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Life history and ultrastructure of *Carpomitra cabrerae* (CLEMENTE) KÜTZING (Phaeophyta, Sporochnales)

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The life history of *Carpomitra cabrerae* (CLEMENTE) KÜTZING was investigated in a laboratory culture. Macroscopic plants were diploid sporophytes forming unilocular sporangia. Zoospores developed into filamentous microthalli which were haploid monoecious gametophytes. After one month culture, oogonia and antheridia were differentiated protandrously on the same gametophyte. By successive transverse cell division of zygote, the sporophyte grew first into uniseriate unbranched filament. Before long, it produced the tuft of apical hairs, and continued trichothallic growth. In about 4-month-culture, the sporangial sorus which was composed of unilocular sporangia and paraphyses was differentiated at the tip of each of branch, beneath the tufts of hairs. Chromosome counts gave ca. 15 in the nuclei of gametophytes, ca. 30 in sporophytes and ca. 15 in unilocular sporangia. Furthermore, ultrastructures of chloroplasts, Golgi bodies and microbodies of gametophytes and sporophytes were chiefly described.

Key Index Words: Carpomitra cabrerae; *chromosome number*; *fertilization*; *life history*; *oogamy*; *ultrastructure*.

Carpomitra cabrerae (CLEMENTE) KÜTZING (Sporochnales) is found along the Atlantic coast of Europe, the Mediterranean Sea, New Zealand and Japan (SAUVAGEAU 1926a). In Japan, it is described from the Pacific coast of the middle and southern Honshu (OKAMURA 1936), western Kyushu (SEGAWA 1956) and Oki Islands (HIROSE and KAJIMURA 1973) which are influenced by the warm currents (Kuroshio C. and Tsushima C.). There have been reported a few culture studies of species belonging to the order Sporochnales (SAUVAGEAU 1926a, b, 1927a, b, 1931, CARAM 1965). In these studies, the life history of *Carpomitra cabrerae* was reported only by SAUVAGEAU (1926a) and many reviews (SMITH 1938, FRITSCH 1945, LEE 1980) have quoted its life cycle, on the basis of his results, as a representative character of the order. However, SAUVAGEAU did not observe the motile sperm in his culture and reported only apogamous development of the female cells (unfertilized eggs ?) of monoecious gametophytes.

In the present studies on *C. cabrerae*, its complete life history, nuclear phases, and cell ultrastructures of two generations are described.

Materials and methods

Fertile sporophytic plants of *Carpomitra cabrerae* were collected at Amakusa (32°28'N 130°E), Kyushu, Japan in July, 1982 by KAWAGUCHI. These plants were found to twine about a fishing-dragnet, therefore, their actual habitat was not clear. According to the previous description (OKAMURA 1936, HIROSE and KAJIMURA 1973), this species usually grows in the depth of 15-20

m. The plants collected were sent immediately to our laboratory, the Institute of Algological Research, Muroran by air mail and culture experiments were started immediately.

Fertile branch with a sporangial sorus (an apex of thallus) was cut off and rinsed several times in autoclaved seawater. Each piece was introduced to a small Petri dish containing 10 m*l* sterile seawater and it discharged zoospores after about 10 minutes. These zoospores were washed 3-5 times in sterile seawater with a capillary pipette and then they were inoculated on glass slide with a few drops of seawater or medium. The glass slides adhering some zoospores were placed in culture vesseles (6.5×8.0 cm) containing 180 m*l* medium and unialgal cultures were established.

The culture medium employed was PESI (TATEWAKI 1966) and was renewed every 3 weeks. Culture experiment was conducted in 10 incubators equipped with cool white 40 W fluorescent lamps (40-80 μE $m^{-2}s^{-1}$) under the following temperature and photoperiod regime: 5°C 14:10 (No. 1), and 10:14 (No. 2), 10°C 14:10 (No. 3) and 10:14 (No. 4), 14°C 14:10 (No. 5) and 10:14 (No. 6) 18°C 14:10 (No. 7) and 10:14 (No. 8), 22°C 14:10 (No. 9) and 10:14 (No. 10).

For cytological observations, whole or fragements of plants in various developmental stages were fixed with an aceto-alcohol solution (1:3) and WITTMANN's aceto-iron-haematoxylin-chloral hydrate solution (1965) was used for staining (YABU and TOKIDA 1966).

Methods of fixation, dehydration and embedding for electron microscopic observations were similar to our previous description for *Laminaria angustata* (MOTOMURA and SAKAI 1984). Thin sections were cut on a Poter-Blum MT-1 ultramicrotome using glass or diamond knives, and were double-stained with uranyl acetate and REYNOLD's lead citrate solution (1963), and observed with a Hitachi H-300 electron microscope.

Results

The sporophyte used for the present study was about 10 cm in height and a flattened cylinder with several dichotomous branches (Fig. 1). All branches were provided with a midrib and an apical tuft of hairs. The sporophyte had been forming only unilocular sporangia in a sorus below the tuft of hairs terminating a fertile branches. The sorus was composed of many unilocular sporangia and branched paraphyses having enlarged terminal cells (Fig. 2). Mature unilocular sporangia were elongate oboid or elliptical, measuring 36.0-44.0 μm×12.3-15.8 μm (average 40.0 μm×13.3 μm) and each sporangium produced 32 zoospores.

Development of gametophyte: Zoospores were pear-shaped or ovoid, measuring 5.0-7.0 μm×3.6-5.0 μm (average 6.1 μm×4.1 μm). They had a single chloroplast, one eyespot and two lateral flagella (Fig. 3). The eyespot was usually adjacent to the attaching point of flagella. The anterior flagellum was longer (ca. 15 μm) than the posterior one (ca. 5 μm). After a short period of movement, they became sluggish and settled on the substratum. Settled zoospores were spherical and measured about 5 μm in diameter (Fig. 4). Within 2 days, they began to germinate under warm temperature conditions (higher than 10°C), but did not germinate at lower temperature (5°C). Most germlings took an elongated shape without the cytoplasmic migration and divided transversely into 2-4 cells which also produced lateral-branches (Fig. 5, double arrows). Some other germlings produced a germination tube, into which all the cytoplasm migrate, leaving the oringinal cell empty (Fig. 5 arrow). The first divided cell of these germlings elongated and divided into 2-3 cells which soon produced side-branches. Further development of these two types of germlings showed no remarkable difference and they developed into minute prostrate thalli (gametophytes) composed of branched uniseriate filaments. Vegetative cells of gametophytes varied in size and measured

7-13 μm in thickness. They contained one or two plate-like chloroplasts which were irregularly dissected. Fig. 6 shows a 3-week-old gametophyte grown in No. 5 incubator. The gametophytes grew well at high temperatures (Nos. 5-10 incubators) and were not effected any by photoperiods, but their growth was suppressed at low temperature (10°C).

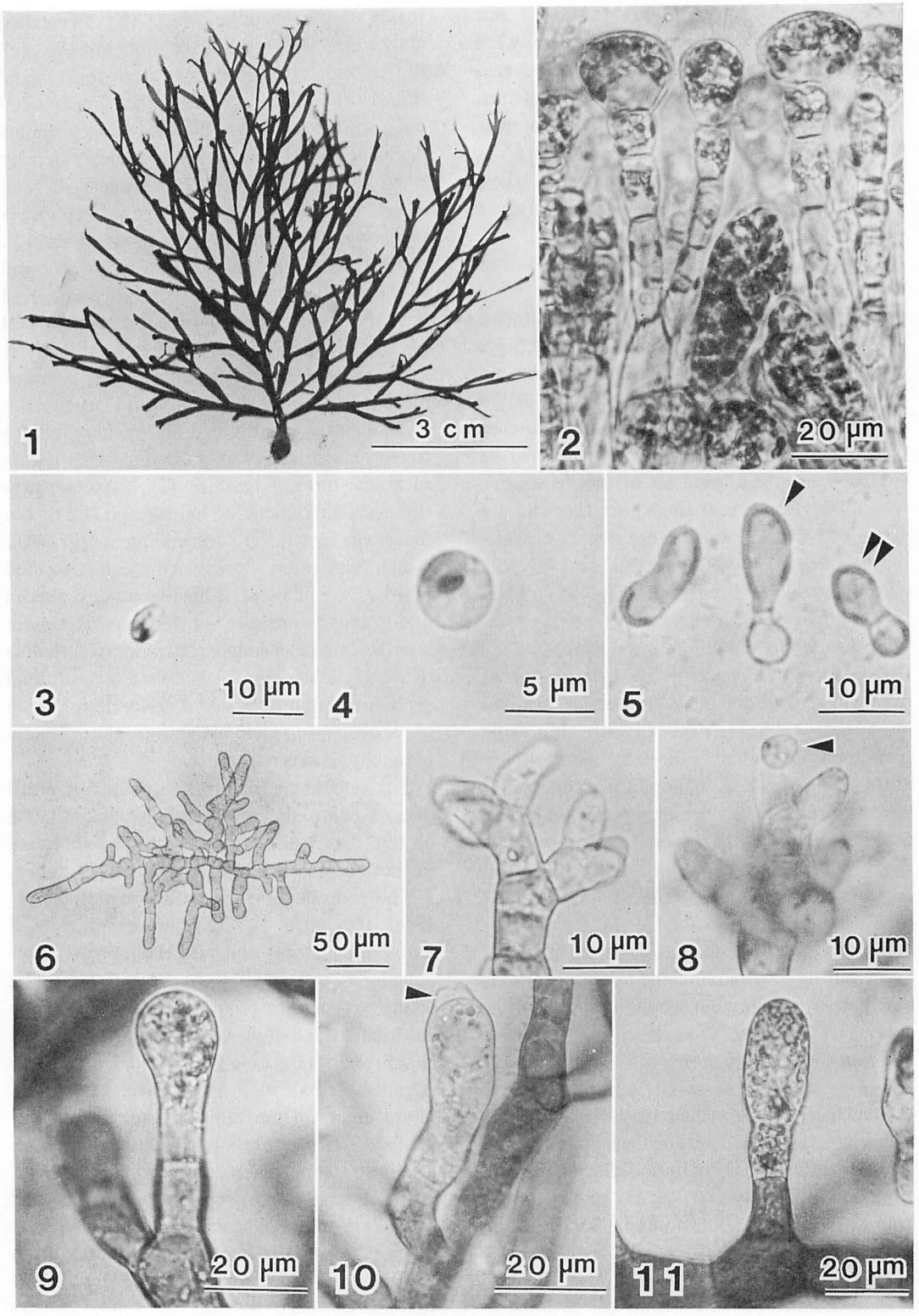
The gametophytes were monoecious, but seem to be protandrous. Antheridia were observed firstly in one-month-old cultures. They were ordinarily conical form, 4.0-9.0 μm×4.0-6.0 μm (average 7.2 μm×4.8 μm) in size, and were formed singly or in clusters on terminal or lateral part of the branches (Fig. 7). Each antheridium contained a single sperm. Liberation of motile sperms was observed several times, but they did not swim actively. Sperms were ovoid, measuring about 5.3 μ×4.5 μm and had a pale chloroplast, but no eyespot (Fig. 8). They had heterokontic flagella, short flagellum (ca. 4 μm) and long flagellum (ca 11 μm).

In several days after the occurrence of antheridia, oogonia were formed on terminal or lateral cells of branches of the same gametophyte which already bore many antheridia. Mature oogonium could easily be detected by its enlargement and pale color compared with other vegetative cells (Fig. 9). Formation of antheridia and oogonia (maturation of gametophytes) occurred most remarkably at 14°C short-day condition (No. 6 incubator). An extrusion of egg from the oogonium could not be observed, but apical opening of oogonium was often observed (Fig. 10). Fertilization between egg and sperm was not demonstrated directly, however, it must have occurred at this stage which had been formed apical opening on oogonium, because the chromosome number of vegetative gametophyte cells was about 15±5, being haploid (Fig. 22) and that of young sporophyte cells was about 30±5, being diploid (Fig. 23).

Development of sporophyte: A fertile egg was ordinally obovate form, ca. 27.5 μm× 15 μm in size, and pale color. It germinated inside of the oogonium. At the two-celled stage, the basal cell attaching on the cell of gametophyte produced a rhizoid initial (Figs. 11, 12), whereas the upper cell developed into a erect thallus. Erect thallus developed in the same manner described by SAUVAGEAU (1926a). By successive cell divisions, the sporophyte grew first into a uniseriate unbranched filament (Fig. 13). Afterwards, some short cells were formed at the middle part of the erect filament, and one of them developed into the mother cell of meristem (Fig. 14). Firstly, this short cell produced several hairs to form primary meristem (Figs. 14, 15), and then the meristematic cell divided in various planes to form a broadening meristem with a tuft of apical hairs (Figs. 16, 17). Accompanying with increment of hairs, each cell of the meristem produced descending outgrowth, which elongated downwardly and formed multiseriate filament. This filament a coalesced and gradually ensheathed the uniseriate main axis to form a pseudoparenchymatous thallus (Figs. 17, 18). Fig. 19 shows a longitudinal section through an apical meristematic region of sporophyte, demonstrating the pseudoparenchymatous structure.

The cells of sporophyte contained numerous discoid chloroplasts, as contrasted with one or two dissected plate-like chloroplasts found in those of gametophyte as mentioned above.

The sporophytes grew most rapidly at 14-18°C and in a 14:10 photoperiod (Nos. 5 and 7 incubators) and also their growth was enhanced remarkably by aeration. The young sporophyte from a fertilized egg was cultured by bubbling in an Erlenmeyer flask containing 1000 m*l* medium at No. 5 incubator. After about four month's culture, this sporophyte grew up into almost the same morphology with the plant collected in nature, attaining about 10 cm long and fertile (Fig. 20). The sporangial sorus was differentiated at the tip of each branch beneath the tuft of hairs. Unilocular sporangia obtained in the present culture were 35.0-50.0 μm×12.0-18.0 μm (average 40.8 μm×15.4 μm) in size (Fig. 21).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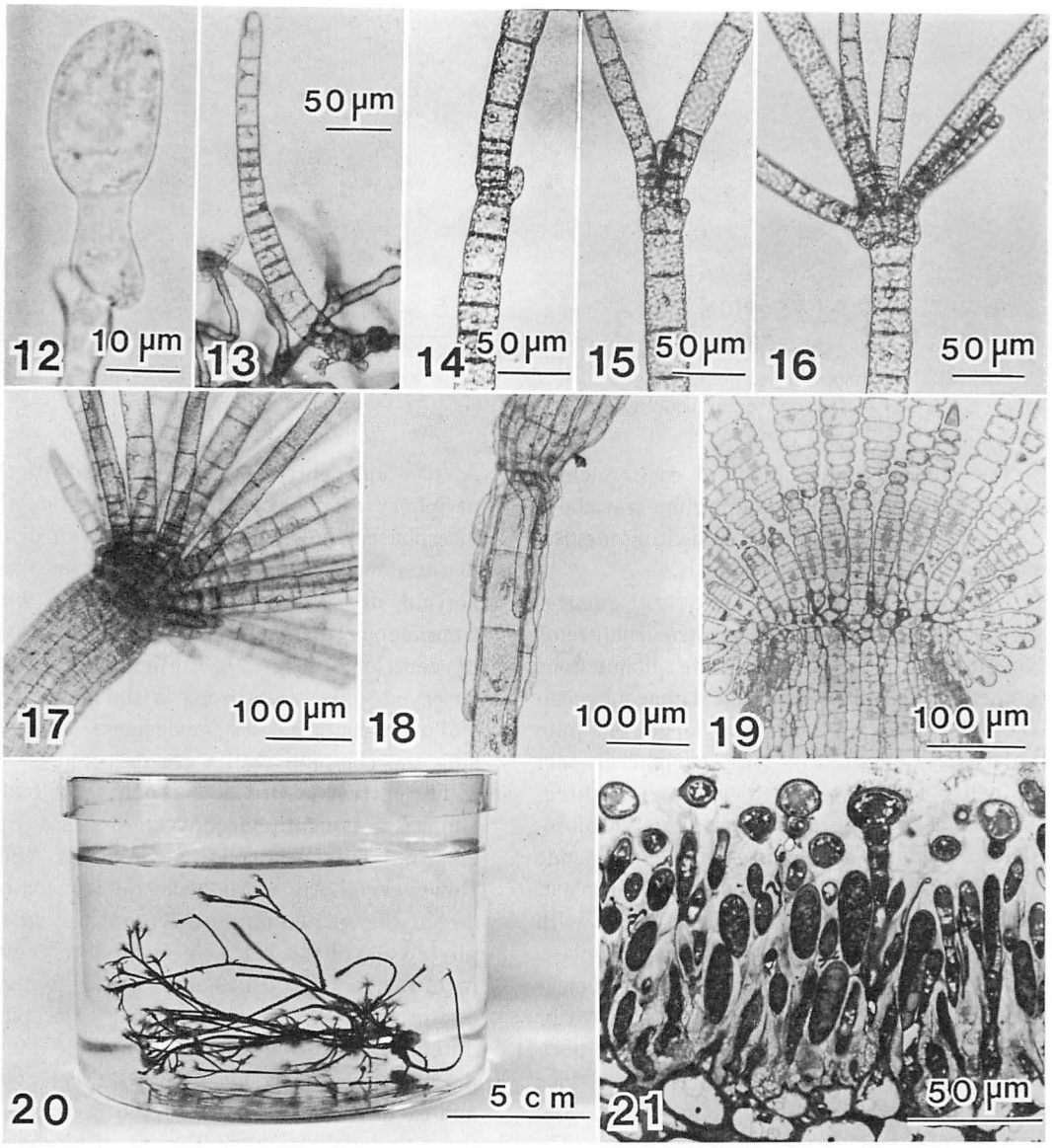


Fig. 1. Mature sporophyte from field. Fig. 2. Unilocular sporangia and paraphyses of sporophyte from field material. Fig. 3. Zoospore from unilocular sporangium. Fig. 4. Settled zoospore. Fig. 5. Germlings from settled zoospores. There are two types of germination. 1) All the cytoplasm migrate into a germ tube and the original cell becomes empty (arrow). 2) Settled zoospore germinates by elongation and divides into two cells transversely (double arrows). Fig. 6. Gametophyte derived from zoospore after 3 weeks in 14°C, 14 : 10 LD condition. Fig. 7. Antheridia on gametophyte. Fig. 8. Just released sperm (arrow) from the antheridium. Fig. 9. Oogonium on gametophyte. Fig. 10. Full-matured oogonium on gametophyte with a opening at the tip (arrow). Fig. 11. Two-celled sporophyte on gametophyte. Fig. 12. Two-celled sporophyte. Its lower cell is differentiating to the rhizoid. Fig. 13. Uniseriate erect sporophyte. Fig. 14. Initial formation of the meristematic cell on uniseriate sporophyte. Fig. 15. Young meristem on uniseriate sporophyte. Several trichothallic hairs are formed. Fig. 16. More developed meristem. Fig. 17. The meristem on ca. 1 cm sporophyte. Fig. 18. Lower part of Fig. 17. Descending threads are forming. Fig. 19. Section of meristematic part of sporophyte stained with 1% toluidine blue 0 in 1% borax. Fig. 20. Mature sporophyte after 4 month's culture in 14°C, 14 : 10 LD condition from fertilized egg. Fig. 21. Section of sorus part of cultured sporophyte stained with 1% toluidine blue 0 in 1% borax.

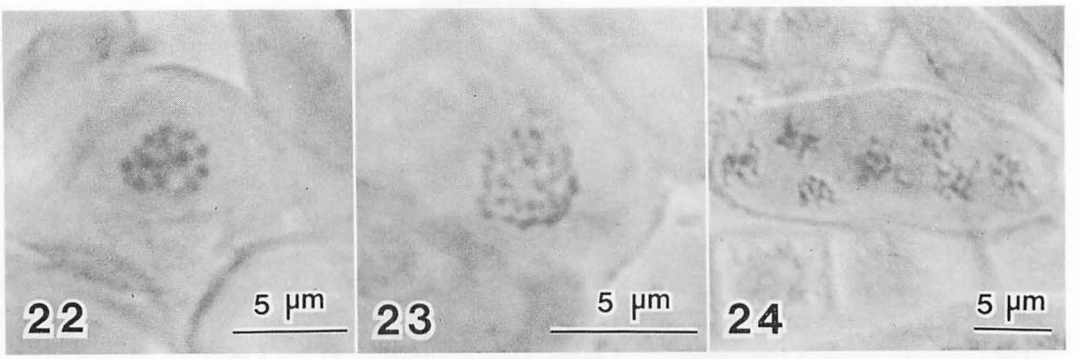


Fig. 22. Chromosomes of gametophyte. Fig. 23. Chromosome of Sporophyte. Fig. 24. Chromosomes of each nucleus in the unilocular sporangium.

The chromosome number of each nucleus found in the unilocular sporangium was about 15, being haploid (Fig. 24), indicating meiosis occurred in the zoosporogenesis.

Ultrastructure of vegetative cells of gametophyte and sporophyte: The ultrastructure of vegetative cells of uniseriate filamentous gametophytes showed a typical phaeophycean feature. Fig. 26 shows a large laminate chloroplast situated at the peripheral part of cell. There were 4-8 (average 6) three-thylakoid lamellae per chloroplast. Chloroplast envelope and chloroplast endoplasmic reticulum (CER) surrounded the chloroplast. Pyrenoid did not occur. The nucleus with one nucleolus was adjacent to the chloroplast. Occasionally, the connection between nuclear envelope and CER was observed. Two or three Golgi bodies were located in the perinuclear region and they appeared to produce small vesicles. These vesicles often contained electron dense material (Fig. 27).

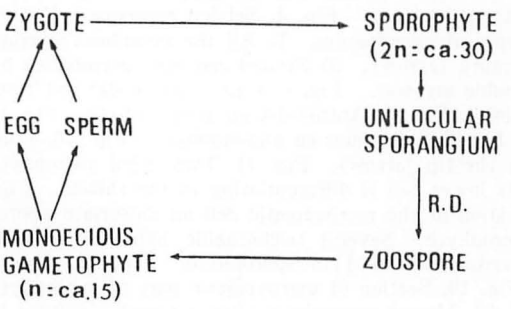


Fig. 25. Summarized diagram of life cycle of *Carpomitra cabrerae*.

A pair of centrioles was detected in the periphery of nuclear envelope even in the interphase of nucleus and the electron dense material was found especially at the basal portion of centrioles. Microtubules were conspicuous in the cytoplasm nearby a pair of centrioles (Fig. 29). Microbodies were observed only as a mass without any crystalloid structure. Plasmodesmata transversing the common wall were detected.

The ultrastructure of sporophyte cell also showed a typical phaeophycean feature (Fig. 29), as described on gametophyte cells. However, there were some differences between the gametophyte cells and the sporophyte cells of the apical meristematic region in ultrastructure. As demonstrated by light microscopic observations, the chloroplast differed from that of gametophyte. Many discoid chloroplasts lay along the cell wall and each of them contained 3-5 (average 4) three-thylakoid lamellae (Fig. 30). Chloroplast envelope and CER surrounded the chloroplast. CER was often associated with ER. But there was no connection between CER and nuclear envelope, because the nucleus with one nucleolus was ordinarily located in the center of cell and was separated from peripheral chloroplasts. The Golgi bodies were located in the perinuclear region (Fig. 29). Especially in the cells of apical hairs (trichothallic hairs), a large number of Golgi bodies were detected and they appeared to produce actively electron transparent vesicles. Several microbodies were observed in the

basal cells of apical hairs and generally associated with mitochondria (Fig. 30). These microbodies contained the regular crystalloid structure, but they did not contain such a crystalloid structure in the cells of other part of sporophyte.

The other ultrastructural features of sporophyte were common with those of gametophyte cells. For example, pyrenoid did not occur, a pair of centrioles was demonstrated even in the interphase of nucleus and plasmodesmata also existed in the cell wall as shown in Fig. 31.

Discussion

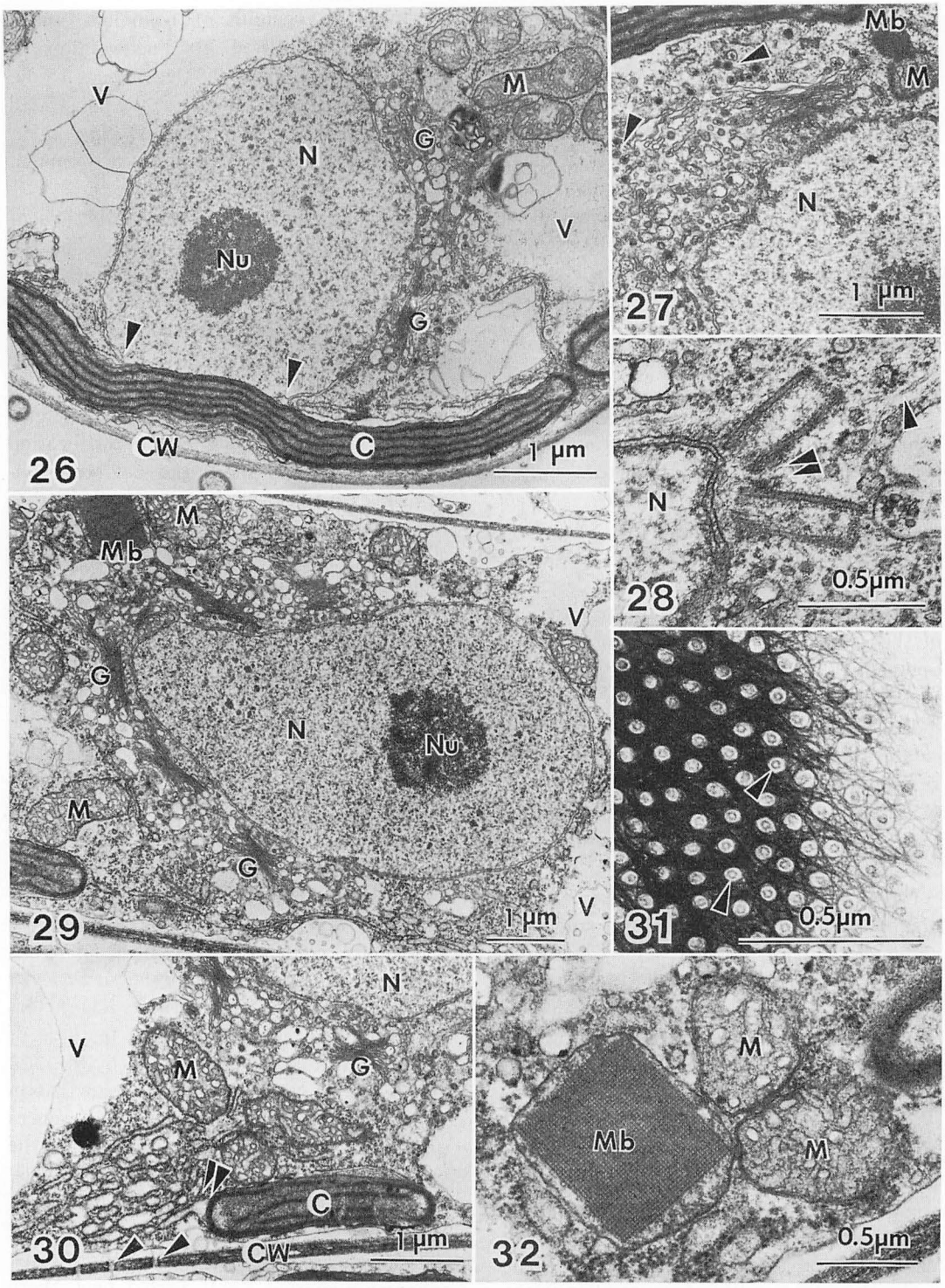
In the order Sporochnales, a few studies on the life history have been reported: *Carpomitra cabrerae* (SAUVAGEAU 1926a): *Nereia filiformis* (SAUVAGEAU 1927a, b); *Sporochnus pedunculatus* (SAUVAGEAU 1931, CARAM 1965). SAUVAGEAU (1926a) ordinally described heteromorphic biphasic life history for one of the representative characters of the order Sporochnales, but it was not complete, especially on oogamous evidence. After that it has been confirmed for *Sporochnus pedunculatus* by CARAM (1965). According to her results, the life history showed an alternation of heteromorphic generations and meiosis took place in the unilocular sporangia of the diploid macrothallus.

In the present study, the same type of life history was confirmed by culture study and cytological observations in *Carpomitra cabrerae* from Japan. SAUVAGEAU (1926a) noted that in *C. cabrerae* an oogonium was formed as an enlarged terminal cell of each filament of prothallus (gametophyte) and an egg developed only apogamously in the oogonium. In our cultures, oogonia differentiate from terminal or lateral cells of branched filamentous gametophytes. These oogonial cells can easily be distinguished from vegetative cells even in their early developmental stage by their swollen shape and pale color resulting from smaller chloroplasts than those of vegetative cells. The oogonium neither extruded nor released mature egg as described by SAUVAGEAU, however, an opening of oogonium which apparently permitted the penetration of sperm was observed by the present study. Such apical opening has been demonstrated also in mature oogonium of *Sporochnus* species (CARAM 1965, TATEWAKI unpubl. data).

According to SAUVAGEAU, antheridia of *C. cabrerae* formed terminal clusters on the branches of monoecious gametophyte, but a liberation of motile sperm from antheridia had not been observed. In the present study, the antheridia occur singly or in clusters on terminal or lateral positions of the branches and motile sperm provides heterokontic flagella. Although actual fertilization between egg and sperm has not been confirmed, cytological observations indicate that the sperm must fuse with the egg to produce a fertilized egg. Meiosis occurring in the unilocular sporangium of the sporophyte has been confirmed in other species of Sporochnales; *Sporochnus pedunculatus* (MAGNE 1953) and *Nereia filiformis* (CARAM 1965).

From the present results, the life cycle of *Carpomitra cabrerae* examined can be summarized as follows; heteromorphic alternation combined with oogamous monoecious microscopic gametophyte and unilocular sporangium-bearing macroscopic sporophyte as shown in the diagram of Fig. 25.

In this study, we examined the ultrastructures of vegetative gametophyte cells and sporophyte cells especially of the apical meristematic region of *Carpomitra cabrerae* and demonstrated that these characters basically agree with the typical features of phaeophycean algae described by BOUCK (1965). However, it has been found that in ultrastructures there were some differences and some common features between the gametophyte cells and the sporophyte cells. As we demonstrated above by light microscopic observation, one or two large lamellate chloroplasts were in the gametophyte cells, whereas numerous small discoid ones were in the sporophyte cells. Furthermore, there were some ultrastructural differences be-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tween the two generations. In gametophyte cells, there were 4-8 three-thylakoid lamellae per chloroplast and the connection of nuclear envelope with CER could easily be observed. In sporophyte cells, however, the number of them were 3-5, and the connection of CER with the nuclear envelope could not be detected, but the connection with ER was frequently observed. These three-thylakoid lamellae of this species, however, seem to be not well developed ones as compared with those of other brown algae growing in the intertidal zone. This fact is considered to be resulted from deep habitat (15-20 m) of *C. cabrerae*.

HORI (1972a, b) surveyed the presence or absence of pyrenoid in many phaeophycean algae, and reported that pyrenoid did not occur in the order Sporochnales including a sporophyte of *C. cabrerae*. In the present study, it is confirmed that pyrenoid does not occur in the cells of both generations of this species.

Golgi bodies exist always in perinuclear region and some of them in the vegetative gametophyte cells appear to produce small vesicles containing electron dense material. These characteristic vesicles have been reported in the cells of vegetative female and male gametophytes of *Laminaria angustata* (MOTOMURA and SAKAI 1984) and they were considered to have adhesive function to a substratum. On the other hand, a large number of Golgi bodies in the sporophyte cells, especially those of apical hairs, are detected to produce electron transparent vesicles, but they never produce the vesicles containing electron dense material.

Microbodies could be observed in both generations and they always existed in adjacent part of mitochondria. Especially, in the cells of basal part of apical hairs, several comparatively large ones which contained the regular crystalloid structure were considerably noticeable. This may relate to the site of active cell division, namely the trichothallic growth region of sporophyte of *C. cabrerae*. Microbodies containing these crystalloid structure are common in higher plants (NEWCOMB and FREDERICK 1971), but are only detected in *Fucus* and *Giffordia* in Phaeophyta (BOUCK 1965). Several papers (BOUCK 1965, BISALPUTRA *et al.* 1971, GALATIS *et al.* 1977, PRUD'HOMME VAN REINE and STAR 1981, KATSAROS *et al.* 1983) on the ultrastructure of microbodies in phaeophycean algae commented that they have clear relationship to mitochondria, in contrast to that they are adjacent to chloroplast and mitochondria in higher plants (NEWCOMB and FREDERICK 1971).

The order Sporochnales is a highly specialized and relatively small group with about six genera. The species of this order are sometimes included in the Desmarestiales

Fig. 26-32. Electron micrographs. C=chloroplast, CW=cell wall, G=Golgi body, M=mitochondria, Mb=microbody, N=nucleus, Nu=nucleolus, V=vacuole. Fig. 26. Vegetative cell of gametophyte. Note large laminate chloroplast without pyrenoid along the cell wall, large vacuoles, one nucleus with one nucleolus, several Golgi bodies and mitochondria in cytoplasm. The connection between nuclear envelope and chloroplast endoplasmic reticulum is evident (arrow). Fig. 27. Vegetative cell of gametophyte. Golgi body appears to produce small vesicles, and some of them contain electron dense material (arrow). Fig. 28. A pair of centrioles in interphase nucleus of vegetative cell of gametophyte. Note electron dense material which is noticeable at the base of centrioles (double arrows) and microtubules (arrow). Fig. 29. Cell of trichothallic hairs of sporophyte. Note one nucleus with one nucleolus, large vacuoles, many perinuclear Golgi bodies, mitochondria and a microbody containing the regular crystalloid structure. Golgi bodies appear to produce actively large electron transparent vesicles. Fig. 30. Cell of trichothallic hairs of sporophyte. Note the discoidal chloroplast without pyrenoid, several mitochondria and Golgi bodies. The connection between chloroplast endoplasmic reticulum and endoplasmic reticulum (double arrows) is visible and plasmodesmata exist in the cell wall (arrow). Fig. 31. Transverse view of plasmodesmata penetrating cell wall of trichothallic hair of sporophyte. Note the plasmalemma (arrow) throughout the cell wall. Fig. 32. Microbody in the cell of trichothallic hair of sporophyte. Note the regular crystalloid structure in it. Mitochondria exist adjacent to it.

(RUSSELL and FLETCHER 1975, LEE 1980). Because, in both orders, the life history shows an alternation of a macroscopic sporophyte with a microscopic filamentous gametophyte reproduced by oogamy and the sporophyte develops by means of trichothallic growth into a pseudoparenchymatous structure. Although these two orders differs from each other in such features as a developmental type of unilocular sporangium and an apical structure of sporophytes, our present study supports the conception that the Sporochnales is closely related to the Desmarestiales.

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本村泰三*・川口栄男・阪井與志雄*：イチメガサ *Carpomitra cabrerae* (褐藻・ケヤリモ目) の生活史と微細構造**

イチメガサの生活史を室内培養により観察した。天然より採集した藻体は単子のうを有し，これより放出された遊走子は匍匐する単列糸状の微小な体へと発生した。14°C 短日条件下で約1ヶ月の培養の後，糸状体は成熟し造卵器と造精器を形成した。受精卵は直立する単列糸状の体へと発生し，まもなく分裂組織が形成され頂毛生長を行う。受精卵の培養開始後，約4ヶ月で直立体は成熟し単子のうを形成した。染色体数は，匍匐糸状体では約15，直立体では約30，単のう内では約15であった。微細な匍匐糸状体は配偶体，大型の直立体は胞子体であり，両者の間で世代交代が行われていることがわかる。また両世代の細胞内微細構造についても報告した。(*051 室蘭市母恋南町 1-13 北海道大学理学部付属海藻研究施設 **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)

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