basal portion). H. Adventitious branch originated from the suprabasal segment of the main axis (14-day old). Scale in H applies to all of A-H.

significant differences in the segment length among plants cultured at different six conditions mentioned above were observed.

Polysiphonia akkeshiensis

The following observations are based on Akkeshi 2991 strain which was cultured at 15°C, 16:8 LD. Liberated carpospores were deep red in color and averaged 57.6 μm (range 52.5–65.0 μm ; 140 spores measured) in diameter (Fig. 6A). Isolated carpospores germinated and grew into plants (Figs. 6B–H, 7A–H) in a manner similar to that of *Polysiphonia japonica* described above. The following features were observed for growing tetrasporophytes of the 2991 strain: recurved sporelings at a very young stage (Figs. 6C–E), irregular number of pericentral cells on suprabasal segments of the main axis, repeating replacement between ordinary branches and vegetative trichoblasts, adventitious branches originating from an axial cell of the lower segments of main axes (Figs. 6H, 7F) and from a basal cell of vegetative trichoblasts before (Fig. 7G) or after (Fig. 7H) the shedding of trichoblasts.

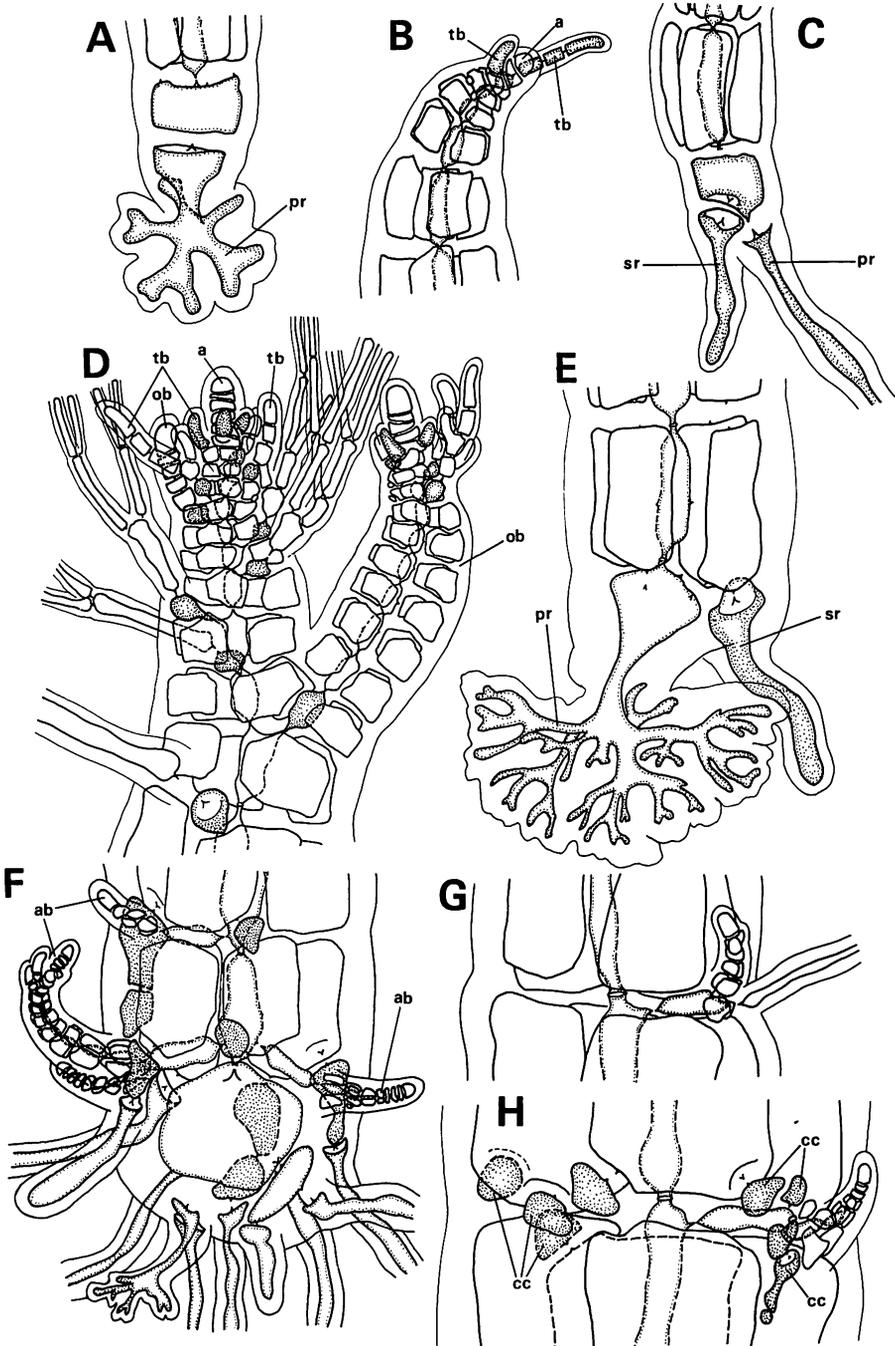
Plants began to form tetrasporangia 28 days after inoculation. They formed tetrasporangia more abundantly within a further week and released many tetraspores. At this stage the fertile plants had reached 15–23 mm in length (Fig. 8A) and possessed 18–27 branches of the first order and many short cicatrigenous branches. The tetrasporangia were first produced on the upper portion of ordinary branches (Fig. 8B) and later on the short cicatrigenous branches. Liberated tetraspores were slightly smaller than the parent carpospores and averaged 49.3 μm (range 37.5–57.5 μm ; 80 spores measured) in diameter (Fig. 8C). These tetrasporophytes formed cortical cells, which cut off rhizoidal cells, from pericentral cells of the lower segments of the main axis (Fig. 7F). They also formed cortical cells from pericentral cells and scar cells of the middle segments of the main axes (Fig. 7H). More developed cortical cells are shown in Figs. 8D, E. No propagules were observed on the tetrasporophytes of the 2991 strain.

Tetraspores inoculated onto glass slides germinated and grew into gametophytes in a pattern similar to that of the parent tetrasporophytes. The gametophytes began to produce procarps and spermatangial branchlets on separate plants 14 days after inoculation. The spermatangial branchlets were borne on male trichoblasts replacing ordinary branches or vegetative trichoblasts (Fig. 8F). Two to seven male trichoblasts were formed successively, then replaced by ordinary branches or vegetative trichoblasts, after which they were formed successively again. This process was repeated continuously as long as the plants grew well (Fig. 8G). Mature spermatangial branchlets were nearly cylindrical and 165–283 μm long \times 53–70 μm wide. The procarps were borne on the suprabasal segments of female trichoblasts (Fig. 8H) which arose from the growing apex of main axes and branches. The female trichoblasts were repeatedly replaced by ordinary branches and/or vegetative trichoblasts and were usually formed individually.

When female gametophytes bearing procarps were placed in dishes with male gametophytes releasing numerous spermatia and shaken they formed cystocarps (Fig. 8I). Viable carpospores were released 16 days after the initiation of mixed cultures. Mature cystocarps were ovate and 260–430 μm long \times 250–440 μm wide (Fig. 8J). Isolated female gametophytes did not produce cystocarps.

Propagules were often formed both on female and male gametophytes; they grew into fertile gametophytes bearing reproductive organs of their respective parents. The propagules formed on male gametophytes are shown in Figs. 8K, L.

Akkeshi 2990 strain initiated from tetraspores showed the same developmental pattern as did the aforementioned 2991 strain. All strains derived from branch apices grew well and reached reproductive maturity 1–2 months after inoculation at 15°C, 16:8 LD. Some of these strains were clonally cultured and used for hybridization experiments



A, D, 50 μ m

B,C,E,G, 100 μ m

F, H, 100 μ m

(Fig. 9).

The growth and reproductive responses of the tetrasporophytic (the second generation of 2990 strain) and gametophytic (the second generation of 2991 strain) phases to varying temperatures and photoregimes were examined as has been described earlier for *Polysiphonia japonica*. The responses of both phases were similar. The plants grew most rapidly at 15°C, 16:8 LD and most slowly at 10°C, 8:16 LD. Tetrasporangia were formed first at 15°C, 16:8 LD, 20°C, 16:8 LD and 20°C, 8:16 LD, 28 days after inoculation and lastly at 10°C, 8:16 LD, 77 days after inoculation. Spermatangia and procarps were formed first at 15°C, 16:8 LD, 20°C, 16:8 LD and 20°C, 8:16 LD, 14 days after inoculation and lastly at 10°C, 8:16 LD, 63 days after inoculation.

Hybridization experiments

Our results from crosses between 11 female and 12 male clones derived from 8 local populations of *Polysiphonia japonica* and *P. akkeshiensis* are shown in Fig. 9. Cystocarp development was evident on female plants in compatible crosses after 7 days at 15°C, 16:8 LD and carpospores were released 7-14 days afterward. Cystocarps, however, did not develop on female plants in other crosses even 2 months after the initiation and these crosses were then terminated. Since no cystocarps were observed in isolated female controls, the results indicate that cross-fertilization occurred in the compatible crosses and did not occur in the incompatible crosses. In crosses between female plants from Oshoro, Kannonzaki,

Shiaku and Iwagasaki (the southern group) and male plants from Abashiri, Utoro, Akkeshi and Erimo (the northern group) were completely negative. About half of their reciprocal crosses between female plants of the northern group and male plants of the southern group, however, was positive and viable carpospores were released. In negative crosses between these groups pericarp development was observed on the female plants in 7-14 days, but their gonimoblasts did not become mature. Any of these crosses repeated showed the same results. These breeding groups did not correspond to taxonomic groups defined by field-collected plants (Tables 1, 2). Abashiri and Erimo populations, which can be identified as *P. japonica*, belong to the northern group including *P. akkeshiensis*.

Carpospores resulting from compatible crosses were cultured at 15°C, 16:8 LD. No significant differences in developmental pattern and morphology among the sporelings (=F₁ tetrasporophytes) were observed. All F₁ tetrasporophytes obtained formed tetrasporangia and released viable spores within 30-40 days. Tetrasporelings were grown at the same culture condition. The tetrasporelings (=F₁ gametophytes) derived from many compatible crosses grew rapidly and formed procarps and spermatangia on separate plants within 14-21 days after germination, whereas those derived from the northern females × southern males (except for Akkeshi females × Iwagasaki males) were less vigorous. F₁ gametophytes of Akkeshi 1979 female × Kannonzaki 2422 and 2427 males grew slowly and eventually died

Fig. 7. Carposporelings of *Polysiphonia akkeshiensis* grown at 15°C, 16:8 LD (Akkeshi 2991 strain). A. Basal portion of a 2-day-old sporeling. B. Apical portion of a 3-day-old sporeling which issues two trichoblasts. C. Basal portion of a 5-day-old sporeling which produces a secondary rhizoid from the basal cell. D. Apical portion of a 7-day-old sporeling which forms spirally arranged trichoblasts and ordinary branches. E. Basal portion of a 10-day-old sporeling with a primary expanded disc-like rhizoid and a secondary rhizoid produced from the pericentral cell. F. Basal portion of a 17-day-old sporeling which forms four adventitious branches and cortical cells; note secondary rhizoids cut off from the pericentral cell, cortical cells and basal cell. G. Middle portion of a main axis issuing an adventitious branch from the basal cell of a trichoblast before its shedding (20-day old). H. Middle portion of a main axis issuing an adventitious branch from a scar cell (the basal cell of a trichoblast after its shedding) and cortical cells from the pericentral cells and from the scar cell (21-day old).

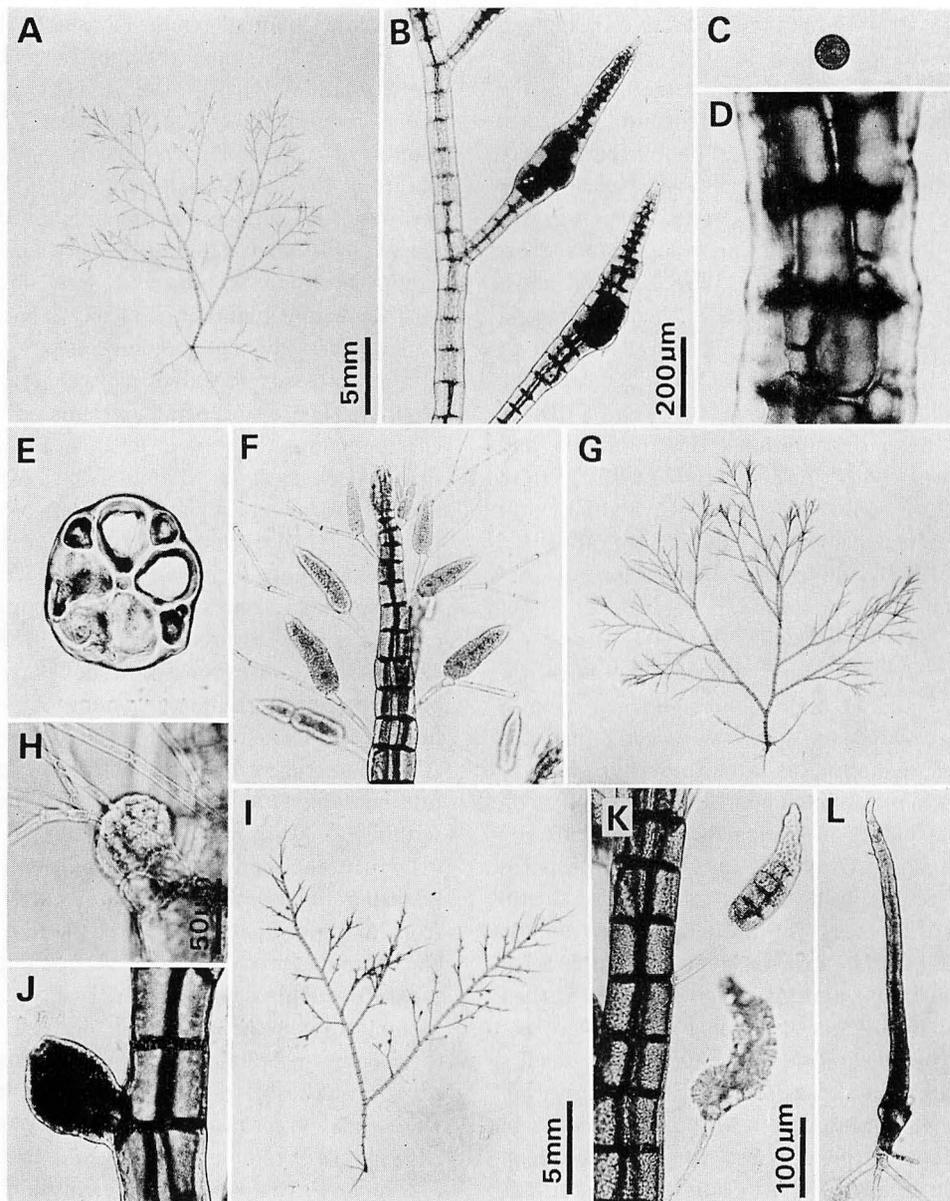


Fig. 8. *Polysiphonia akkeshiensis* cultured at 15°C, 16:8 LD (Akkeshi 2991 strain). All photographs from living material. A. Fertile tetrasporophyte cultured for 34 days. B. Tetrasporangia formed on the ordinary branches. C. Liberated tetraspore. D, E. Cortication of the main axis of a 53-day-old tetrasporophyte (D, surface view; E, cross section). F. Spermatangial branchlets formed on the uppermost portion of the main axis (21 day old). G. Fertile male gametophyte cultured for 34 days. H. Procarp borne at the upper portion of an ordinary branch. I. Fertile female gametophyte cultured stationarily for 14 days and then mixed with a male gametophyte for 16 days on a shaker. J. Mature cystocarp. K. Propagules formed on the upper portion of a male gametophyte. L. Germinating propagule. Scale in A applies also to G; scale in B applies also to D-F, J and L; scale in K applies also to C.

hybrid breakdown up to F_3 gametophytic generation.

Propagules were frequently formed on female and male gametophytes of interpopulation hybrids. Propagules on tetrasporophytes were observed in a single case: F_1 tetrasporophytes of Akkeshi 1980 female \times Oshoro 2714 male. The propagules were less abundant than those of gametophytes. Released propagules gave rise to fertile tetrasporophytes.

Discussion

Our morphological study of the life history stages of *Polysiphonia japonica* and *P. akkeshiensis* reveals that these two species are similar at every stage to each other. The two species are also similar in growth and reproductive responses to varying temperatures and photoregimes. *P. akkeshiensis* has been characterized by having laxly expanded to subflabellate thalli and a flaccid texture (SEGI 1951). These characters are brought about long segments of which length/diameter ratios range between 2.6 and 4.7 at the middle portion of the main axes. Cultured plants of this alga possessed shorter segments than did field-collected plants and could not be distinguished from *P. japonica*. This strongly suggests that these features show phenotypic plasticity and that such unstable characters are inappropriate for use as taxonomic criteria. Alternative criteria, however, have not been found. It may be concluded that employing morphological features, the two algae refer to the same taxonomic species. Our artificial hybridization experiments, however, show that incompletely isolated northern and southern breeding groups are present among the local populations studied. Samani 2590 and Enoshima 2499 strains, which are not shown in Fig. 9, probably belong to the northern group and southern group respectively according to a few crosses attempted. The two breeding groups are entirely allopatric in the range of our collections (Fig. 1). Their geographical patterns should be con-

firmed by more extensive sampling and hybridization experiments. Isolating mechanisms are diverse: incompatibility, hybrid inviability, hybrid sterility and hybrid breakdown. However, no reproductive isolation exists between Akkeshi and Iwagasaki populations, which are geographically distant (Fig. 1). It can be speculated that natural hybridization between these local populations does not occur. These results suggest the possibility that two virtually non-interbreeding groups separated by various isolating mechanisms exist in Japan, but the local populations sampled are small and hybridization experiments are as yet incomplete. These groups may have reached a certain stage of gradual speciation before morphological differentiation. This situation is similar to that of the red algal species *Gymnogongrus flabelliformis* HARVEY of Phylloporaceae (MASUDA, unpubl.). Based on the subtle morphological differences and reduced viability of F_1 gametophytes, RUENESS (1973) concluded that Texas *Polysiphonia boldii* WYNNE et EDWARDS was reduced to varietal status of Scandinavian *P. hemisphaerica*. On the basis of morphological, cytological and hybridization studies, KAPRAUN (1978b) reported that *P. ferulacea* and *P. harveyi* BAILEY consist of reproductively isolated sibling species groups respectively. It is premature to decide the formal taxonomic status of the groups of *Polysiphonia japonica* complex until a biosystematic investigation of the species complex throughout the whole coasts of Japan can be undertaken.

Some critical structural features of the species under study should be added to SEGI's description (1951). Two types of adventitious branches originate endogenously from axial cells of lower segments of the main axis and exogenously from scar cells (=basal cells of shed trichoblasts) as pointed out by YOON (1984). The latter is referred to as cicatrigenous branches (HOLLENBERG 1942). In cultured plants it occurs often before the shedding of trichoblasts. The same phenomenon was reported for field-

collected plants of Danish *Polysiphonia elongata* (HUDSON) HARVEY and *P. nigrescens* (HUDSON) GREVILLE (ROSENVINGE 1923-24) and those of Hawaiian *P. tuberosa* HOLLENBERG (1968). Dichotomous branching, which was described by SEGI (1951) and adopted as a characteristic feature of *P. japonica* by YOON (1984), is entirely absent, but the main axis and any of the branches grow monopodially. Their descriptions are probably based on specimens one of whose lower branches grow conspicuously. Propagules were frequently found on trichoblasts of cultured male and female plants and rarely on tetrasporangial plants and recycled the respective phase that produced them. A similar structure was reported for cultured and field-collected plants of North Carolina *P. ferulacea* (KAPRAUN 1977). Cicatrigenously originated propagules were described for field-collected plants of Australian *P. propagulifera* WOMERSLEY and *P. mollis* HOOKER et HARVEY ex HARVEY (WOMERSLEY 1979). It can be speculated that propagules of these three species are really asexual reproductive organs in the field populations, but this has not been confirmed for the species complex under study in the field.

It is noteworthy that cortical cells of cultured plants developed slowly. Cultured plants, which began to form reproductive organs, had weakly developed cortical cells from the lower segments of the main axis. Similar fertile plants are also found in nature. This suggests a close relationship between *Polysiphonia japonica* complex and *P. savatieri* HARIOT. The latter is characterized by the absence of cortical cells (HARIOT 1891), although its gross morphology seems to be similar to that of *Polysiphonia decumbens* SEGI and young plants of *P. japonica* as pointed out by SEGI (1951) and YOON (1984). The existence of cortical cells in the Korean *P. savatieri* varies according to the habitat (YOON 1984); specimens growing on *Chondria* sometimes have a slight cortication near the base of older axes, although those growing on *Codium* do not

produce cortical cells. YOON (1984) proposed that *P. savatieri* should be reduced to varietal status of *P. japonica*, although his paper, which has not been printed and has been distributed by photostatic copies, is not an effective publication according to Article 29.1 of the International Code of Botanical Nomenclature (ICBN, VOSS *et al.* 1983). Our data obtained in the laboratory and field support his opinion. More detailed studies, however, are needed to evaluate their genetic affinities.

SEGI (1951) reported *Polysiphonia novae-angliae* W.R. TAYLOR from a single locality, Okushiri Isl., Hokkaido. His identification is based on the similarity in texture (spongy rather than slippery) and cystocarp shape (elongato-urceolate) (SEGI 1951). TAZAWA (1975) described spermatangial branchlets of this alga on the basis of specimens collected at Otaru, Hokkaido. Judging from TAZAWA's voucher specimens preserved in SAP (028547), his identification may be based on the spongy texture. Older specimens of *P. japonica*, however, always have a spongy texture. The shape and dimension of cystocarps of *P. novae-angliae* given by SEGI (1951) can be frequently found in our collections of *P. japonica* (Table 2). Thus, *P. novae-angliae* auct. japon. is included in the circumscription of *P. japonica* complex.

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工藤利彦・増田道夫：紅藻キブライトグサとアッケシイトグサの分類学的研究

キブライトグサとアッケシイトグサの生活史を培養実験によって比較した結果、両者は異なる培養条件（温度、10-20°C；日長、16:8 LD と 8:16 LD）で、形態、生長及び成熟の反応においてよく似ていた。後者の特徴とされている形質は、節間が前者よりも長いことに起因することがフィールド個体で確認された。しかし、培養個体ではその差異は認められなかった。これは両者の識別に用いられてきた基準形質が不安定であることを示す。代わりうる形質もみつからなかったため両者は同一の分類学的種として扱われる。一方、様々な機構によって生殖的に融離されている異所的な2つの交配群が存在することが交雑実験で明らかになった。またナガツボイトグサも今回調べられた種群に含まれる。(060 札幌市北区北10条西8丁目 北海道大学理学部植物学教室)

On the systematic position of the parasitic red alga *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA

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KAWAGUCHI, S. and YOSHIDA, T. 1986. On the systematic position of the parasitic red alga *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA. Jap. J. Phycol. 34: 311-318.

Reproductive morphology of *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA, a parasitic red alga on the host *Prionitis angusta* (= *Carpopeltis angusta*), was studied in detail based on the specimens collected at Wakayama and Chiba Prefectures. In these specimens, the auxiliary cell and the 2-celled carpogonial branch were separately produced (non-procarpic) in the secondarily developed cell clusters (ampullary structures characteristic of the Halymeniaceae), and after fertilization the connecting filament was necessary for activating the auxiliary cell to produce gonimoblasts. This result is different from that described by the original authors who interpreted the reproductive structure as procarpic and therefore this species as a member of the Gigartinales.

To clarify this difference in the interpretation of the reproductive structure, we examined the original materials and found that they possessed the same reproductive features as our materials. Thus, we concluded that this species should be placed in the Halymeniaceae (=Cryptonemiaceae).

Key Index Words: Aadelphoparasite; alloparasite; Cryptonemiales; Halymeniaceae; *Kintokiocolax aggregatocerantha*; parasitic red alga; reproductive morphology; Rhodophyceae.

Kintokiocolax aggregatocerantha TANAKA et Y. NOZAWA (1960) was described as a parasite on the *Prionitis angusta* (HARVEY) OKAMURA (= *Carpopeltis angusta*)* based on the specimens collected at Hananose, Kagoshima Prefecture, Southern Kyushu. They placed this monotypic genus in the order Gigartinales (sensu SCHMITZ in ENGLER) on account of their interpretation that this species has procarpic nature. Since then, as far as is known, no investigation has been published on this species except for a short comment by FELDMANN and FELDMANN

(1963).

Recently, small, whitish, seemingly parasitic plants were found on the specimens of *P. angusta* collected at the two localities in the central Pacific coast of Honshu. Gross morphological and inner vegetative features of these specimens were in good accordance with those of *K. aggregatocerantha*, while the reproductive structures were clearly different from those interpreted by TANAKA and NOZAWA (1960). A careful comparison of our specimens with the Holotype and the Isotype of *K. aggregatocerantha* revealed that both of the type specimens had the same reproductive features as ours. We noticed that the reproductive structures of this species were characteristic of the Halymeniaceae, Cryptonemiales.

* In the original description, the binominal *Carpopeltis angusta* (HARVEY) OKAMURA was used, but according to the recent study by KAWAGUCHI (unpubl.), it is most appropriate to treat this species under the genus *Prionitis* as did ABBOTT and HOLLENBERG (1976, p. 444).

Materials and Methods

The materials used for the present study were:

- 1) Hananose, Kagoshima Prefecture, 10 June, 1959, collected by T. TANAKA & Y. NOZAWA (Holotype and Isotype deposited in the herbarium of Faculty of Fisheries, Kagoshima University).
- 2) Hikigawa, ca. 15 m deep, Wakayama Pref., 26 Nov., 1984, collected by T. YOSHIDA (SAP 047798).
- 3) Ohara, 25–32 m deep, Chiba Pref., 27 Aug., 1985, collected by M. OHTA (SAP 047801).

The materials used for anatomical study were preserved in formalin-seawater except for the type materials. Sections were made by hand using a razor blade and stained with cotton blue solution. They were mounted in 50% glycerol-seawater on microscope slides.

Observations

The following observations are based on the specimens collected at Hikigawa and Ohara.

Habit: Plants are found scattered over the host thallus, forming small, irregular-shaped wart-like masses (Fig. 1, arrowheads). Each plant consists of a basal cushion-like part, up to 5 mm in diameter, and short erect columnar shoots. The erect shoots, one to twenty in number, develop from the basal part, up to 5 mm high and 1 mm in diameter, and the apex of a shoot is blunt or sometimes pointed (Fig. 2A). They are somewhat cartilaginous in texture, with rather smooth surface. The color is

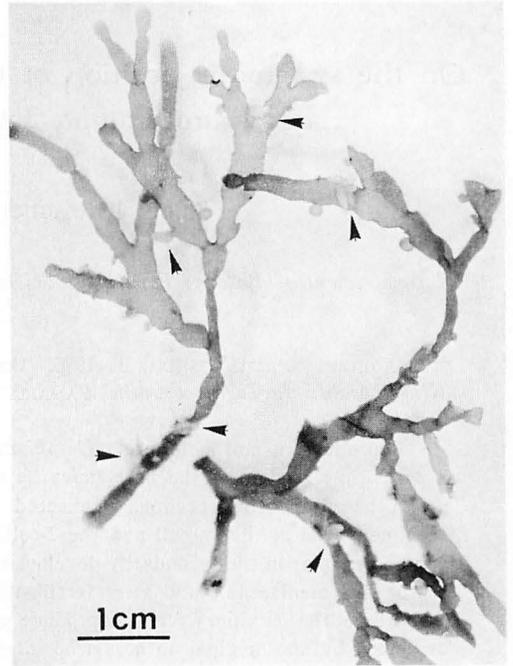
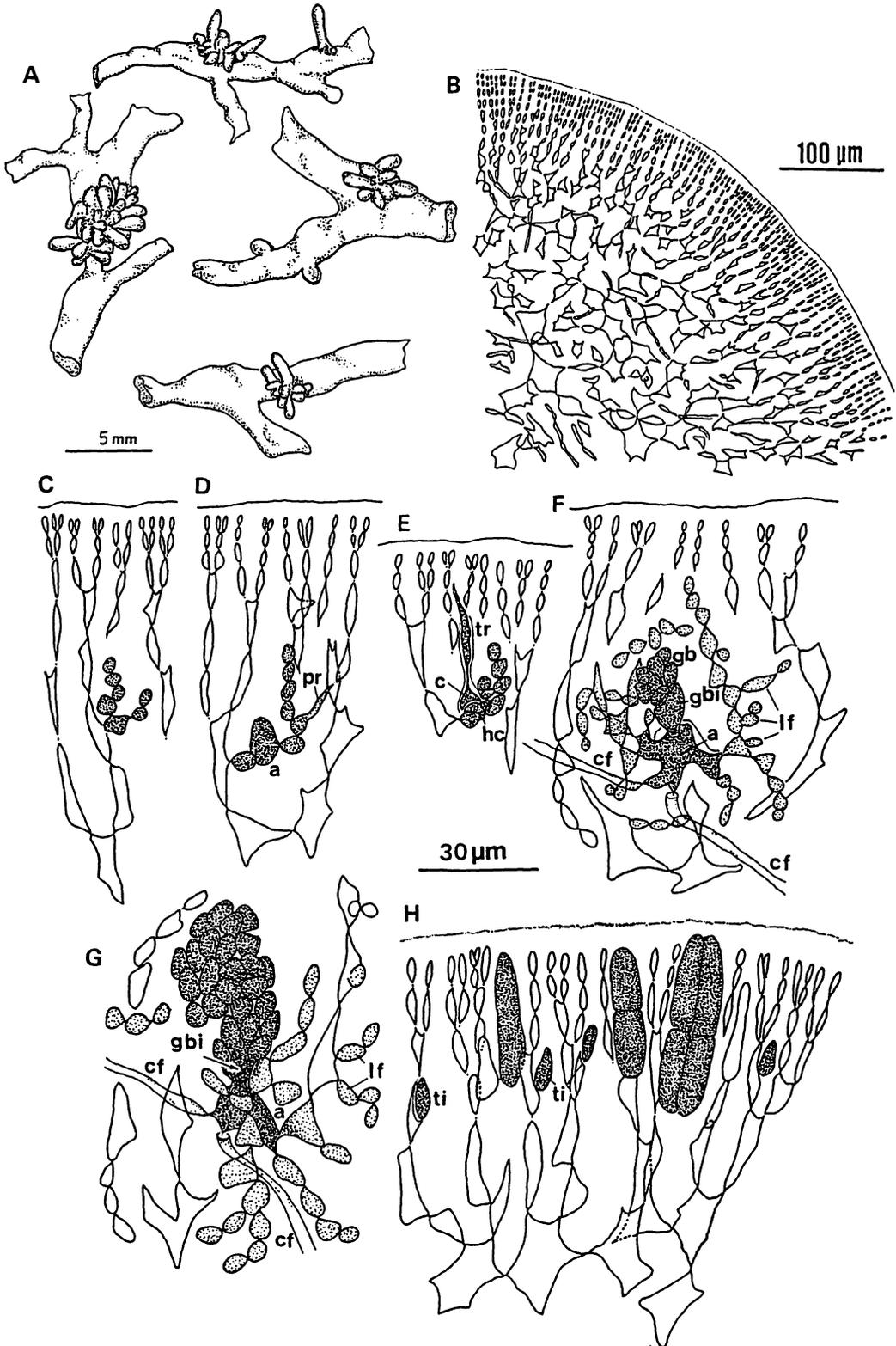


Fig. 1. *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA. Habit of parasitic plants (arrowheads) scattered over the host *Prionitis angusta* (HARVEY) OKAMURA collected at Hikigawa.

usually yellowish white or at times pale pink.

Vegetative structures: In longitudinal section through the host thallus, the parasite seems to attach to the host by its flattened layer, showing no connections with the host in some areas (Fig. 3A). While in other areas of the same plant, the parasite tissue can hardly be distinguishable from the host tissue and seems to be continuous with the outer cortical cells of the host. In the latter case, however, we could not determine whether connections between the host

Fig. 2. *Kintokiocolax aggregatocerantha* (Hikigawa specimens). A. Habit of parasitic plants on hosts. B. Cross section of erect shoot. C. Young branch system secondarily produced from inner cortical cell. D. Auxiliary cell (a) branch system composed of a single filament. Note that a lateral protuberance (pr) develops from a cell in the branch system. E. Carpogonial branch system bearing carpogonium (c) and hypogynous cell (hc). F. Young stage in gonimoblast development. Lateral filaments (lf) produced from cells in the branch system. G. Advanced stage in gonimoblast development. Pit-connection between auxiliary cell (a) and gonimoblast initial cell (gbi) becoming wide. Lateral filaments (lf) produced from neighboring vegetative cells. H. Tetrasporangial formation. Tetrasporangial initials (ti) cut off from cortical cells as a single side branch.



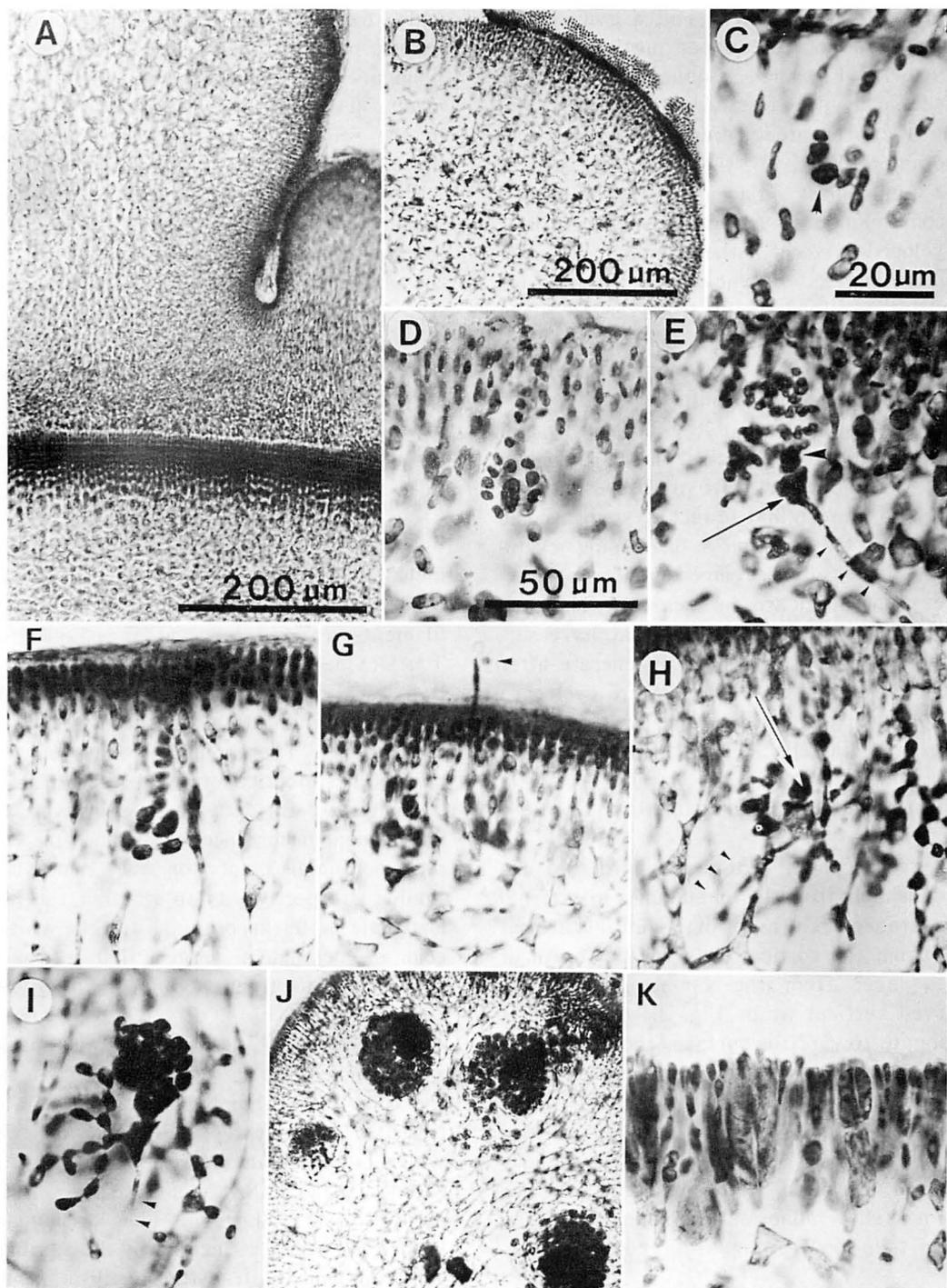
and the parasite were established or not with certainty. No rhizoidal filaments were detected, although many sections were inspected. The erect shoot consists of cortical and medullary layers. The outer cortex is composed of regularly dichotomously branched filaments of small ellipsoid cells ($5-8\ \mu\text{m}$ long \times $3-4\ \mu\text{m}$ broad), about five cells long, laterally free from one another. This outer layer grades to an inner cortex three to five layers deep composed of larger ellipsoid or polygonal cells ($8-15\ \mu\text{m} \times 5-8\ \mu\text{m}$) frequently connected to adjacent cells by secondary pit connections, and in turn grading into a medullary region of irregular-shaped cells also secondarily connected with one another. The cells in the medulla, some of which are very large, reaching $90\ \mu\text{m}$ in diameter, are interconnected by occasional filamentous cells (Fig. 2B). Most of the cells in the cortex and the medulla are almost colorless except for those in the outermost two or three cortical layers. The presence of red pigmentation in the latter cells may show that they play an assimilatory role to a certain degree, although no evidence is available to us.

Reproductive structures: In the specimens at hand, both cystocarpic and tetrasporangial plants were independently found on the same host thallus. The auxiliary cell and the carpogonial branch are formed in the separate branch systems which are secondarily developed laterally from the inner cortical cells (Fig. 2C, D, E). These branch systems are identical to the structures called ampullae

of the Halymeniaceae. The carpogonial branch is two-celled, consisting of a carpogonium and a hypogynous cell (Fig. 2E). The hypogynous cell seems to be intercalarily situated because it has a single side branch (Fig. 2E). The carpogonium, usually conical in shape, projects a trichogyne from the upper portion toward the thallus surface. The branch system bearing an auxiliary cell is basically the same in structure as that bearing the carpogonial branch, and consists of a few filaments branched at most to the second order (Fig. 3F). As shown in Fig. 2D, the auxiliary cell branch system is often composed of only a single filament. The auxiliary cell is intercalary, usually the second cell of the primary filament, or the first cell of the second order filament issued from the first cell of the primary one (Fig. 2D). In some cases, the first cell of the primary filament functions as an auxiliary cell. The auxiliary cell is easily distinguished from other cells in the branch system by its larger size and denser protoplasmic content.

The early stage of post-fertilization development was not clarified (a supposed spermatium attaching close to the top of a trichogyne was found only in one case (Fig. 3G)), but the connecting filaments were clearly observed attached to auxiliary cells (Figs. 2F, G; 3I). The connecting filament may cease to grow when the contact with an auxiliary cell has been established, but in many cases a new connecting filament is cut off from other side of the auxiliary cell. After receiving fertilized nucleus through

Fig. 3. *Kintokiocolax aggregatoceranthe* (A and F-K: Hikigawa specimens; B-E: Holotype and Isotype). A. Longitudinal section of the plant (above) through its host (below) showing that it attaches to the host by its flattened layer. B. Cross section of female shoot. C. Young branch system bearing auxiliary cell (arrowhead). D. Auxiliary cell branch system. E. Young stage in gonimoblast development. Gonimoblast initial cell (large arrowhead) cut off from auxiliary cell (arrow) after contact with connecting filament (small arrowheads). F. Sparsely branched auxiliary cell system. G. Supposed spermatium (arrowhead) attached to a trichogyne projected from the surface. Note that the branch system below is out of focus. H. Early stage in gonimoblast development showing that gonimoblast initial cell (arrow) has just been cut off from auxiliary cell after contact with connecting filament (arrowheads). I. Young stage in gonimoblast development. Connecting filament (arrowheads) attached to auxiliary cell. J. Cross section of erect shoot showing mature cystocarps embedded in the interior of the thallus. K. Tetrasporangia embedded in cortex. Scale bar in B applies also to J, and D to E-I and K.



the connecting filament, the auxiliary cell slightly enlarges and cuts off a gonimoblast initial cell from the upper portion by concave wall (Fig. 3H). Gonimoblast cells are successively developed from the initial cell and they repeatedly divide to form carposporangia (Figs. 2F, G; 3I). Some cells of the gonimoblast adjacent to the initial cell become elongated and remain sterile. In a developed cystocarp, the gonimoblast initial cell is elongated to some degree and becomes difficult to discriminate from the auxiliary cell lying beneath it (Fig. 2G).

Concurrently with the gonimoblast development, the neighboring vegetative cells together with those of the branch system produce simple or branched lateral filaments (Fig. 2F, G). The cells of these filaments and also the original branch system become elongated to surround a developing cystocarp. In a fully developed cystocarp, however, the pericarp is scarcely observed probably because those cells that have surrounded a young cystocarp degenerate after supplying nutrition. The mature cystocarp is spherical to hemispherical in shape, 150–180 μm in diameter, embedded in the interior of a thallus (Fig. 3J).

Male plants were not found in the present study.

Tetrasporangial plants can hardly be distinguishable from the female ones in external appearance. Tetrasporangial initials are cut off from the cortical cells in the fourth or fifth layer from the surface by slightly curved vertical walls (Fig. 2H). They first elongate toward the surface, then enlarging into narrowly ellipsoid sporangia. The mature sporangium is 37–40(–45) \times 10–15 μm in size, cruciately or decussately divided (Figs. 2H; 3K). In some plants, irregularly divided sporangia were abundant, and they seem to show abnormal development judging from their poor protoplasmic contents.

Observations on the type materials

The habit and the vegetative structures of the Holotype and the Isotype were the

same as the original description by TANAKA and NOZAWA (1960). The only different feature obtained by us is that no rhizoidal filaments were observed in the sections we made. The parasite attaches to the host in the same way as described earlier on the specimens from Hikigawa and Ohara.

The reproductive structures of the type specimens obviously differed from those interpreted by TANAKA and NOZAWA in that the auxiliary cell and the carpogonial branch were separately formed in the secondarily developed ampullary cell clusters (Fig. 3D), and that the connecting filament was necessary for activating the auxiliary cell to produce gonimoblasts (Fig. 3E).

Discussion

As far as the materials examined by us, including the Holotype and the Isotype, are concerned, we could not find any rhizoidal filaments as was reported and figured by TANAKA and NOZAWA (1960, p. 110, fig. 4A, B). According to our observations, the plant appears to attach to the host by its flat surface. There remains some doubt on the distinct identity of the present alga or the nature of its parasitism. However, the independent occurrence of cystocarpic and tetrasporangial plants on the same host thallus irrespective as to whether the host is female or tetrasporangial and the whitish color of the thallus suggest that it is most appropriate to treat *K. aggregatoceranthera* as a parasite.

In the original description, this species was considered to belong to the Gigartinales and thus to represent an example of allo-parasite (FELDMANN & FELDMANN, 1958), which is minor in the red algal parasites (GOFF, 1982). TANAKA and NOZAWA (1960) described as follows: "The carpogonial branch is directly connected by the auxiliary cell lying beneath it. After fertilization, the auxiliary cell produces another two or three nourishing cell groups and forms a large fusion-cell which brings forth the gonimoblast." Their fig. 3B, C (p. 108), however,

does not give any exact image on the post-fertilization events. FELDMANN and FELDMANN (1963, p. 558-559) stated that "A en juger par les figures publiées, cette attribution du genre *Kintokiocolax* aux Gigartinales ne nous paraît pas justifiée", on the grounds that the disposition of the differentiated short filaments is not that of the Gigartinales but shows the structure very similar to the carpogonial ampulla characteristic of the Halymeniaceae. As is clear from our observations, the above suggestion by FELDMANN and FELDMANN proves to be true. The auxiliary cell and the carpogonial branch are separately formed in the "subsidiary" (KRAFT and ROBINS, 1985) ampullary branch systems. This clearly shows that this species is non-procarpic and has the reproductive features possessed by the members of the Halymeniaceae. The process of gonimoblast development also quite agrees with those hitherto reported in many species of the family (cf. BALAKRISHNAN, 1961, 1961a; KAWABATA, 1962, 1963; CHIANG, 1970). This species is an adelphoparasite as are most of the red algal parasites (FELDMANN and FELDMANN, 1958; GOFF, 1982).

In separating the genera of the family Halymeniaceae, the auxiliary cell structure is considered to be of value by CHIANG (1970). According to him, the auxiliary cell ampullary structures can be divided into 5 types in the family from the shape and the degree of branching, and sparsely-branched ampulla is more advanced than densely-branched one. If based on his system, the auxiliary cell ampulla of this species clearly falls within the range of advanced category, or is rather more advanced than any type because it is often composed of only a single filament as shown in Fig. 2D. This reduced type of ampulla has never been reported in the members of this family nor has been observed in the host species *P. angusta* (KAWAGUCHI, unpubl.). It might be possible to say that such a reduction of ampullary filaments represented by this species is due to its parasitism.

Until our present investigation, this species escaped from the attention of other workers. The reason probably lies in its rare occurrence, but also in the fact that it is only found on the *Prionitis angusta* collected from deeper places as is known from the collection data. Diligent search in the subtidal zone might bring more specimens suitable for further investigation.

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We wish to express our cordial thanks to Prof. Emeritus M. KUROGI, Hokkaido University, for his kind guidance and to Dr. M. MASUDA, Hokkaido University, for his valuable suggestions during the course of our present study. Special thanks are due to Dr. M. OHTA, Central Laboratory, Marine Ecology Research Institute, who contributed the specimens at our disposal. We are also grateful to Prof. K. NOZAWA, Kagoshima University, for the loan of the type specimens.

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川口栄男・吉田忠生：寄生紅藻キントキヤドリ *Kintokiocolax aggregatocerantha*
 TANAKA et Y. NAZAWA の分類学的位置

キントキ *Prionitis angusta* (= *Carpopeltis angusta*) 上の寄生紅藻として知られる本種は、助細胞と造果枝が直接連結する (procarpic) という原著者らの解釈に基づき、スギノリ目 Gigartinales の種として発表された。しかし、和歌山県と千葉県で新たに採集された材料を詳しく調べた所、その雌性生殖器官の構造には、原報告と明らかに異なる点が見出された。すなわち、助細胞と造果枝は離れて、それぞれ別の二次的に形成された枝叢中に存在した (non-procarpic)。

この違いを基準標本について検討した結果、著者らの観察事実と一致した特徴を有することが確認された。従って、本種はカクレイト目 Cryptonemiales ムカデノリ科 Halymeniaceae に属するとの結論に達した。(060 札幌市北区北10条西8丁目 北海道大学理学部植物学教室)

新刊紹介

R. F. SCAGEL, D. J. GARBARY, L. GOLDEN & M. W. HAWKES (1986) A Synopsis of the Benthic Marine Algae of British Columbia, Northern Washington and Southeast Alaska. Phycological Contribution No. 1, The University of British Columbia, Vancouver, Canada. 444 pp. 22.5 カナダ\$ (含船郵送料, 邦貨約 2,800 円)

本書はカナダの太平洋沿岸における初めての本格的な海藻のチェックリストである SCAGEL, R. F. (1957) "An annotated list of the marine algae of British Columbia and northern Washington" の続編である。1957年以降にこの海域から報告されている海藻の採集記録のほとんどすべてを網羅している。前書に収録されている 189 属 478 種をはるかに上回る 270 属 627 分類群が収録されている。その内訳は黄緑色藻類 3 属 6 分類群、緑藻類 45 属 102 分類群、褐藻類 66 属 130 分類群、紅藻類 156 属 389 分類群となっている。

本書は大きく 2 つの部分に分けられる。前半は各分類群の採集報告が 180 頁にわたって記載されており、後半に約 2000 点の文献のリストが 146 頁にわたって載

せられている。前半部の分類群名の後には、著者名や出典は勿論のこと Basionym やカナダ以外での世界各地の分布も書かれてあり、海藻の名前調べや分布調べにとっても便利である。言うまでもなく分類群の索引としても第 1 級の精度を持っている。しかしここまで述べてきた内容を持っているものは本書以外にもかなりある。本書のもっとも大きな特色は、収録されている文献の種類が分類学だけでなく、遺伝学、形態学、分布地理学、生化学、生理学、生態学など多方面にわたっていることである。様々な分野の研究材料として採集された記録をのこらず載せてあるので、本書は海藻を材料として用いる研究者にとって大いに役にたつ書であると確信できる。最近数多く出版される海藻フロラや海藻チェックリストのなかで本書はその白眉と言えるものである。入用の方は、R. F. SCAGEL, Dept. Bot., Univ. of British Columbia #3259-6270 University Blvd., Vancouver, B. C. V6T 2B1, Canada へ直接申し込むこと。(国立科学博物館植物研究部 田中次郎)

Identification of the alga known as "marine *Chlorella*" as a member of the Eustigmatophyceae

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MARUYAMA, I., NAKAMURA, T., MATSUBAYASHI, T., ANDO, Y. and MAEDA, T. 1986. Identification of the alga known as "marine *Chlorella*" as a member of the Eustigmatophyceae. Jap. J. Phycol. 34: 319-325.

An alga known as "marine *Chlorella*", obtained from Suisan Center (Makishima-machi, Nagasaki, Japan), has been critically investigated in culture and identified on the evidence of ultrastructure and biochemistry as *Nannochloropsis oculata* (DROOP) HIBBERD, a member of the Eustigmatophyceae. Cells are spherical to slightly ovoid, 2-4 μm in diameter, and contain an ovoid or cup-shaped chloroplast. The chloroplast is bounded by two double membranes, the outer representing the CER and showing connections with the nuclear envelope, and the inner representing the chloroplast envelope. Chloroplast lamellae consist of three appressed thylakoids. Girdle lamellae and pyrenoids are absent. Starch was not detected. Optimum growth, with a specific growth rate of 0.9 day^{-1} , occurred at a temperature of ca. 25°C, salinity of 15-30‰, light intensity greater than 12 klux, and initial pH of ca. 8. Predominant photosynthetic pigments were chlorophyll *a*, carotene, violaxanthin, and vaucherixanthin ester. Chlorophyll *b* and lutein were not detected.

Key Index Words: Eustigmatophyceae; growth; marine *Chlorella*; *Nannochloropsis oculata*; pigment; ultrastructure.

A small, planktonic, unicellular alga known as "marine *Chlorella*" has been widely used as food for the rotifer *Brachionus plicatilis* in the culture of many types of fish (WATANABE *et al.* 1978a). Because it is an excellent food for use in the culture of juvenile marine fish, the alga has been the subject of many nutritional studies, which have been revealed to have a high content of eicosapentanoic acid (WATANABE *et al.* 1978b). However, there have been few studies on its biology and biochemistry. In the present report the growth, pigment composition, and ultrastructure of this alga are examined and the results applied to its taxonomic assignment.

Materials and methods

Materials

A sample of the alga used for culture of rotifer *Brachionus plicatilis* was obtained as a nearly pure culture from Suisan Center, Nagasaki City Institute of Fisheries (Makishima-machi, Nagasaki, Japan) in July, 1981, and purified by plating out suitable dilutions. Two other unicells, *Monodopsis subterranea* (PETERSEN) HIBBERD (obtained from the Sammlung von Algenkulturen, Göttingen No. 848-1 as *Monodus subterraneus*) and *Nannochloropsis oculata* (DROOP) HIBBERD (obtained from the Algal Culture Collection at the University of Texas No. 2164 as *Nan-*

nochloris oculata) were used for purposes of comparison in the identification of photosynthetic pigments (WHITTLE and CASSELTON 1975, ANTIA *et al.* 1975).

Culture conditions

The alga was cultured in a medium containing 0.5 g KNO₃, 0.1 g Na₂HPO₄, 15 mg EDTA-Na-Fe, 1 ml of Arnon's solution A₅ (WATANABE 1960), 5 ml of vitamin mixture S-3 (PROVASOLI *et al.* 1957), and 0.5 µg of vitamin B₁₂ per liter of either natural sea water or Jamarin S artificial sea water (Jamarin Laboratory, Osaka) that had air enriched with 0.1–0.5% carbon dioxide bubbling through it. Culture vessels were oblong and flat. Standard conditions of culture were 25°C and continuous illumination (white fluorescent lamp, 6–7 klux). These conditions were altered for certain experiments. For light intensity and pH experiments, glass Erlenmeyer flasks containing unbubbled medium were used. For salinity experiments, Jamarin S artificial sea water containing MBM (WATANABE 1960) and vitamins was used. To determine vitamin requirements, Provasoli's ASP 2 (PROVASOLI *et al.* 1957) was used.

Culture density was estimated by measuring optical density in a spectrophotometer at 700 nm. The specific growth rate was determined during exponential growth. The growth rate during non-exponential conditions was calculated from average growth during the culture period.

Electron microscopy

Cells were washed with 50 mM phosphate buffer containing 0.25 M sucrose (pH 7.2), fixed with 2% glutaraldehyde in the same buffer for 9 hr at ca. 4°C, post-fixed with 2% OsO₄ in the same buffer without sucrose for 24 hr at ca. 4°C, embedded in agar, dehydrated in a graded ethanol series (50% to 100%), transferred to acetone, and embedded in Spurr's resin (SPURR 1969). Following polymerization, sections were cut with a Porter-Blum MT-2 Ultramicrotome, stained with lead citrate for 10 min., and viewed with a JEM 200 CX electron microscope at 100 kV.

Pigment analysis

Pigments were extracted by treating the cells, which were first washed with artificial sea water, with 85% acetone. Extracted pigments were separated on columns of sucrose using 0.5% n-propanol in petroleum ether (b.p. 30–60°C) as the developing solvent. Each fraction was eluted diethyl ether and further separated using thin-layer chromatography (TLC) with cellulose plates (Merck) and a running solvent of petroleum ether: n-propanol (96:4 v/v) or petroleum ether: acetone: n-propanol (90:10:0.45 v/v). Rf values were calculated and absorption spectra examined. Chlorophyll *c* was sought using a spectrophotometer after separation of the extracted pigments by TLC with cellulose plates and a running solvent of petroleum ether: chloroform (1:3 v/v). Carotenoids were extracted for quantitative analysis using acetone: methanol (7:3 v/v), saponified for removal of chlorophyll, and estimated spectrophotometrically after separation by TLC.

Analysis of fatty acids

Lipids were extracted from cells with a methanol chloroform mixture and saponified in the usual manner (KATES 1972). Fatty acids were isolated from the saponification mixture using petroleum ether, methylated, then analysed by gas chromatography (Shimadzu GC-3BF).

Test for starch

Cells were decolorized with methanol, incubated in 0.2% I₂/2% KI for 20 min., then examined with an optical microscope using opal glass slides.

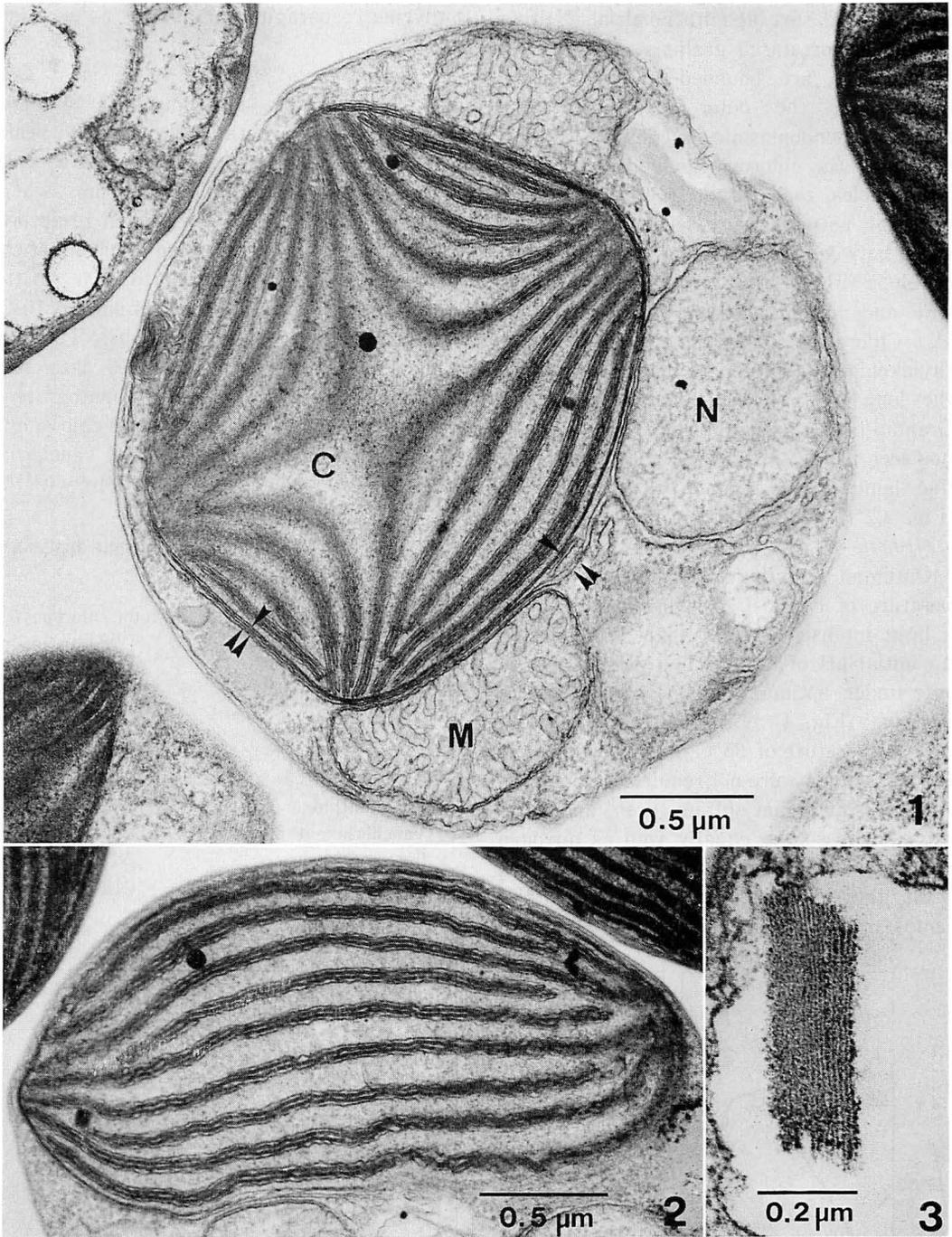
Results

Optical microscopic observations

Live cells are spherical to slightly ovoid and measure 2–4 µm in diameter. They usually contain one chloroplast. Testing with I₂/KI failed to detect starch. Vegetative multiplication takes place by binary fission. No motile cells were seen.

Electron microscopic observations

Cells are enclosed in a thin wall and contain an ovoid or cup-shaped chloroplast, a



Figs. 1-3. Electron micrographs of "marine *Chlorella*". Fig. 1. Section of whole cell. The chloroplast is enclosed by two double membranes: the outer one is the CER (double arrow head) while the inner one is the chloroplast envelope (single arrow head). Direct continuity between the CER and the nuclear envelope is observed. C, chloroplast; N, nucleus; M, mitochondrion. Fig. 2. Section of chloroplast. Bands of three associated thylakoids extend across the entire chloroplast length with no girdle lamellae. Fig. 3. Section showing fine structure of lamellate vesicle in cytoplasm.

nucleus, and several mitochondria. Neither pyrenoids nor starch grains were observed. Chloroplasts are bounded by two double membranes, the outer representing the chloroplast endoplasmic reticulum (CER) and the inner the chloroplast envelope (Fig. 1). No vesicles that might represent a periplastidal network were seen in the narrow space between the CER and the chloroplast envelope (Fig. 1). Continuity between the CER and nuclear envelope is apparent (Fig. 1). Chloroplast lamellae consist of three thylakoids running approximately parallel to the long axis of the chloroplast (Fig. 2). Granum-like stacks or girdle lamellae were not seen (Figs. 1, 2). Vesicles containing fine lamellae are common in the cytoplasm (Fig. 3).

Growth

Optimum growth was obtained at a temperature of ca. 25°C, a salinity of 15-30‰, a light intensity greater than 12 klux, and an initial pH of ca. 8. The specific growth rate under optimum conditions was about 0.9 day⁻¹ (Fig. 4). No growth was apparent at a temperature of 35°C or at a salinity of 0‰. Vitamins were not required. Potassium nitrate, ammonium sulfate, urea, and casamino acids served equally well as nitrogen sources. The alga did not grow in the dark with glucose, galactose, fructose, maltose, lactose, acetic acid, citric acid, ethanol,

glycine, asparagine, or alanine as a carbon source.

Photosynthetic pigments

The absorption spectrum of the total pigment extract in diethyl ether showed peaks at 661 nm, 470 nm, and 429 nm. No peaks or shoulders at 642 nm or 452 nm, where chlorophyll *b* would be expected to absorb, were found. The absorption spectrum of the cell suspension was similar to that of the extract except that the peaks shifted 10-20 nm toward longer wave lengths. The total pigment extract was separated into four fractions by sucrose column chromatography. The fractions were identified as chlorophyll *a*, carotene(s), violaxanthin, and vaucheria-xanthin ester by co-chromatography with the

Table 1. Photosynthetic pigment analysis of "marine *Chlorella*".

Pigment	Percent total chlorophyll or carotenoid
Chlorophyll <i>a</i>	100
Chlorophyll <i>b</i>	ND*
Chlorophyll <i>c</i>	ND
Carotene(s)	11
Violaxanthin	51
Vaucherixanthin ester	26
Lutein	ND
Other carotenoids	12

*Not detected

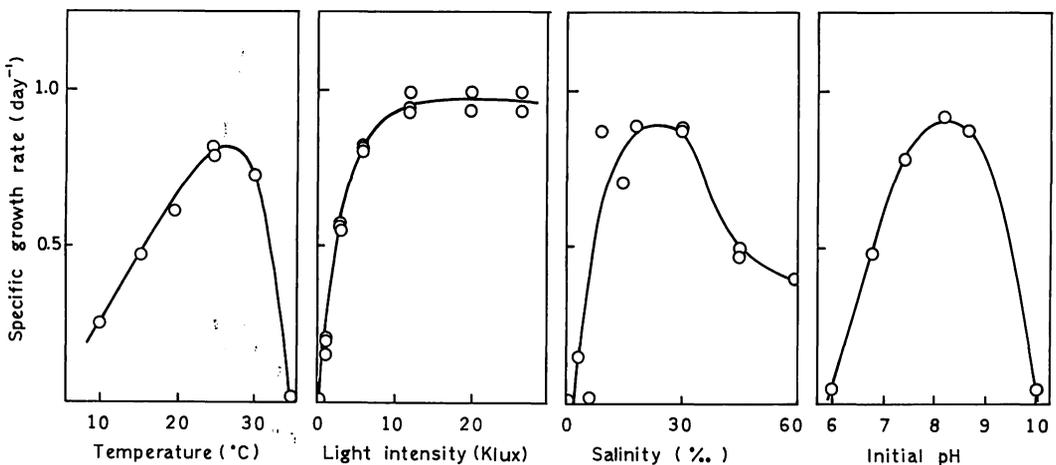


Fig. 4. Effect of culture conditions on the growth rate of "marine *Chlorella*"

Table 2. Fatty acid composition of "marine *Chlorella*".

Fatty acid	Percent total fatty acid
14:0	5.0
16:0	17.8
16:1	24.9
18:0	tr
18:1	4.9
18:2 ω 6	3.2
18:3 ω 3	1.2
20:3 ω 3)	4.2
20:4 ω 6)	
20:5 ω 3	37.1

pigments of *Monodopsis subterranea* and *Nannochloropsis oculata*. The major xanthophyll was violaxanthin. Chlorophyll *b*, chlorophyll *c*, and lutein were not detected (Table 1).

Fatty acids

The major fatty acids were eicosapentaenoic acid (20:5 ω 3), palmitoleic acid (16:1), and palmitic acid (16:0). A small quantity of the stearate family of acids were represented (Table 2).

Discussion

Since this alga grows well at a salinity of 15 to 30‰ but does not grow at a salinity of 0‰, and since the pH of optimal growth (ca. 8) agrees with that of sea water, it appears to be a marine form that grows well at moderate temperatures (ca. 25°C) and high light intensity (12–27 klux). The proportions of fatty acids, with 20:5 ω 3, 16:1, and 16:0 as the major fatty acids, are similar to those of "marine *Chlorella*" that have been reported previously (WATANABE *et al.* 1978b).

As is evident from its biochemistry and ultrastructure, however, this alga cannot be assigned to the Chlorophyceae and hence is incorrectly placed in the genus *Chlorella*. The alga lacks chlorophyll *b* and lutein, which are always present in Chlorophyceae. Chloroplasts are surrounded by two double membranes rather than one as in Chlorophyceae, and the lamellae consist of three thylakoids rather than one. Starch, which is the storage product of all Chlorophyceae, is absent. The pigments and cytological features are similar to those of *Nannochloropsis*

Table 3. Comparison of main taxonomic characteristics between *Nannochloropsis oculata* (Millport No. 66) and "marine *Chlorella*".

Characteristics	<i>Nannochloropsis oculata</i> (Millport No. 66)	"marine <i>Chlorella</i> "
Cell dimension	2–4 μ m*	2–4 μ m
Cell shape	globose*	globose or slightly ovoid
Chloroplast	single, ovoid or cup-shaped parietal**	single, ovoid or cup-shaped
Propagation	binary fission*	binary fission
Pyrenoid	rarely observed**	not observe
Chloroplast ER	present (continuous with the nuclear envelope)**	present (continuous with the nuclear envelope)
Thylakoid arrangement	3-thylakoid lamellae**	3-thylakoid lamellae
Girdle lamellae	absent**	absent
Lamellate vesicles	in chloroplast**	in cytoplasm
Predominant photosynthetic pigments	chlorophyll <i>a</i> carotene violaxanthin vaucherixanthin ester**	chlorophyll <i>a</i> carotene violaxanthin vaucherixanthin ester

*DROOP, 1955 **ANTIA *et al.*, 1975

oculata (DROOP) HIBBERD, an alga which has been assigned to the Eustigmatophyceae on the basis of pigment composition and ultrastructure (ANTIA *et al.* 1975). A comparison with *N. oculata* is made in Table 3. The characteristics agree with two exceptions. First, pyrenoids have been seen in *N. oculata*, although rarely (ANTIA *et al.* 1975), whereas they have not been found in the alga under study. Second, lamellate vesicles, which in the present study were found abundantly in the cytoplasm (in agreement with other eustigmatophytes; [HIBBERD and LEEDALE 1972, HIBBERD 1974]), occur only in the chloroplast of *N. oculata* (ANTIA *et al.* 1975). The pyrenoid of *N. oculata* is similar to the polyhedral pyrenoid characteristic of eustigmatophytes. Its rare appearance suggests that it is a transient feature related to metabolic condition (ANTIA *et al.* 1975). It is possible that a pyrenoid will be detected in the present alga during further study. The discrepancy between the position of the lamellate vesicles cannot be resolved at the present time. HIBBERD (1981) commented that a great deal of uncertainty still remains regarding the small forms classified in the Monodopsidaceae, which includes *Nannochloropsis*, since they are difficult to fix for EM and have relatively few non-ultrastructural anatomical characters.

Additional similarity to the Eustigmatophyceae is found in the composition of fatty acids. Like *N. oculata* (unpublished data) and the related freshwater alga *Monodopsis subterranea* (NICHOLS and APPLEBY 1969) the alga under study contains 20:5 ω 3, 16:1, and 16:0 as major fatty acids and contains a small quantity of the stearate family of acids.

Since the similarities outweigh the discrepancies, it seems appropriate to identify the alga under study as *Nannochloropsis oculata* on the basis of its pigment composition and cytological characteristics.

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丸山 功・中村寿雄・松林恒夫・安藤洋太郎・前田直彦：いわゆる海産クロレラの分類学的性質

水産種苗の初期餌料として重要なシオミズツボワムシの生産に広く用いられる海産クロレラと呼ばれる藻の一つについてその性質を調べた。この藻は通常1個のカップ型または卵型の葉緑体を有する球形あるいはだ円型の細胞であり、主な光合成色素として chlorophyll *a*, carotene, violaxanthin, vaucherixanthin ester を含んでいた。電顕観察の結果、核膜と連結したクロロプラストERが葉緑体を取り囲み、葉緑体を囲む膜は葉緑体包膜とクロロプラストERで4枚に観察された。ラメラは三重チラコイドラメラ構造をしていた。この藻は形態、微細構造、色素組成の特徴から現在のところ、真正眼点藻綱 *Nannochloropsis oculata* HIBBERD と同定するのが適当と思われる。(833 福岡県筑後市久富1343番地 クロレラ工業株式会社)

新 刊 紹 介

K. KRAMMER and H. LANGE-BERTALOT (1986) **Bacillariophyceae I. Teil: Naviculaceae.** In H. Ettl, J. Gerloff, H. Heynig and D. Mollehauser [eds.] Süßwasserflora von Mitteleuropa. Bd. 2. Gustav Fischer Verlag, Stuttgart, New York. 876 pp. 206 図版 2976 図。(含船郵送料邦貨約18000円)。

本書は“Süßwasserflora von Mitteleuropa”シリーズ24巻中の1つである。今回出版されたのは2巻1号で Naviculaceae を網羅しており、今後他の科についても2号、3号で出版される予定となっている。

内容は大きく2つに分けられており、第1部では、用語、殻の構造、生殖、細胞構造、殻形成、運動、生態、研究方法などが概説され、第2部でそれぞれの種について記述がなされている。ここで扱われている属は *Navicula*, *Stauroneis*, *Anomooneis*, *Frustulia*, *Amphipleura*, *Neidium*, *Scolioleura*, *Diploneis*,

Pleurosigma, *Gyrosigma*, *Cymbella*, *Amphora*, *Gomphonema*, *Gomphoneis*, *Didymosphenia*, *Rhoicosphenia*, *Caloneis*, *Pinnularia*, *Mastogloia*, *Diatomella*, *Oestrupia*, *Entomoneis* の22属である。全ての種類が光顕写真で示されており、一部には類似した種類間での相違点が電顕写真によって示されている。

本書は HUSTEDT の Bacillariophyta (1930) 及び Kieselalgen (1930~1966) が元になっており、材料の多くは HUSTEDT のコレクションの中から選ばれている。そして特筆すべきことはその中に多くのタイプ標本が含まれ、それが写真によって示されていることである。これは大変貴重なものであり、本書の価値を非常に高めるものであり、利用者にとっては大変有用なものとなるであろう。

(筑波大学生物科学系 出井雅彦)

チミケップ湖のカラフトマリモ

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KANDA, F. 1986. *Cladophora sauteri* (NEES) KÜTZING f. *kannoi* (TOKIDA) SAKAI in Lake Chimikeppu, Hokkaido. Jap. J. Phycol. 34: 326-331.

Lake Chimikeppu, which lies about 20 km south of Kitami in Hokkaido, is a freshwater lake, 22 m deep and covers 1.2 km². An alga identified with *Cladophora sauteri* f. *kannoi* has been reported in this lake based on the specimen collected on August, 1937. Since then no one could collect the alga in the Lake Chimikeppu. The author collected the alga at one point in the lake on 24 October, 1985.

The morphological details and distribution of the alga in the Lake Chimikeppu were investigated.

Most plants of the alga grow on gravel or stones. Individual filaments are 0.5-1.5 cm long, branched densely. Many adventitious rhizoids descend from any portions of fronds, and some of them attach to coarse sand grains. Branches are alternate, sometimes opposite, composed of cylindrical or sometimes slightly clavate cells. The diameter of the cells of branches of the alga is 40-100 μm (mean value: 63 μm) and the length of the cells is 100-800 μm (mean value: 429 μm). The ratio of length to diameter of the cells of branches is 2-14 (mean value: 6.9). Branchlets are composed of cylindrical cells. The diameter of the cells of branchlets of the alga is 39-70 μm (mean value: 51.7 μm) and length of the cells is 200-900 μm . The ratio of length to diameter of the cells of branchlets is 4-18 (mean value: 9.3).

The diameter of the apical cells of branchlets of the alga is 35-58 μm (mean value: 46.3 μm), and the length of the apical cells of branchlets is 380-1570 μm (mean value: 852.2 μm). The ratio of length to diameter of the apical cells of branchlets is very high, 8.0-30.8 (mean value: 17.1).

The present alga is identified with *Cladophora sauteri* (NEES) KÜTZING f. *kannoi* (TOKIDA) SAKAI in many points and it differs chiefly from the other forms of *Cladophora sauteri* in its longer cells especially in apical cells, reaching 30.8 times as long as diameter.

Key Index Words: *Cladophora sauteri*; *Cladophora in Japan*, freshwater alga; lake ball; Lake Chimikeppu; Marimo.

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チミケップ湖は北見の津別町にあり、周囲を針広混交林に囲まれ、比較的原生環境の保たれた湖である。この湖にマリモ類が産することは1934年の菅野の論文で初めて報告され、その後、SAKAI (1964) によりカラフトマリモ (*Cladophora sauteri* (NEES) KÜTZING f. *kannoi* (TOKIDA) SAKAI) として報告されている。しかし正式な採集記録としてはSAKAI (1964) の論文中にみられる1937年のMATSUDAによるもの以降採集されていなかった。この間、1965年に山田と道・国の文化財関係者はマリモ調査を行っているが、発見し

ていない(徳井, 1965)。また、徳井も採集することが出来なかったと述べている(徳井 1965)。近年、安原・新崎 (1979) もこの湖にマリモ採集に行ったが見つけることはできなかった。筆者も1981年に文献などからチミケップ湖で最もマリモが生育している可能性の高い北部一帯を調査したが採集できなかった。しかしながら、1985年10月にチミケップ湖に於て再び調査を行った結果、この湖からマリモ類を採集できたので採集地点や形態の観察結果をここに報告する。

調査地と調査方法

チミケップ湖は北海道東部、北見市の南方約 20 km の津別町にある。東経 143 度 52 分～54 分、北緯 43 度 38 分～39 分に位置し、長軸 2.3 km、最大幅 0.8 km で北西～南東へやや細長い形をしている (Fig. 1)。面積は 1.2 km² で、湖岸線は 7.5 km ある。最大深度は 21.3 m である (北海道生活環境部, 1984)。この湖には無名のいくつかの小さな川が入り込んでおり、流出河川はチミケップ川である。チミケップ川はその後、網走川に合流している。

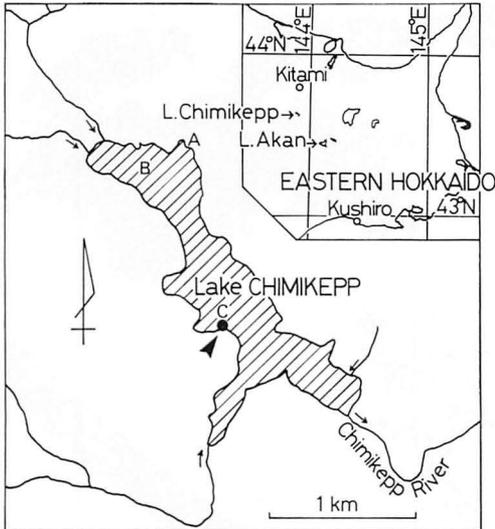


Fig. 1. Maps showing the locality of Lake Chimikeppu and the collection site (arrow) of *Cladophora sauteri* f. *kannoii*.

チミケップ湖は本邦におけるヒメマスの原産湖で、湖の周囲は道有林として非常に良く保護されており、湖畔の一部に鹿鳴荘と名づけられている宿泊所と YMCA の建物以外は北部にキャンプ場があるのみである。湖周囲の森林は針葉樹としてトドマツ、エゾマツを主体とする針広混交林で、広葉樹としてはシナノキ、エゾイタヤ、ヤチダモ、カツラ、センノキ、オヒョウ、ケヤマハンノキがある (館脇, 1954)。

マリモの採集は1985年10月24日に行った。採集方法は、ゴムボート上で、採取網を用いて行った。採取網は直径 21.5 cm の金属枠で囲われた布製のもので、中央部は径約 10 cm の金属メッシュになっている。メッシュの目の大きさは 0.67 mm である。

結 果

マリモの生育地点

従来、マリモが生育していたであろうとされる地点は Fig. 1 の A 地点の YMCA のロッジのあるキャンプ場周辺である (安原・新崎, 1979)。ここは湖岸にヨシ (*Phragmites communis*) がよく繁茂しており、水深も 2 m 前後の所である (Fig. 2A)。湖岸に沿ってこの付近一帯を採集用網を用いて探したが、1981年に引き続き今回も発見出来なかった。また、チミケップ湖の B 地区は湖の中央部であるが、この水深は浅くなっており、1.1～1.3 m しかなく、水深から言ってマリモ類が生育している可能性があるが、採集出来なかった。

今回マリモ類を採集出来たのは Fig. 1 の C 地点である。湖岸から 5～10 m の所に幅約 20 m にわたって分布していた。この水深は 90 cm であつこ。10月24

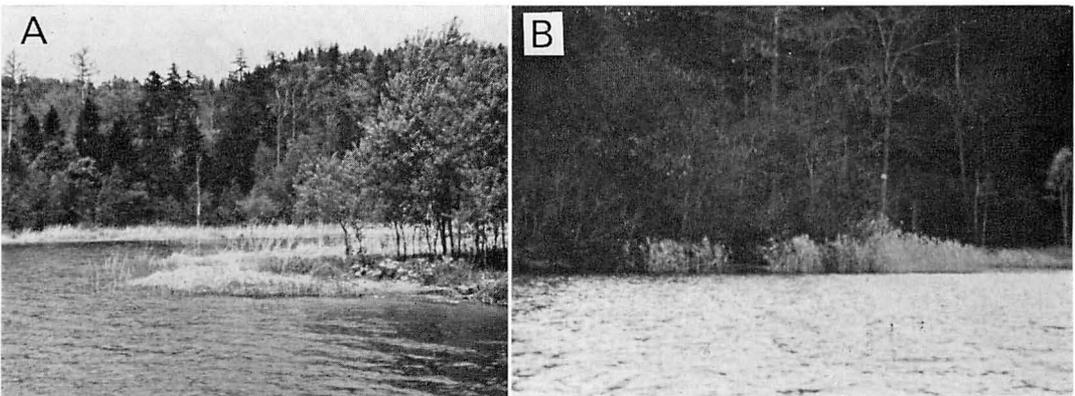


Fig. 2. A. The northern site of Lake Chimikeppu (site A in Fig. 1); B. The collection site of *Cladophora sauteri* f. *kannoii* (Site C in Fig. 1).

日の水温は湖表面で 10.8°C であった。当日の気温は 5°C で天気は雨〜みぞれであった。湖岸の植生はヨシで (Fig. 2B), この湖水中には他の水草は見られなかった。生育地の底質は岩や石で非常に堅かった。

マリモの形態

採集された *Cladophora sauteri* は全て石に附着していた。石は大きい物でも径 5 cm 程で、1 mm 以下の砂に附着しているものもあった (Fig. 3A, 3B)。阿寒湖やシラルトロ湖に見られる様ないわゆる石などに附着しない、浮遊状のものは見られなかった。Fig. 3C に示したように、ここの *Cl. sauteri* は糸状体の長さ

が 0.5~1.5 cm で、附着部分は仮根からなっていた (Fig. 3D)。仮根は藻体のいろいろな部分から不規則に出ていた。糸状体は一系列細胞で密に枝分かれしていた。分枝のしかたは互生 (Fig. 3F) あるいは偏生 (Fig. 3G) で基部では対生の場合もあった。枝分かれの仕方は糸状体によって異なっており、割合に規則的に枝分かれしているものと、非常に不規則になっているものがあった。前者では枝と小枝との成す角度も鋭角で阿寒湖やシラルトロ湖のものと殆ど区別がつかなかった。後者はいろいろな所から仮根を出して小さな石に附着している場合にみられ、小枝と枝との成す角度も鋭角のも鈍角のもあった (Fig. 3D)。

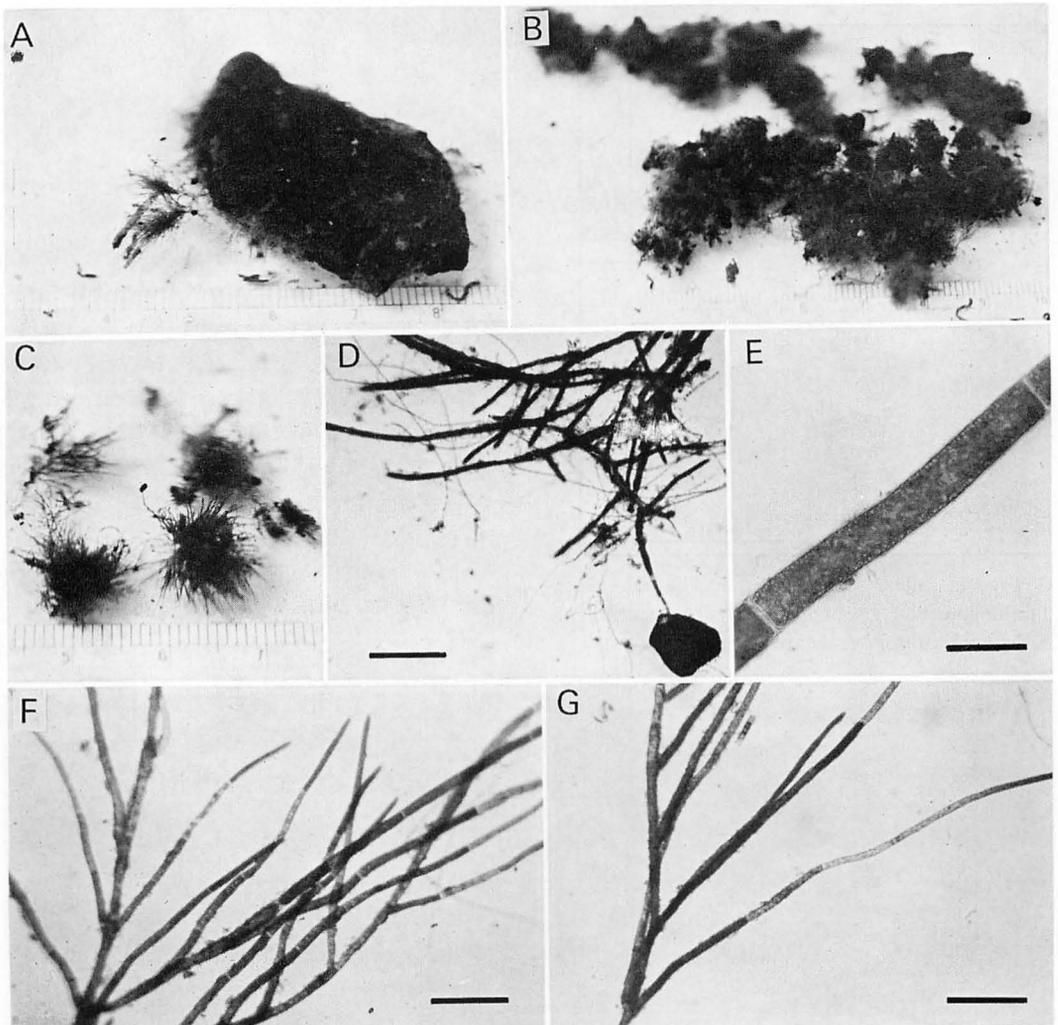


Fig. 3. A. *Cladophora sauteri* f. *kannoi* growing on a stone collected from the bottom of Lake Chimikeppu; B-C. Aggregation of filaments attaching to gravel or sand; D. Lower portion of filaments (scale, 500 μ m); E. Cylindrical cells (scale, 100 μ m); F. Middle portion of filament; G. second type branching of the alga.

糸状体を構成している細胞は基本的には円柱状であり (Fig. 3E), 基部に近い細胞ではやや棍棒状をしているものもあった。最末小枝の細胞の径は Fig. 4B に示したように大部分が 40~70 μm に集中して分布していた。計測した 101 細胞の平均は 51.7 μm であった。最末小枝の細胞の長さは Fig. 5B に示した様に 200~900 μm の範囲にあり, 多くは 300~600 μm に分布していた。平均では 474.3 μm であった。

最末小枝を除く枝の細胞の径は, Fig. 4A に示したように 40~100 μm に分布しており, 最末小枝に比べると均一性に欠けていた。計測した 92 細胞の平均は

63.2 μm で, 最末小枝よりもやや大きかった。枝の細胞の長さは Fig. 5A に示したように 100~800 μm に分布しており, 最末小枝と殆ど同じようなパターンであった。平均は 429.1 μm であった。

細胞の長さとの比は Fig. 6 に示したようなパターンとなり, 最末小枝で, 4~18 に分布しており, 平均では 9.32 であった。枝の細胞の場合は 2~14 に分布しており, 平均で 6.91 であった。これらのことから最末小枝の細胞の長さは枝の細胞と同じであるのに細いために比の値が小さくなって, より細長い細胞となっていることがわかる。

このマリモ類で目立つのは最末小枝の先端細胞は長いものが多いことである。300~1600 μm までみられた。平均でも 852.3 μm となった。従って細胞の長さとの比も非常に大きく 8.0~30.8 までみられ, 平均でも 17.1 であった。

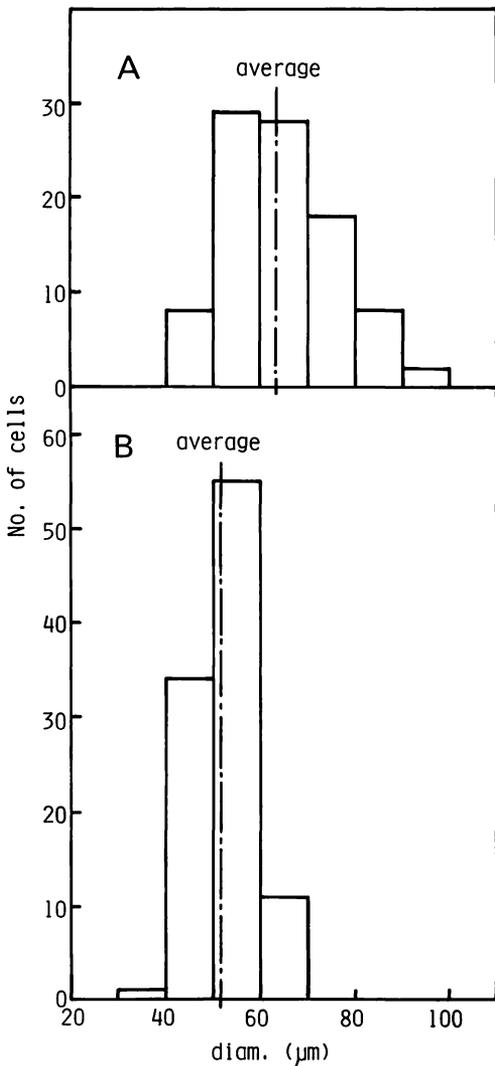


Fig. 4. Distribution in diameter of filaments of the alga from Lake Chimikeppu: A. Cells of branches; B. Cells of branchlets.

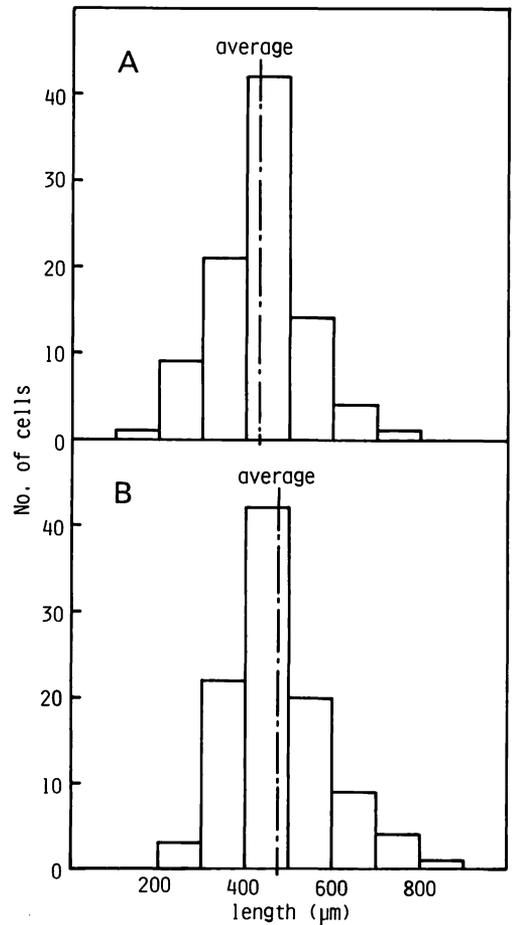


Fig. 5. Distribution in length of cells: A. Cells of branches; B. Cells of branchlets.

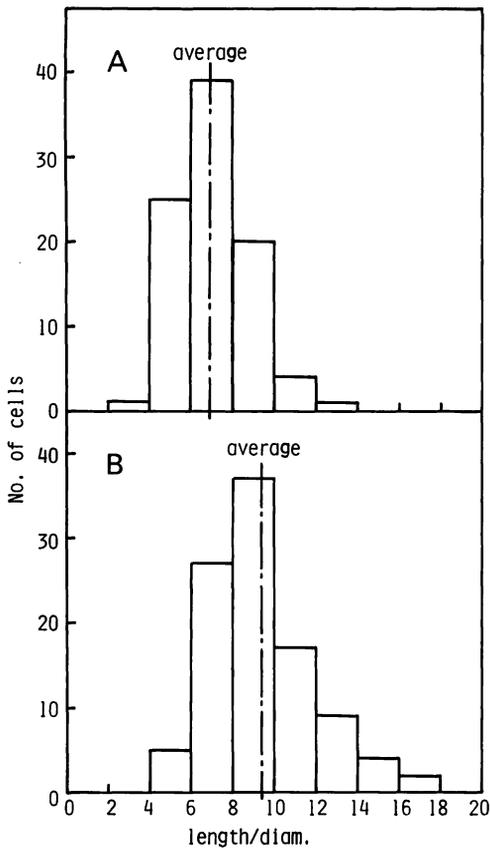


Fig. 6. Distribution in the ratio of length to diameter of cells: A. Cells of branches; B. Cells of branchlets.

考 察

チミケップ湖のマリモに関して、最初に記述したのは菅野 (1934) で、その中で、彼はチミケップ湖のマリモは昭和2年千高エトロフ島内保湖で採集された *Aegagropira sauteri* var. *Borgeana* (BRAND) NORDSTEDT と同じものとしている。この報告の中ではチミケップ湖のマリモについては不規則形の扁平集団が多く稀に球状集団があると記しているのみで、糸状体についての記載はなされていない。一方、SAKAI (1964) はチミケップ湖のマリモを *Cladophora sauteri* f. *kannoi* (TOKIDA) SAKAI (和名: カラフトマリモ) とし、内保湖産のものを *Cladophora sauteri* f. *kurilensis* (NAGAI) SAKAI (和名: チシママリモ) として区別している。SAKAI (1964) はその報告の中で、カラフトマリモと他の品種での大きな違いは細胞の長さとの比が大きいことをあげている。すなわ

ち、f. *kannoi* では細胞の長さとの比は(4-)7-20(-26)であり、他の f. *kurilensis* と f. *sauteri* では(3-)6-12(-17)であるとしている。この点に関して、今回詳しく調べた所では、枝や最末の小枝の細胞に関しては、チミケップ湖から採集されたものと、*Cl. sauteri* f. *sauteri* や *Cl. sauteri* f. *kurilensis* とでは、ややチミケップ湖のものの方が大きい傾向がみられた程度であった。しかしながら、小枝の先端細胞の長さとの比に関しては、その値が非常に大きく、30.8にも達した。この点に関して SAKAI (1964) はこの特徴をチミケップ湖のものとの品種を区別する点としてあげており、筆者も今の所、この特徴で他の品種と区別しておいた方が良いと思う。ただ、菅野 (1934) や SAKAI (1964) の記述に見られるような球形ないしは不規則形の扁平集団は全く見られなかった。このような僅かな違いが系統的にどれほど意味があるか疑問であるが、かといってこれらの品種を同じ物とする (VAN DEN HOEK, 1963) にはまだ調査が不十分と思われる。従って現在の所、別品種として扱っておくのが妥当ではないかと筆者は考えている。

最後にマリモの生育環境について若干考察してみたい。マリモの生育環境に関しては水質が重要な要素と考えられる。チミケップ湖の水質を調べた例としては、1982年北海道生活環境部の調査結果がある (北海道生活環境部, 1984)。それによれば湖の中央部で表面から水深5mまでの範囲で、pH; 7.8~7.9, DO; 7.6~8.4 mg/l, COD; 3.0~3.5 mg/l, BOD; <0.5~0.6 mg/l となっている。また、全リンは 0.004~0.023 mg/l, 全窒素は 0.147~0.221 mg/l である。これを阿寒湖のデータ (青井・中村, 1976) と比較してみると、pH では阿寒湖の方がやや高く (1973年7月7日のデータで、8.2~8.3), DO では 9.2~10.0 mg/l, COD; 3.3~5.2 mg/l, BOD; 0.5~1.1 mg/l と何れも大差はなかった。全リンは比較するデータが無いが、全窒素は阿寒湖で 1.19~2.9 mg/l と阿寒湖の方が約10倍も高い。pH についてはマリモはアルカリを好むと言われており (VAN DEN HOEK, 1963), この点からは阿寒湖の方がアルカリでありマリモの生育に適しているのではなかろうか。窒素量は阿寒湖で非常に高く、マリモの現存量も阿寒湖の方がチミケップ湖よりはるかに多いことから阿寒湖の窒素量の方がマリモの生育に適しているようにみえるが、昨年 (1985) 10月に筆者が阿寒湖で調べた際にはアオコが僅かではあるが湖表面に見られ、マリモ生育地の近くに魚の養殖場が在ること、水質に関しての一般的な点から見ると窒素のこの

ような値は決して水質のきれいなことを示しているものではなく逆に富栄養化を示していると思われることなどから、マリモにとって阿寒湖の方が窒素の条件が整っているとは必ずしも言えないであろう。

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川嶋昭二： 外国産コンブ目植物の漂着記録 (2). オニワカメについて Shoji KAWASHIMA : Drifting records of alien species of the Laminariales (2). *Alaria fistulosa* POSTELS et RUPRECHT.

(2) *Alaria fistulosa* POSTELS et RUPRECHT オニワカメ

オニワカメはアラスカ南東部からアリューシャン列島を経て千島列島エトロフ島までの北太平洋沿岸に分布するが、さらにオホーツク海を距てて宗谷海峡の二丈岩にも生育している (WIDDOWSON 1971)。

葉体は全長 25 m に達し、日本周辺では最大の海藻として知られるが、*Alaria* 属の他種と違って中肋が太く、中空で、竹のような隔壁があることや、成実葉または附着器の形などから、たとえ細片でもそれと見分けられる明瞭な特徴をもっている。

この海藻は北海道から手のとどくような近くに分布しながら、今のところ北海道沿岸では利尻島のコンブ養殖用フロートに着生していた例 (山本・鳥居 1983)

を除き、自生地は全く発見されていない。しかし、宮部 (1902) が北見地方への漂着をのべているように流れ藻としては古くから知られている。岡村 (1936) が産地としている釧路も漂着した地方を示すと思われる。ただ、宮部も岡村も実際の地点は示していない。Fig. 1 には、これらの文献以後に発表された漂着地 (○印) と、著者の集めた新たな漂着地 (●印) をそれぞれの漂着年月日とともに示した。これらのうち、他から得た情報はそれぞれ本文中に記してある。

この図によると、オホーツク海北部の枝幸から道東太平洋の床潭 (厚岸町) の間で、1944年から1985年までに11回の漂着記録があり、その多くは6~8月に集中している。しかし実際はこれよりはるかに多く、季節を問わず発見できると思われる。オホーツク海沿岸

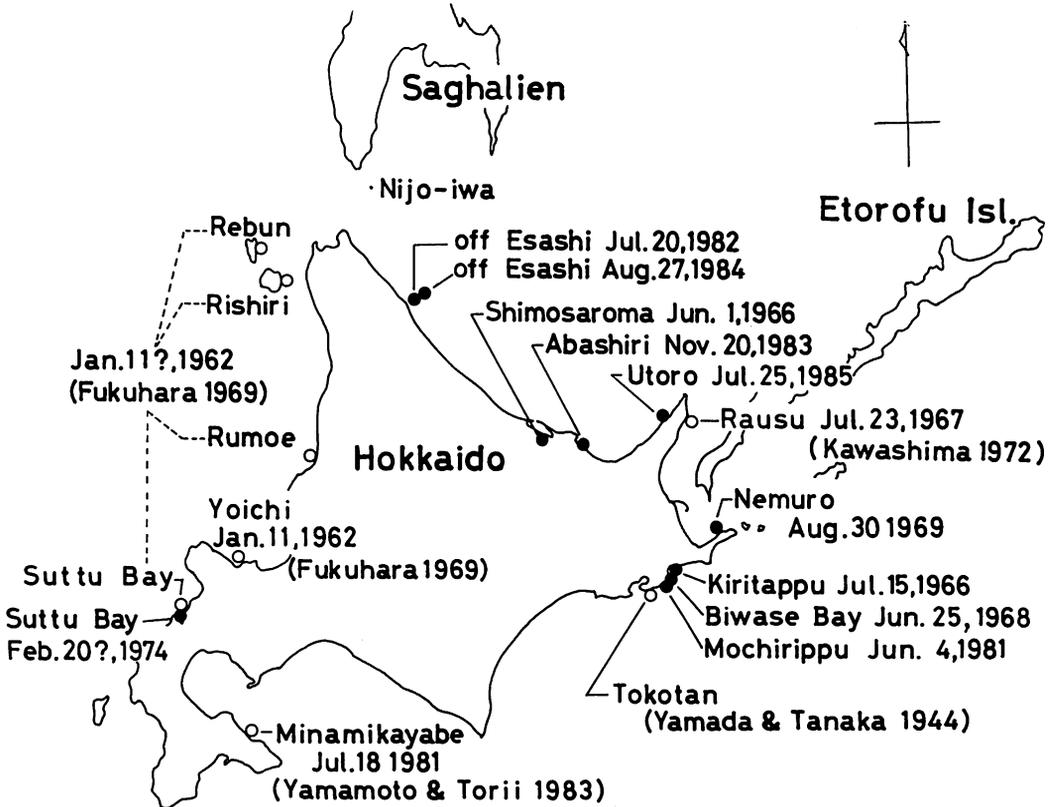


Fig. 1. A map of Hokkaido showing localities where *Alaria fistulosa* were drifted ashore. ○, already known locality by the past literature; ●, new locality by the author.

に漂着するものは二丈岩周辺から宗谷暖流に乗って、また道東太平洋沿岸で発見されるものは千島から親潮に運ばれてくるものであろう。ちなみに漂着の南端記録は渡島管内南茅部町である (山本・鳥居 1983)。

これにくらべて日本海沿岸への漂着は今のところ2回しか記録がない。しかし、福原 (1969) が報告した1962年1月11日前後の漂着例は、大量の流れ藻として利尻、礼文両島から留萌、余市、寿都の各地にまで打ち上げられており、これほど広範囲に、ほぼ同時に漂着した例は他に記録がない。また1974年2月20日頃に再び寿都湾沿岸に打ち上げられた時も、かなりの量であったらしい (北海道新聞 1974年2月26日付)。福原も述べているように、対島暖流の北上するこれらの沿岸に北方から大量の流れ藻が漂着するのは珍らしいことである。しかし、それが比較的まれな年に、また厳冬期にだけ記録されることは海流よりもむしろ、日本海に大しけをもたらす大陸からの季節風 (北西風) の

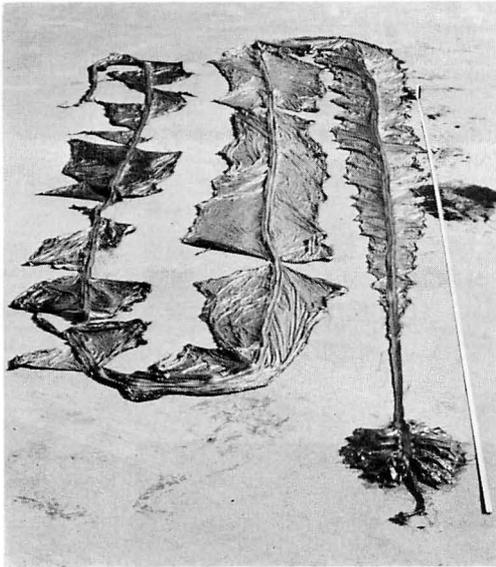


Fig. 2. A driftage of *Alaria fistulosa* at Esashi (枝幸), the Okhotsk coast of Hokkaido, July 20, 1983. (14.7 m in length)

影響かも知れない。

漂着する藻体の大部分はオホーツク海や道東太平洋ではおそらく2年目以上の大きなものであるが、破損が烈しくて中肋だけ、あるいはわずかに葉片が残っていたり、成実葉や附着器も失われていることが多い。そのような中で、Fig. 2 に示した藻体 (1982年7月20日、宗谷管内枝幸沖、鳥居茂樹氏提供) のように全長 14.7 m、葉幅 60 cm を越える新鮮、かつ完全なものが多数発見された例もある。また藻体が小さな例としては同じ枝幸沖で1984年8月27日に発見された漂流中の *Laminaria* sp. の茎に着生していた 1-35 cm の20個体ほどの幼体 (四ツ屋義則氏提供) があり、中肋の隔壁形成を知る上で貴重な標本である。福原 (1969) の報じた余市に漂着した藻体が 1.5-2 m くらいの若いものであったのは、おそらく前年発生のものであると考えられる。

情報と標本の収集に協力いただいた鳥居茂樹氏と四ツ屋義則氏にお礼申し上げる。

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(042 函館市湯川町1丁目 2-66 北海道立函館水産試験場)

— 学 会 録 事 —

1. 昭和62・63年度会長及び評議員選挙

去る7月15日に投票用紙と選挙人名簿を発送し、次期会長と評議員の選挙を実施した。8月15日に投票を締め切り、8月20日に渡辺 信（国立公害研究所）及び宮地和幸（東邦大・理・生）の両氏立会いのもとに開票が行われ、次の方々を選出された。

会 長 梅崎 勇

評議員 三本菅善昭・藪 熙（北海道地区）

谷口和也（東北地区）

千原光雄・山岸高旺・原 慶明・小林 弘

三浦昭雄（関東地区）

横浜康継・喜田和四郎（中部地区）

榎本幸人・巖佐耕三・石川依久子（近畿地区）

大野正夫・秋山 優（中国・四国地区）

右田清治・奥田武雄（九州地区）

2. 日本藻類学会第2回秋季シンポジウム

10月6日、日本植物学会第51回大会の関連集会として日本藻類学会秋季シンポジウムが野澤治治氏（鹿児島大学水産学部）と新村 巖氏（鹿児島県水産試験場）を世話人として鹿児島大学水産学部において開催された。昨年の新潟に続いて2回目の開催である。鹿児島は水産学研究所の盛んな地であるため、世話人のお二人にはそろって演者もお願いすることになった。演題は野澤治治、竹内 幹、新村 巖の三氏による「漸深帯

海藻群落の植物社会学的研究」と新村 巖氏による「南日本におけるガラモ場造成に関する問題点」であった。座長は奥田武雄氏（九州大学農学部）であった。会員の多くにとっては遠方で行われたにもかかわらず全国から51名の参加者があり、2時間にわたって講演と論議が行われた。シンポジウム終了後記念写真の撮影を行い、引き続いて同大学生協食堂において野呂忠秀氏（鹿児島大学水産学部）の司会で懇親会が開催された。会は世話人の野澤治治氏の挨拶に始まり、田中剛氏の乾杯の音頭で幕を開け、薩摩料理を楽しみながら2時間近くにわたってなごやかに行われた。

懇親会出席者は次のとおり。秋山 優、新崎盛敏、鯨坂哲朗、井浦宏司、猪川倫好、石川依久子、市村輝宜、出井雅彦、井上 勲、梅崎 勇、榎本幸人、恵良田真由美、奥田一雄、奥田武雄、長田敬五、大島海一、太田雅隆、大塚晴江、笠井文絵、加崎英男、勝俣亜生、加藤季夫、小林艶子、新村 巖、須田彰一郎、税所俊郎、高橋永治、田中 剛、坪 由宏、長島秀行、南雲保、野崎久義、野澤治治、野呂忠秀、原 慶明、福島博、藤田隆夫、舟橋説往、堀 輝三、本多正樹、真部永地、溝口裕代、宮地和幸、山岸高旺、吉川浩二、吉崎 誠、古武佐紀子、吉田忠生、渡辺 信。

野澤治治氏、新村 巖氏、野呂忠秀氏には会場の手配から当日の運営にわたる全てに行き届いた配慮を頂いた。記してお礼申し上げる。



会 員 異 動
新 入 会

住 所 變 更

退 会

小保方潤一（北海道），新田勇次（東京都），水島富人（愛知県），伊藤善夫（島根県），R. TOWNSEND, H. B. S. WOMERSLEY (オーストラリア), J. McLACHLAN (カナダ), W. F. FARNHAM (イギリス), R. E. NORRIS (南アフリカ), H. W. JOHANSEN (アメリカ)

賛助会員

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第13期初めての勧告・要望出る

昭和61年11月 日本学術会議広報委員会

日本学術会議は、去る10月22日から24日まで第101回総会（第13期の4回目の総会）を開催しました。

今回の「日本学術会議だより」では、今総会で採択され、政府に勧告した「国立代用臓器開発研究センター（仮称）の設立について」及び要望した「我が国における学術研究の推進について一大学院の充実等を中心として一」を中心として、同総会の議事内容をお知らせします。

また、来年1月に開催を予定している本会議主催の公開講演会等についてお知らせします。

総会報告

総会はその初日に、会長からの経過報告、各委員会報告に続き、規則などの改正、勧告・要望の提案がなされ、午後の各部会での審議の上、2日目午前中にこれらの採決が行われた。なお、前日、21日午前中に全員が出席する連合部会が開催され、これらの案件の予備的な説明・質疑が行われた。3日目は午前中、常置委員会、午後は特別委員会が開催された。

総会の冒頭に先に逝去された、第3部会員高宮 晋氏（部長）を追悼した後、新たに任命された野口 祐会員が紹介された。また、チェルノブイリの原子力発電所事故について、原子力工学研究連絡委員会委員長から8回の会合における検討に基づく、この研連の見解「原子力の平和利用と安全性」が委員長の国際原子力機関での事故調査検討状況と共に報告された。

総会で決定された事項は、すべて「日本学術会議月報」11月号に詳しく掲載されるので、主要な項目の説明にとどめる。まず、第1常置委員会で鋭意検討されてきた、会則の改正、規則及び内規等が次のように採択された。会則の改正は、「衛生学研連」から「環境保健学研連」への名称変更である。規則の改正は、昭和63年度の第14期会員推薦手続きの手直しであって、その第1は、学術研究団体（学・協会）の登録に際し、従来の方式に加えて会員名簿などの添付を要請すること、会員推薦の場となる「推薦研連」に登録する学・協会を確保する方策などである。第2は、この登録された学・協会が会員候補者を届け出る際の記載事項を追加して、推薦人の判断資料を充実させることである。最後に推薦研連が熱工学研連から機械工学研連へ、衛生学研連から環境保健学研連へと変更された。

内規の改正は、日本学術会議の活動の周知と学・協会との連絡・協力を維持・強化するために、「連絡学・協会」の名の下に多くの学・協会との緊密な連絡を保ってきたが、今回、これを「広報協力学術団体」と改称し、別項のようにさらに広い範囲の学・協会と連携を図るようにしたものである。

特別委員会のうち、国際協力事業特委は任務を終了したので、それに代わり、人材養成などを含めて総合的・学際的・広域的な地域の研究機関のあり方を検討するために、「地域の研究推進特委」が設置され、直ちに委員を選出して活動を開始した。

本総会では、第7部提案の「国立代用臓器開発研究センター（仮称）の設立について（勧告）」、第4常置提案の「我が国における学術研究の推進について一大学院の充実等を中心として一（要望）」が採択され、直ちに内閣総理大臣始め関係諸機関等に送付した。これらの詳細は別項及び月報所載のとおりである。

第2日目午後、「高度情報社会の展望と課題」について自由討議を行った。

国立代用臓器開発研究センター（仮称）の設立について（勧告）

人体のある臓器が障害を受け、従来の治療によっては、もはやその機能の回復が不可能になった場合には、当然、死に至るわけであるが、近代医学は、その臓器の機能を他のもので代替することによって、未だ完全の状態と言えないまでも生命の維持を可能にしている。その一つの手段が人工臓器であり、もう一つが臓器移植である。両者は代替という同じ目標を持ちながら、全く異なった研究アプローチで、それぞれ独立したテーマとして発足し、今日の進歩をみている。例えば腎臓移植と人工臓器との関係では、両者の技術は全く異なっている。しかし、慢性腎不全の治療における両者の相補的效果は極めて高いものである。人工臓器と臓器移植とはあたかも車の両輪のような関係にあるので、医療の場において両者を一体化した医療システムが強く要求されている。

このような関係にある両者を合わせ、代用臓器と呼んでいるが、この研究が今後飛躍的に進めば、臓器疾患に悩む患者の治療に貢献することは間違いない。一方これら研究の我が国の現状をみると、個別的に極めて優れた成果を挙げているものもあるが、全体的にはまだ十分の研究体制が整っているとはいえない。その理由を考えてみると、臓器移植の面では、臓器取得に関連して、我が国の脳死問題を含む死の判定等人の考え方の相違に基づくと思われる問題が大きいことである。人工臓器の面では、基礎材料の研究に始まり、エネルギー、エネルギー変換機構、駆動機構や臓器機能の制御システムの開発などは、各分野の専門家による有機的な組織のもとでの研究が必要であるにもかかわらず、そのような研究体制が我が国にはなかったのである。

医学、薬学、生物学、理学、工学、農学にわたる分野の研究者が緊密な協力研究を行い、臓器置換を安全に、有効に行うため生体生理機構を解明しつつ、システムとテクノロジーを確立することが緊急に必要と考えられる。ただ本研究は臓器置換という生命の尊厳に係わる医の倫理問題が関係しているため、本研究センターの運営には、人文社会科学系の方々の参加を求め、また、本研究センター内の活動に係わっては、研究者の倫理的思考の行き過ぎを抑制し、社会の理解を深めるなど医の倫理を検討する組織の設置を計画し、運営機構が一方では開発研究にあたって独創的研究を積極的に推進し、臓器置換という医療がここに飛躍的に進展するよう期待したい。

詳細は日本学術会議月報11月号を参照されたい。

我が国における学術研究の推進について —大学院の充実等を中心として—(要望)

次の代を担う若い人達をどうしたら立派に育成することができるかという問題は、その国の将来を決める上で重要である。日本学術会議においても第13期活動計画の中にこの種の問題の重要性をうたっているが、これからは経済的のみならず学術的にも大きく世界に貢献する立場に置かれているだけに、独創的な若い人達を育成する必要が一段と強まっている。

学術研究推進のための一つの大きな柱として若い研究者の育成、特に大学院の充実等を中心としてまとめる際、むずかしい基本的な問題点は、学問分野によって事情が著しく異なるが、今回の「要望」はおおむね各分野に共通する問題であり緊急性の高いものにしてまとめてみた。その中では学問の急速な進歩に対応し得るよう、長期的展望にたつて大学院(必要な人員、設備、建物面積や経常費等)を抜本的に強化充実を図る必要性を強調し、さらに大学院における人材養成について基本的問題を踏まえて、大学が大学院の内容を自主的に検討し、改善すべき点は積極的かつ的確に実現していくことが必要である。

一方研究者の層をもっと厚くし、研究基盤を強化し、特に基礎的科学的分野の充実を図ることが急務である。研究者の交流その他、種々の問題があるが、一つの新しい建設的提言として地域の研究機構の設立がある。研究機器が年々性能が向上すると共にその価格が高くなる情勢下において、効率よく使う仕組みが要求されている今日、日帰りで使える地理的範囲に先端的機器を配置すると共に、その場を、その地域に特徴的なしかも世界的レベルの独創的研究を育成する場とし、研究者の日常的交流、協力を、国内、国外、産官学の広い範囲にわたって図ろうとするものである。その他年々加速度的に盛んになる国際交流についても、特に若い研究者達が日常的に国際的競争の場の中で育成される条件を整えることが重要である。

この要望は大学院の充実という、考えようによっては当然の事柄が、現在あまりにも不十分である現実を前にして、国に対して、また大学自身に対して出されたものである。

詳細は、日本学術会議月報11月号を参照されたい。

広報協力学術団体の申込について

本会議では、第101回総会で内規の一部改正が行われ、従来「連絡学・協会」は、名称を「広報協力学術団体」と改め、資格要件も大幅に緩和されました。「広報協力学術団体」とは本会議活動の周知を図るとともに、各分野の学術研究団体との緊密な連絡・協力関係を維持し、強化するため広報活動に協力してもらうために指定する団体です。詳細は事務局にお問い合わせください。

なお、登録学術研究団体、従来からの連絡学・協会は自動的に指定されたものとみなします。

公開講演会開催のお知らせ

本会議は、9月27日「21世紀の学術」をテーマとした公開講演会を開催したが、第2回目の公開講演会を次のように企画しているので、多数の方々の御来場をお願いしたい。

- ☆ テーマ 学問の自由と科学者の責任
- ☆ 日時 昭和62年1月24日(土)13時30分～17時
- ☆ 会場 日本学術会議講堂
- ☆ 演題及び演者
 - 科学研究の環境と科学者の責任(大木道則 第4部会員、東京大学理学部教授)
 - 学問の自由と教育の自由(大田 堯 第1部会員、東京大学名誉教授)
 - 生命科学の進歩と科学者の責任(渡辺 格第4部会員、北里大学衛生学部教授)

自由討議—高度情報社会の展望と課題—

この自由討議は今期に設置された、高度情報社会特別委員会のメンバーが、個人の立場で、来るべき高度情報社会の展望と課題についての意見を発表したものである。第3部竹内 啓(可能性と展望)、第5部平山 博(技術的展望と問題点)、第2部正田 彬(人権)、第4部坂井利之(人間)、第1部東 洋(教育)の各会員がそれぞれ付記したサブテーマについて問題を提起した。これに続いて、第7部梅垣洋一郎(医学・医療)、第6部飯田 格(情報と図書館)の各会員からコメントが提出された。

すべての部にまたがる広汎な分野からの発表であるから、その対象・論旨は多様であったが、あえて要約すると以下のようである。

これまでの「人」と「物」の社会に、これらと独立して「情報」が生まれた。情報の処理、通信(伝送)、記憶の超高速、巨大化と認識・識別の高度の発展により、労働形態・教育・医療も含めて社会を大きく変化させることが予想される一面、人権、人間疎外を始めとする影の部分にも十分に配慮する必要があると強調された。

なお、この自由討議は別途刊行される予定である。

財団法人日本学術協力財団設立

日本学術会議と密接に連携しつつ、本会議の成果を国民に還元するため出版事業や国際会議の計画策定などを行う財団法人学術協力財団(〒106 東京都港区西麻布3-24-20 TEL 03(403)2860)が10月17日、内閣総理大臣所管の公益法人として設立されました。

この財団は事業の一つとして、日本学術会議総会時における自由討議等を「日学双書」としてシリーズで発行・販売することとしており、当面、脳死をめぐる諸問題(11月初旬発行)、21世紀の学術(12月中旬発行予定)及び高度情報社会の展望と課題(2月中旬発行予定)が予定されています。

学術研究団体調査についてのお願い

日本学術会議事務局では、昭和61年7月1日現在で全国の学術研究団体(いわゆる学・協会)の調査を実施しています。

この調査は、全国の学術研究団体の最近の活動状況を把握することを目的としており、主要な項目については、「総覧」として刊行することを計画しております。

当事務局で承知している各学術研究団体には、既に調査依頼を行っておりますが、最近足した学術研究団体などで調査依頼が未着のところがございましたら、当事務局推薦管理事務室あてに御連絡くださるようお願いいたします。

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多数の学協会の御協力により、「日本学術会議だより」を掲載していただくことができ、ありがとうございます。

なお、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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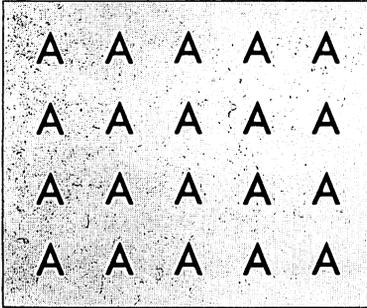
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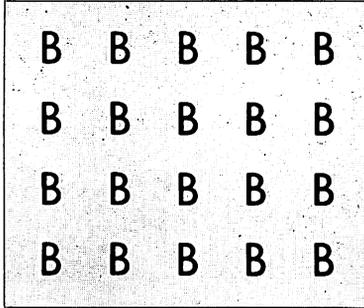
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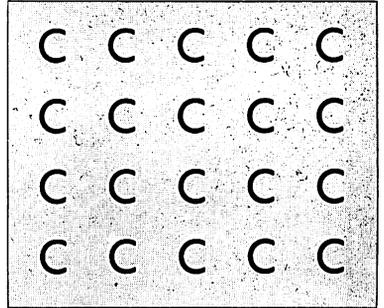
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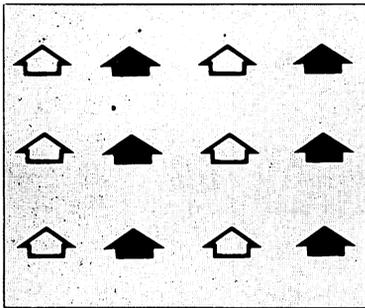
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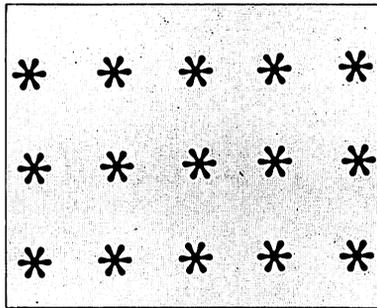
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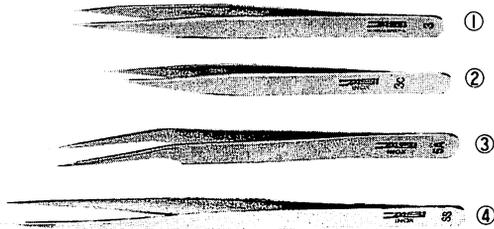


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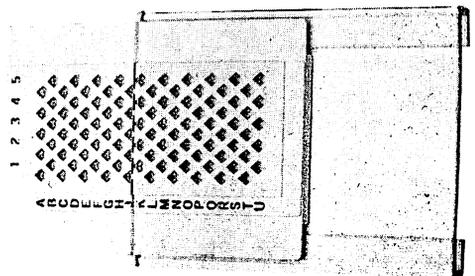
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