The Japanese Journal of PHYCOLOGY

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Morphological observations on the adelphoparasite Gracilariophila oryzoides (Gracilariales, Rhodophyta)

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Gracilariophila oryzoides belongs to the Gracilariaceae based on features of early reproductive development and is interpreted as a recently evolved adelphoparasite of Gracilariopsis lemaneiformis. Based on reproductive morphology the parasite closely resembles its host; the cystocarp lacks tubular nutritive cells that fuse with cells of the pericarp, gonimoblast filaments are organized into comparatively straight chains, and gonimoblast conjunctor cells fuse with cells in the floor of the cystocarp. Lack of a specialized nutritive tissue in the cystocarp is discussed with regard to the parasitic lifestyle. Spermatangia are cut off singly by transverse division from spermatangial parent cells produced from surface cortical cells. Penetration and connection between parasite cells and vegetative host cells, and subsequent growth into a pustule are documented.

Key Index Words: Adelphoparasite—Gracilariaceae—Gracilariophila—parasitism—red algae—reproductive morphology—systematics.

Historical Perspective

SETCHELL and WILSON in WILSON (1910 p. 81) described Gracilariophila as a small parasitic red alga from San Francisco, California, thought to infest both Gracilariopsis lemaneiformis (BORY) DAWSON, ACLETO et FOLDVIK (as Gracilaria multipartita) and Gracilaria papenfussii Abbott (as G. confer-They recognized one species, voides). Gracilariophila oryzoides, which they characterized by the presence of penetrating rhizoids, lack of pigmentation, and antheridia scattered over the entire spermatangial thallus. Whereas the holotype specimen is apparently lost in the Herbarium of the University of California at Berkeley (UC), an isotype specimen collected by GARDNER from Fort Point, San Francisco, is housed in US (US 851G).

Though not assigning *Gracilariophila* to any existing family, WILSON (1910) noted a close taxonomic relationship with *Gracilaria* GREV.,

then placed in the suborder Sphaerococcoideae. *Gracilariophila* was ignored in subsequent classification schemes, until SMITH (1944 p. 268) placed it in the Gracilariaceae, a taxonomic opinion accepted by DAWSON (1949).

Gracilariophila was the first parasitic red algal genus reported growing on members of Gracilariaceae, the second being Holmsella STURCH (1926 p. 603) [type species: H. pachyderma (REINSCH) STURCH (1926 p. 604) on Gracilaria verrucosa (HUDSON) PAPENFUSS (as G. confervoides)], and the third Gracilariocolax WEBER VAN BOSSE (1928 p. 393) [type species: G. henriettiae W.v.B. from Malaysia on Gracilaria radicans HAUCK]. Originally placed Feldmann in the Gigartinaceae, and FELDMANN (1958) transferred Gracilariocolax to the Gracilariaceae, although it is currently placed under Incertae sedis (see FARR et al. 1979 p. 741).

Gracilariophila oryzoides is reported from Smith Island, Washington, to Bahia Rosario, Baja California del Norte, Mexico (Аввотт and HOLLENBERG 1976). In addition to G. oryzoides, five other species of Gracilariophila have been described. SETCHELL (1923 p. 393) described G. gardneri on Gracilaria textorii var. cunninghamii (FARLOW ex J. AGARDH) DAWSON [as G. cunninghamii J. AG.] collected near Santa Monica, California, based on its larger size and more strongly projecting Cystocarps. Weber van Bosse (1928) erected four new species and one new variety from the Malay Archipelago, while not ruling out the possibility that the various habits could represent different developmental stages. She recognized two clusters of species based on manner of host penetration: the Californian species by means of rhizoids, and the Malaysian species by establishment of pit-connections with host cells, and placed the four Malaysian species in her section Arhiza, a reference to the lack of rhizoids. Subsequently, CHANG and XIA (1978) identified three of WEBER VAN BOSSE's species in China, and found that Gracilariophila infidelis (W.v.B.) W.v.B. and G. deformans W.v.B. both possess deep spermatangial conceptacles.

FELDMANN and FELDMANN (1958) recognized two major groups of florideophycean parasites, adelphoparasites and alloparasites. They placed *Gracilariophila* among the adelphoparasites, a group in which the parasite and host are closely related taxonomically.

Discussing his new genus Congracilaria, YAMAMOTO (1986:287) suggested that four genera of Gracilariacean adelphoparasites may ultimately be distinguished based on mode of penetration and spermatangial configuration: 1) Gracilariophila SETCHELL et WILSON, possessing rhizoids and superficial spermatangia, 2) Gracilariophila sensu WEBER VAN BOSSE (1928), lacking rhizoids and with superficial spermatangia, 3) Gracilariophila sensu CHANG and XIA (1978), in which rhizoid presence has still to be investigated, but with spermatangia in conceptacles and 4) Congracilaria YAMAMOTO, lacking rhizoids and with spermatangia in conceptacles. Although WEBER VAN BOSSE (1928) did illustrate deep spermatangial conceptacles in Gracilariocolax, YAMAMOTO (1986) did not hint at the possible congenerity of Congracilaria and Gracilariocolax.

Materials and Methods

Material used in this study was fixed and preserved in 5% formalin/seawater. Transverse hand sections were stained with acetoiron-hematoxylin chloral-hydrate (WITTMAN 1965) and mounted in 1:1 Hoyer's mounting medium:water according to the procedure of Hommersand Frederico (1988). and Material of Gracilariophila oryzoides investigated includes female and male specimens on Gracilariopsis lemaneiformis from Pebble Beach, Monterey, California, 20. vii. 74, M. H. Hommersand, and in the drift, south of Hotel Coronado, Coronado, San Diego Co., California, 26. ix. 69, and tetrasporophytes from Execution Rock, Bamfield, Vancouver, British Columbia, Canada, 4. vi. 85, M. H. Hommersand. All specimens are deposited at NCU.

The latter specimens are the first reported for British Columbia and represent its most northern known distribution record (GABRIELSON, pers. comm.)

Results

Vegetative morphology

Gracilariophila oryzoides parasites are characterized by smooth hemispherical, spherical or warty crescent-shaped tubercles or 'pustules' protruding from the infected host (Fig. 1). Although mostly concentrated in the lower thallus portions of the host or in regions priorly epiphytized, such pustules also occur singly or in aggregated clusters over the entire surface of the host. Whereas cystocarpic and tetrasporophytic pustules are variously pigmented, spermatangial ones are typically unpigmented. All pustules investigated were dioecious or tetrasporophytic.

Spore attachment, germination and host penetration were not seen. According to ZUC-CARELLO and GOFF (1988) nuclei are transfer-





red directly from the infection peg and 1-2 derivative cells into host cells which, in turn, produce filamentous rhizoidal cells that penetrate the host tissue making secondary pit-connections with host cells. Young pustules stained with hematoxylin reveal what appear to be numerous infection discs on the surface of a single pustule (Figs. 2, 3 and 5). This is interesting in that combined male and female sexes or mixed phases were never seen in the same pustule. Perhaps the discs are non functional.

The intrusive part of the infection cycle in G. oryzoides starts when a rhizoidal cell or infected host cell becomes darkly staining in contrast to cells of the host cortex. Because a remaining empty spore wall could not be detected on the host cuticle, it seems likely that the entire spore content invades the outer tissues of the host. Initially subspherical, a parasite cell (Figs. 3 and 5, arrows) becomes more irregular in shape by adopting the outline of the intercellular space it occupies (Fig. 2). Once embedded within host tissue. the parasitic component is commonly referred to as a 'rhizoidal cell' (GOFF, 1982), or if a filamentous file of rhizoidal cells, as a 'rhizoid' (Fig. 4).

A recently embedded rhizoidal cell that lies two to three cells beneath the host cuticle soon cuts off a derivative cell that extends toward the surface (Fig. 2 on left) where it cuts off a pair of initials bilaterally to the outside (Fig. 5, arrowhead). Each of these initials then divides longitudinally by concavo-convex septa to form files of cells that barely emerge

beyond the host surface (Figs. 2 and 6, arrowheads; Fig. 5, double arrowhead). Meanwhile, the embedded rhizoidal cells become multinucleate (Figs. 2 and 5-7) and initiate conjunctor cells that establish secondary pitconnections (Figs. 6-7) with neighboring host cells. Outer cortical host cells overgrown by erumpent parasite cells are stimulated to divide transversely, forming an amplified zone composed of small, squarish cortical cells with which both intrusive (Figs. 5-7) and erumpent parasite cells initiate secondary pitconnections. Under light microscopy, pit plugs of such secondary pit-connections (Fig. 7) do not appear different from those between the host cells themselves. Formation of secondary pit-connections between parasite and host cells takes place throughout development, and results in the continuous deposition of parasite nuclei into host cells.

In addition to initiating conjunctor cells that fuse with host cells, rhizoidal cells simultaneously also cut off derivative cells that grow thallus-inward and continue to proliferate within the confines of intercellular spaces (Figs. 8-13). Once rhizoidal cells have reached the medulla, direction of growth for further expansion shifts from thallus-inward to the margins of the infected areas (Figs. 10 and 11), a shift that allows the infection area to expand in width. The most terminal rhizoidal cells that grow laterally and thallus-outward are uninucleate and elliptical to irregularly shaped with an angular portion (Figs. 10-11). They continue to divide while their subterminal derivatives quickly expand,

Figs. 8–15. Gracilariophila oryzoides from British Columbia. Fig. 8. Intrusive penetration of rhizoidal cells in host tissue. Fig. 9–10 (Fig. 10 is close-up of Fig. 9). Young pustule consisting of dark-staining parasite cells and light-staining host cells. Rhizoidal cells extending toward surface (arrowheads) and into the medulla (arrow) of host. Fig. 11. Rhizoidal cells (arrowheads) extending toward surface of host. Fig. 12. Small-celled parasite cells (arrowheads) confined to small intercellular spaces. Fig. 13. Formation of conjunctor cells (arrowheads) from parasite cells encircling a medullary host cell. Fig. 14. Establishment of secondary pit-connection (arrow) between parasite cell and host cell. Fig. 15. Intrusive growth of parasite ceases in medullary region of host (arrow). Distinction between host cells and vegetative cells has become blurred.

Figs. 1–7. Gracilariophila oryzoides from British Columbia. Fig. 1. Surface view of mature tetrasporangial pustule on host Gracilariopsis lemaneiformis. Fig. 2. On left: binucleate rhizoidal parasite cell (arrow) with derivative growing towards surface of host. On right: multinucleate rhizoidal cell (arrowhead) with erumpent cell file. Fig. 3. Discs (arrows) and penetrating rhizoidal cells (arrowheads) in host tissue. Fig. 4. Rhizoidal filament (arrow). Fig. 5. In center: rhizoidal cell (arrowhead) with lateral pair of derivative cells. On left: rhizoidal cell (double arrowhead) with file of derivative cells. On right: cellular discs (arrow) that have not yet connected with host cortex. Fig. 6. Rhizoidal cell linked by secondary pit-connection (arrowhead) to cortical cell of host. Fig. 7. Same as in Fig. 6, with rhizoidal cell bearing erumpent derivatives (arrowheads).



becoming spherical (Figs. 11–13). They also continue to initiate conjunctor cells (Figs. 12– 13), establishing numerous secondary pit-connections (Fig. 14) with host cells. Rhizoids also course intercellularly into the starch-rich cortex of the host and stop abruptly at the vacuolated, presumably nutrient-poor medulla (Figs. 9 and 10, arrows). Whenever rhizoids penetrate the host tissues without at the same time cutting off derivatives that grow outwards toward the thallus surface, they appear to loose the ability to erupt secondarily above the host cortex (Fig. 4).

While a difference in shape and cyto-

plasmic content is obvious between host cells and parasite cells during the early infection stages, the vegetative tissues of both parasite and host eventually become indistinguishable once both infection and abundant formation of secondary pit-connections has ceased (Fig. 15). Remnant traces of the parasitic component are then revealed by the darkly staining extremities of rhizoidal derivatives (Fig. 15).

Female reproductive apparatus

Mature cystocarpic pustules are variously pigmented, hemispherical and resemble cystocarps of the host. A single continuous pericarp surrounds either one (Figs. 18 and 27) or several carposporophytes (Fig. 19). The latter phenomenon indicates that several carpogonia were simultaneously fertilized and that cells of the sterile branches flanking the carpogonial branch and neighboring cortical cells were concomitantly activated to divide periclinally.

A transverse section through a cystocarpic pustule of *Gracilariophila oryzoides* reveals that the floor is little modified cytologically (Figs. 17, 18 and 27). The cells are morphologically similar to medullary cells, and the cytoplasmic contents of both sporophytic and gametophytic tissues stain darkly.

Functional carpogonial branches were not present in the available research material. Unfertilized carpogonial branches are typically two-celled (Fig. 16), consisting of a distal conical carpogonium with a straight trichogyne extending towards the thallus surface, and a hypogynous cell. Such carpogonial branches are borne on a multinucleate supporting cell that also bears a pair of sterile branches (Fig. 16 arrowheads).

The earliest stages leading to the establishment of a postfertilization fusion cell were also absent in our material; however, a supporting cell subtending a distinct hypogynous cell and fusion cell (Figs. 17 and 18) is a clear indication that fusion cell initiation follows a typical Gracilariacean pattern, in which the sterile cells fuse directly onto the persistent carpogonium. It is evident that the fusion process in *Gracilariophila* typically circumvents both the hypogynous cell and supporting cell (Fig. 17), as neither cell is incorporated into the fusion cell.

Within the cystocarpic cavity, the initial branching pattern of the gonimoblast can be reconstructed from Figure 20. After gonimoblast initials are cut off from the fusion cell, each continues to divide to form files of gonimoblast cells. Division proceeds by concavo-convex septa, followed by oblique or transverse division of the residual subapical The result is a branching pattern in cell. which a basal gonimoblast cell bears two rows of predominantly transverselv dividing gonimoblast cells bilaterally (Fig. 20). In addition, intercalary suprabasal gonimoblast cells have the potential to cut off laterals (Fig. 24) that initiate supplementary chains of gonimoblast cells.

In every instance, the lowermost gonimoblast cells closest to the cystocarp floor cut off conjunctor cells from their lower surface (Figs. 20–23) which fuse (Fig. 21, arrow) onto multinucleate floor cells, leaving behind secondary pit-connections. A transversely positioned metaphase plate in a lower

Fig. 16–22. Gracilariophila oryzoides from California. Fig. 16. Carpogonial branch apparatus consisting of supporting cell bearing non-functional carpogonial branch and a pair of sterile branches (arrowheads). Fig. 17. Close up of Fig. 18 showing fusion cell bearing gonimoblast, hypogynous cell and supporting cell. Arrowhead points to metaphase stage in basal gonimoblast cell. Fig. 18. Cystocarp with fusion cell (arrow) bearing gonimoblasts. Distinction between floor of cystocarp and medulla has become blurred. Fig. 19. Three cystocarps beneath one pericarp trigger expansion of outer cortex of host (arrowhead), resulting in sharp demarcation between its cortical and medullary region. Fig. 20. Obliquely longitudinal division of apical and subapical gonimoblast cell, and formation of conjunctor cells from lower surface of lowermost gonimoblast (arrowheads). Fig. 21. Initiation of conjunctor cell (arrowhead) and fusion of conjunctor cell (arrow) with a multinucleate upon division.

Abbreviations: cp = carpogonium, cs = carposporangium, fu = fusion cell, g = gonimoblast cell, hy = hypogynous cell, su = supporting cell, t = trichogyne.



Figs. 23–27. Gracilariophila oryzoides from California. Fig. 23. Abundant formation of secondary pit-connections (arrowheads) cut off from lower gonimoblast cells. Fig. 24. Suprabasal gonimoblast cell that has cut off small lateral derivative (arrowhead) by a concavo-convex septum. Fig. 25. Metaphase plate (arrowhead) in lower gonimoblast cell will initiate conjunctor cell upon division. Progressive maturation of gonimoblast into short chains of elongate carposporangial initials. Fig. 26. Basipetal transformation of gonimoblast cells into chains of spherical carposporangia. Fig. 27. Mature cystocarp with well developed central ostiole (arrow), and chains of carposporangia.

For abbreviations see the legend of Figs. 16-22.

gonimoblast cell (Figs. 22 and 25) indicates that gonimoblast cell division and conjunctor cell formation are independent processes. Lower gonimoblast cells become progressively vacuolate, while the distal ones stain darkly (Figs. 23 and 24) and are progressively transformed into elongate carposporangial initials (Fig. 25) that become spherical carposporangia (Fig. 26) upon release through the ostiole (Fig. 27). The pericarp is formed entirely of host tissue surrounded by an outer cuticle that is continuous with that of the vegetative axis (Fig. 19). At maturity, the pericarp consists of about 9–12 layers of small isodiametric cells. Terminal pericarp cells are typically elongate and pointed (Figs. 19 and 27). Numerous carposporophytes beneath one pericarp trigger expansion of the outer cortex of the host, and result in sharp demarcation between its cortical and medullary regions (Fig. 19).

Male reproductive apparatus

Male pustules (Fig. 28) are hemispherical and smooth. The entire outer cortex becomes transformed into a zone of spermatangial parent cells (Figs. 29 and 30) that are barely distinguishable from surface cells of the host. Each pair of spermatangial parent cells (Figs. 31 and 32) is the product of



Figs. 28–32. *Gracilaria oryzoides* from California. Fig. 28. Confluence of spermatangial pustule with host cortex (arrowheads). Fig. 29. Same as in Fig. 28. Fig. 30. Spermatangial pustule with superficial spermatangial parent cells (arrow), and aborting cystocarp of host (arrowhead). Fig. 31. Superficial spermatangial parent cells with transversely divided spermatangia (arrowhead). Fig. 32. Same as in Fig. 31.

an oblique longitudinal division by a concavoconvex septum in a uninucleate outer cortical cell. Both spermatangial parent cells are basally pit-connected, remain uninucleate and each cuts off a single colorless, uninucleate spermatangium distally by a single transverse division (Figs. 31 and 32).

Tetrasporangia

Tetrasporangial pustules are typically crescent-shaped and warty (Figs. 1, 33 and 34). Each tetrasporangial initial (Fig. 35, arrowhead) is transformed from the terminal product of a longitudinal concavo-convex division of an outer cortical cell (Fig. 35, arrowhead). Usually, the resulting subapical bearing cell also divides by a longitudinal concavo-convex septum (Fig. 36), with the apical derivative potentially becoming a new sporangium after release of tetraspores from the first tetrasporangium. Tetrasporangial initials (Fig. 35) typically are larger and stain darker than surrounding cortical cells. The tetrasporocytes typically undergo two successive divisions, giving rise to four cruciately arranged tetraspores of approximately equal size (Fig. 37), although these are frequently divided in an irregular fashion (Fig. 37).

Discussion

Gracilariophila clearly belongs to the Gracilariaceae based on features of early reproductive development. Family characters include a supporting cell bearing a two-celled carpogonial branch flanked by a pair of



Fig. 33–36. Gracilariophila oryzoides from British Columbia and Fig. 37 from California. Fig. 33. Tetrasporangial pustule consisting of mixture of host cells and parasite cells. Sharp demarcation between inner parasite cells and host tissue (arrowheads). Fig. 34. Tetrasporangia (arrowheads) embedded between cortical filaments. Fig. 35. Tetrasporangial initial subtended (arrow) by its bearing cell. Fig. 36. Potential tetrasporangial initials (arrowhead) and bisporangium (on left). Former subapical cell has undergone an oblique division potentially resulting in tetrasporangial initial (arrowhead). Fig. 37. Regularly and irregularly cruciately divided tetrasporangia.

sterile branches, direct fusion of cells of sterile branches onto the persistent carpogonium, and formation of a generative multinucleate fusion cell that cuts off gonimoblast initials (FREDERICQ and HOMMERSAND 1988a).

Recently, ZUCCARELLO and GOFF (1988) corraborated by cross inoculation experiments the observations of DAWSON (1949) that *Gracilariophila* is an obligate parasite of its closely related host *Gracilariopsis lemaneiformis* (as *Gracilaria lemaneiformis*). The present study reinforces this idea of adelphoparasitism. The cystocarps of most red algal parasites typically consist of multiple lobes [e.g. *Gardnerella* (GOFF and HOMMERSAND 1982), *Tikvahiella* (KRAFT and GABRIELSON 1983)] because each individual carposporophyte is surrounded by a separate pericarp. In contrast, the carposporophyte of *Gracilariophila* is hemispherical and surrounded by a single, continuous pericarp.

In transverse section the cystocarpic pustule in *Gracilariophila* is scarcely distinguishable from the cystocarp of its host, *Gracilariopsis*. Both lack the tubular nutritive cells characteristic of *Gracilaria* that fuse with cells of the pericarp. In both, gonimoblast filaments are organized into comparatively straight chains, the initial shape of lowermost gonimoblast cells is retained, and gonimoblast conjunctor cells fuse with cells in the floor of the cystocarp.

The fundamental difference between host and parasite genera is seen in features of the floor of the cystocarp. In Gracilariopsis, a special nutritive tissue, the inner pericarp, is generated from the inner portion of cortical filaments that also produce the outer pericarp. Cells of the inner pericarp develop enlarged nuclei, are densely filled with cytoplasm, and appear to function as a 'sink' for the accumulation of nutriment that can support the growth of the carposporophyte during the course of gonimoblast development and the differentiation of the carposporangia (FREDERICO and HOMMERSAND 1989b). In contrast, there is not a sharp demarcation between gonimoblast tissues and the tissues of the floor of the cystocarp in Gracilariophila. Indeed, inner gonimoblast cells are cytologically and morphologically similar to host medullary cells. This continuum between reproductive and vegetative tissues is, so far, unique to Gracilariophila among red algal parasites. This special feature can, perhaps, best be understood as a refinement for supplying nutriment to the developing carposporophyte. Being а parasite, Gracilariophila presumably has a continuous, ambient supply of nutriment at its disposal obtained directly from the host, most cells of which by this time contain parasite nuclei owing to the abundance of secondary pit-connections. The formation of a secondarily transformed nutritive tissue that functions as а 'sink' (Hommersand and FREDERICQ 1989) would be a superfluous nutritive strategy, since food reserves have already been commandeered through the host/parasite interaction.

WILSON (1910) illustrated spermatangia borne in chains flanked by elongated sterile filaments. This pattern was never observed in our material. Instead, the present study documents that the spermatangial parent cells are produced from surface cortical cells, forming a superficial continuous layer, and that they cut off spermatangia by transverse division as in *Gracilariopsis* (FREDERICQ and Hommersand 1989b).

WEBER VAN BOSSE (1928) and YAMAMOTO (1986) both questioned whether the penetration of the parasite comes about by means of rhizoids or by pit-connections. In agreement with ZUCCARELLO and GOFF (1988), we found that connection between a parasite cell and a vegetative host cell is established by means of secondary pit-connections in *G. oryzoides*. A multinucleate rhizoidal cell was never seen to fuse directly with a host cell. Instead it always cuts off one or more conjunctor cells that fuse with the host cells, leaving behind pit-connections.

As was mentioned earlier, WEBER VAN Bosse (1928) subdivided *Gracilariophila* based on the absence (Malaysian species) or presence (California species) of rhizoids. In our opinion the compactness of the cortical region (and hence the size of intercellular spaces) may affect the outline of parasite cells (roundish rhizoidal cells vs. elongate rhizoids). We found both shapes in *G. oryzoides*.

The erumpent component of other red algal parasites is known to consist predominantly of unpigmented parasitic tissue interspersed with pigmented host cells, as for example in Gardnerella (GOFF and HOM-MERSAND 1982) OF Tikvahiella (GABRIELSON and KRAFT 1983), both adelphoparasites Solieriaceae. belonging the to In Gracilariophila, in contrast, the erumpent component is minimal and a well-defined pustule in which parasitic tissue is distinguishable is lacking.

GOFF and COLEMAN (1985) recently discussed the role of secondary pit-connection formation in red algal parasitism as a mechanism for transferring parasite genetic information Using host. fluorescence into the microscopy, Zuccarello and Goff (1988) noted that the only independent stages of Gracilariophila are the spore, the penetrating infection peg which cuts off 1-2 additional cells that transfer nuclei directly into adjacent host cell, establishing a heterokaryotic host cell, and the limited filamentous growth that occurs at the infection site. In their view,

once initial nuclear transfer has taken place by means of secondary pit-connections, the parasite cell then spreads throughout the host tissues as an intracellular parasitic nuclear genome. An alternative interpretation may in addition to establishing be that, heterokaryotic cells, rhizoidal cells may preserve their parasitic individuality until they have completely ceased to undergo cell division. In each instance that we observed, the establishment of a heterokaryotic cell is directed unilaterally, with rhizoidal conjunctor cells fusing with host cells and not vice ver-The main portion of the proliferating sa. rhizoidal system does not appear to harbor vegetative nuclei at the very last stages of infection, do parasite and host tissues eventually become cytologically and morphologically indistinguishable from one another.

The fact that secondary pit-connections do not seem to be structurally modified suggests that few incompatibility barriers exist between host and parasite cells, as would be expected of an adelphoparasite. The evolutionary success of this unusual parasite clearly lies in the abundance and flexible formation of secondary pit-connections at each stage of development. Pit-connections are initially formed when a rhizoidal cell links up with host vegetative cells, when the parasite ramifies and spreads, and when it taps food reserves for the developing carposporophytes.

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Suzanne FREDERICQ^{*1,2}・Max H. HOMMERSAND^{*1}・James N. NORRIS^{*2}: アデルフォ寄生藻 *Gracilariophila oryzoides*(紅藻、オゴノリ科)の形態観察

Gracilariophila oryzoides は生殖器官の初期発達過程からオゴノリ科に属し, Gracilariopsis lemaneiformis の新しい時 代に現われたアデルフォ寄生薬(宿主と極めて近縁な寄生種)と考えられる。寄生種の生殖器官が宿主のそれと 酷似する点は, 嚢果には果皮細胞と融合する管状の栄養細胞を欠き, 造胞糸は比較的直線的に連なって形成され, 造胞糸の結合細胞は嚢果底の細胞と融合しているなどである。嚢果に分化した栄養組織を欠くことを, 寄生とい う生活様式と関連づけて考察した。精子嚢は表層細胞から作られた精子母細胞の横分裂によって切り離される。 胞子の侵入, 寄生種の細胞と宿主の栄養細胞との結合, それに続くイボ状組織への成長についても記載した。 (*1 Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, N.C. 27599–3280, U.S.A.; *2 Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.)

Notes on Odonthalia kamtschatica (RUPRECHT) J. AGARDH (Ceramiales, Rhodophyta)¹

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Odonthalia kamtschatica (RUPRECHT) J. AGARDH (Rhodomelaceae, Ceramiales) is described and illustrated on the basis of specimens recently collected near the type locality. Tetrasporangia are borne on penultimate and ultimate orders of narrow lateral branches and proliferations. Two tetrasporangia are produced in each of 4–16 successive segments of these branches, including one or two segments congenitally fused to the parent axis. These features clearly distinguish O. kamtschatica from other costate species with which it has often been confused, and ally it with O. yamadae MASUDA, which is suggested to be a vicariant species.

Key Index Words: Kamchatka—Odonthalia—Odonthalia kamtschatica—Rhodomelaceae— Rhodophyta—taxonomy.

The red alga Odonthalia kamtschatica (RUPRECHT) J. AGARDH (Rhodomelaceae, Ceramiales) was originally described by RUPRECHT (1850) as Atomaria kamtschatica on of specimens collected basis the at Petropavlovsk, Avacha Bay, on the eastern Kamchatka Peninsula. It was transferred to Odonthalia by J. AGARDH (1863). Since then, it has been reported from various localities of the north Pacific (SETCHELL and GARDNER 1903; Collins 1913; Kylin 1925; Okamura 1932, 1936; Tokida 1934, 1950, 1954; YAMADA and TANAKA 1944; SCAGEL 1957; CHIHARA 1967; WIDDOWSON 1974; SCAGEL et al. 1986). Although RUPRECHT's description of cystocarpic plants is clear, this species has been confused with other species of Odonthalia as discussed by MASUDA and YAMADA (1981).

Further studies based on the cystocarpic lectotype specimen (MASUDA 1981a; MASUDA and YAMADA 1981) have amplified the original description. In this paper, we describe and illustrate tetrasporangial plants for the first time based on recent collections near the type locality. The characteristic features of *Odonthalia kamtschatica* are discussed and compared with several related species.

Materials and Methods

Specimens were collected at four localities Avacha Bay: Cape Seroglazka in (53°02'42"N, 158°35'30"E, vegetative, May 24, 1984, leg. V.I. STRELKOV); Cape Kazak (52°57'40"N, 158°27'30"E, tetrasporangial, May 6, 1988, leg. A.G. BAZHIN); Stones Tri Brata (52°54′00″N, 158°42′02″E, vegetative, September 15, 1987, leg. A.G. BAZHIN); and Harbor Vilyuchinskaya (52°38'35"N, 158°25'32"E, tetrasporangial, May 2, 1988, leg. N.G. KLOCZCOVA; tetrasporangial and cystocarpic, May 4, 1988, leg. N.G. KLOCZ-COVA). Odonthalia kamtschatica grows abundantly on rocks at 3-12 m depth in Avacha Bay.

The exterior morphology of dried herbarium specimens was studied with a dissect-

¹ Dedicated to the memory of the late Dr. Munenao KUROGI (1921–1988), Professor Emeritus of Hokkaido University.



Fig. 1. First-year tetrasporangial specimen of *Odonthalia kamtschatica* with broad vegetative branches and narrow reproductive branches (arrowheads) collected at Cape Kazak, Avacha Bay, eastern Kamchatka on May 6, 1986.

ing microscope. For microscopic examination of anatomical structure, portions were removed, preserved in 70% ethyl alcohol and sectioned by hand using a razor blade and pith stick.

Voucher specimens are deposited in the herbaria of Faculty of Science, Hokkaido University, Sapporo (SAP) and the Kamchatka Department of Environment, Pacific Institute of Geography, Petropavlovsk-Kamchasky.

Observations

Several upright thalli, 8–19 cm high and dark red in color, arise from a common basal disc. Each thallus is monopodial and branched in an alternate-distichous manner (Fig. 1). The main axis is terete just above the basal disc and 0.8–1.6 mm in diameter, becoming immediately compressed above. It is broader at the point of insertion of lateral branches, attaining a width of 2.5-3.3 mm at non congenitally-fused area with its laterals in the lower and middle portions.

The majority of first-order branches are indeterminate, up to 6-12 cm long, and are divided into progressively shorter branches to 5-6 orders. The proximal one or two branches of 2-5 orders remain unbranched. Proliferations are formed from the margins of the main axis. Those initiated in axils formed by the main axis and injured first-order branches resemble indeterminate first-order branches, but have terete bases rather than the flattened bases characteristic of ordinary lateral Many branches. narrow reproductive proliferations develop on the perennating main axes of second-year thalli (Fig. 2).

Midribs are visible on the lower to upper portions of the main axis (Figs. 3-6) and on the lower to middle portions of well-developed



Fig. 2. Second-year tetrasporangial specimen of *Odonthalia kamtschatica* with many reproductive proliferations (arrowheads) collected at Vilyuchinskaya Harbor, Avacha Bay on May 2, 1988.

first-order branches and proliferations. Midribs are produced by successive divisions of cortical cells, and do not develop equally on both sides (Figs. 4, 5). They appear on only one side of the upper portion of the main axis (Fig. 3) and the middle portion of first-order branches and proliferations.

Penultimate and ultimate branches of narrow lateral branches (Fig. 1) produce tetrasporangia (Fig. 7). Tetrasporangia are also formed on penultimate and ultimate branches of proliferations less than 5 mm in length and on longer, narrow proliferations (Fig. 2). Tetrasporangial branches are arranged entirely in an alternate-distichous manner and are compressed, 650-1800 µm long and 180-240 µm wide. Two tetrasporangia are produced in each of 4-16 successive segments of the branches, including one or two segments congenitally fused with the parent axis (Fig. 7). Each sporangium is provided with two cover cells (Fig. 8). Tetrahedrally divided sporangia are $120-170 \,\mu m$ in diameter.

Procarp-bearing branchlets and cystocarps are arranged on narrow branches and short proliferations in a flexuose-racemose manner. Procarp-bearing branchlets are polysiphonous (Fig. 9). As cystocarps form, distal sterile segments of these branchlets develop into long calcars (Fig. 10). Matur-



Figs. 3-6. Cross sections of a main axis of *Odonthalia kamtschatica* collected at Stones Tri Brata, Avacha Bay on September 15, 1987, showing development of a midrib: 3, upper portion; 4, 5, middle portion; 6, lower portion. Scale in Fig. 5 applies also to Figs. 3 and 4.

ing cystocarps are urceolate and have elevated necks; fully mature cystocarps have not been observed. Cystocarps examined are 700–900 μ m long by 580–750 μ m wide and with 280–800 μ m long calcars (Fig. 10).

Discussion

Our observations of polysiphonous procarp-bearing branchlets and urceolate cystocarps with long calcars are identical with earlier reports based on the lectotype specimen of *Odonthalia kamtschatica* (MASUDA 1981a; MASUDA and YAMADA 1981). Our study confirms that tetrasporangia are also borne on narrow reproductive branches (similar to those of cystocarpic plants) that are distinctly different from the broader vegetative

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Figs. 7–10. Reproductive structures of *Odonthalia kamtschatica* collected at Vilyuchinskaya Harbor, Avacha Bay on May 2, 1988 (7, 8) and May 4, 1988 (9, 10): 7, tetrasporangial branches, note tetrasporangia being formed at the congenitally-fused area between the axis and ultimate laterals (arrowheads); 8, two segments of a tetrasporangial branchlet, showing cover cells (c) (the tetrasporangia being out of focus); 9, polysiphonous procarpial branchlet, note the procarp-bearing segment being shown by an arrowhead; 10, two cystocarps with well-developed calcars. Scale in Fig. 9 applies also to Fig. 8.

branches characteristic of this species.

In second-year plants, the broad main axes are eroded and overgrown by proliferous reproductive branches. These thalli, composed of narrow proliferations (Fig. 2, TOKIDA 1934, Pl. V), are sufficiently different from first-year plants to cause confusion as to their identity. Nevertheless, proliferations have terete bases in contrast with the compressed bases of ordinary lateral branches, so that thalli composed chiefly of narrow reproductive proliferations can be identified as perennating individuals of *O. kamtschatica*.

At present, twelve species have been described in the genus *Odonthalia* (MASUDA

1982). They are divided into two groups, depending on the presence or absence of midribs. Odonthalia kamtschatica is included in the costate group together with the following seven species: 1) O. dentata (LINNAEUS) LYNGBYE, the type species, 2) O. kawabatae MASUDA, 3) O. lyallii (HARVEY) J. AGARDH, 4) O. ochotensis (RUPRECHT) J. AGARDH, 5) O. setacea (RUPRECHT) PERESTENKO, 6) O. washingtoniensis Kylin and 7) O. yamadae MASUDA. Although these species can be distinguished by reproductive features (MASUDA 1982), it is often difficult to distinguish species on the basis of vegetative features alone. Hence, non-reproductive

specimens of *O. kamtschatica* have been confused with other closely related species.

We can now use tetrasporangial characters for a more complete comparison of Odonthalia kamtschatica with other costate species. 0. kamtschatica and O. ochotensis are currently distinguished on the basis of cystocarpic characters (MASUDA and YAMADA 1981). Our results show that O. kamtschatica produces tetrasporangia on ultimate and penultimate branches, whereas tetrasporangia in O. ochotensis are restricted to ultimate branchlets (RUPRECHT 1850), i.e. well-defined stichidia with constricted bases. Two kinds of tetrasporangial branches have been described for 0. ochotensis: "flabellato-corymbose stichidia without short pedicels" (OKAMURA 1923, Pl. 196, Fig. 4) and "pinnatofasciculated stichidia with short pedicels" (Okamura 1923, Pl. 196, Fig. 5; 1936, Fig. OKAMURA's voucher specimens, 422. 4). deposited in SAP, were examined, including four tetrasporangial specimens: one from Chirie, Sakhalin (June 15, 1912) and three from Shumsh Island, the north Kuriles (no These specimens have collection date). tetrasporangial branchlets lacking pedicels, comparable to those of O. kamtschatica; no specimens with pedicellate tetrasporangial stichidia are present. We believe that OKAMURA's original description was based on collections composed of more than one species, one of which is O. kamtschatica.

Specimens of Odonthalia setacea and O. lyallii can be distinguished from those of O. kamtschatica by their monosiphonous procarp-bearing branchlets, ecalcarate cystocarps and tetrasporangial stichidia with constricted bases (MASUDA 1981a; MASUDA and MILLER, unpublished), although these species are all similar to one another vegetatively.

Odonthalia kawabatae, with its narrow thalli, broadly ovoid cystocarps, and well-defined tetrasporangial stichidia (MASUDA 1981b), is readily distinguished from O. kamtschatica. Fertile specimens of O. dentata (NEWTON 1931; MASUDA and YAMADA 1981) and O. washingtoniensis (SETCHELL and GARDNER 1903, as O. semicostata; MASUDA and YAMADA 1981) possess minute axillary or marginal reproductive branches that are readily distinguished from the well-developed reproductive lateral branches and proliferations of *O. kamtschatica*. The reported occurrence of *O. dentata* in the North Pacific (RUPRECHT 1850; TOKIDA 1954; PERESTENKO 1977) is questionable (LINDSTROM 1977).

Odonthalia kamtschatica and O. yamadae are closely related and have the following vegetative and reproductive features in common: 1) large, broad thalli, 2) conspicuously developed midribs, 3) narrow reproductive branches, 4) flexuose-racemose arrangement of cystocarps, 5) tetrasporangia produced on both ultimate and penultimate branches, including segments congenitally fused to the species parent axis. These two are distinguished by features of the procarp-bearing branchlets and cystocarps. O. kamtschatica has polysiphonous procarp-bearing branchlets and urceolate cystocarps with long calcars, whereas О. yamadae possesses monosiphonous procarp-bearing branchlets and barrel-shaped or broadly ovoid cystocarps without conspicuous calcars (MASUDA 1982). The occurrence of procarps on polysiphonous branchlets is considered primitive feature in the family а Rhodomelaceae 1963; (Hommersand MASUDA 1982). The distributional range of O. kamtschatica extends from the Kamchatka Peninsula through the middle Kuriles to Sakhalin (MASUDA and YAMADA 1981). As pointed out by WIDDOWSON (1974), records of its occurrence on the east coast of the North Pacific (SETCHELL and GARDNER 1903; COL-LINS 1913; KYLIN 1925; SCAGEL 1957; SCAGEL et al. 1986) need verification. On the other hand, the present known range of O. yamadae is narrowly restricted to the eastern coast of Hokkaido (MASUDA 1982). The monosiphonous procarp-bearing branchlets of O. yamadae may be a derived character associated with its vicariant speciation from the more broadly distributed and primitive O. kamtschatica to the south.

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増田道夫*・Olga N. SELIVANOVA**: 紅藻カムチャツカノコギリヒバ (イギス目フジマツモ科)について

基準標本産地の近くから最近採集された標本に基づいて、紅藻カムチャツカノコギリヒバ Odonthalia kantschatica (RUPRECHT) J. AGARDH の形態的特徴の記載と図示を行った。四分胞子嚢は栄養枝よりも幅の狭い生殖枝 と副枝の最末小枝と末位から二番目の枝に、4-16節連続して二列に形成される。四分胞子嚢枝の基部はくびれ ず、最末小枝の場合には軸と癒合している1-2節にも四分胞子嚢を生じる。これらの特徴は、今まで本種と混同 されてきた他の中肋を持つノコギリヒバ属の種から、本種を明瞭に区別し、アッケシノコギリバ O. yamadae MASUDA との近い類縁を示している。(*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・**Kamchatka Department of Environment, Pacific Institute of Geography, Far East Science Branch, Academy of Sciences of the USSR, Petropavlovsk-Kamchasky, 683000, USSR)

Nitrate uptake by nitrogen-starved plants of the red alga Gracilaria tenuistipitata var. liui

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Nitrate-nitrogen uptake by nitrogen-starved plants of the red alga *Gracilaria tenuistipitata* var. *liui* ZHANG and XIA (formerly called *Gracilaria verrucosa*) was studied under 25 combinations of temperature (10, 15, 20, 25 and 30°C) and salinity (10, 20, 30, 40 and 50%). The plants assimilated all NO₃⁻ (200 μ M) in the medium within 24 hours at the combinations of 15°C, 20°C, 10% and 20%, but the uptake was slow at lower temperature (10°C) and at higher salinity (40 and 50%).

Nitrate uptake by the plants in the "light" and in the "dark" was almost the same during the first 6 hr, but afterwards, the plants in the light assimilated nitrogen much more rapidly than those in the dark. The "light" plants assimilated all of the NO_3^- (200 μ M) in the medium within 20 hr and continued the assimilation in a new medium. In contrast the "dark" plants assimilated NO_3^- slowly during the first 24 hr and stopped the assimilation in a new medium. The basal segments of the N-starved plants absorbed more than 80% of NO_3^- (200 μ M) in the medium within 24 hr, whereas the apical segments absorbed only 40% of it.

Key Index Words: Gracilaria—Gracilaria tenuistipitata var. liui—Gracilariaceae—nitrate uptake— Rhodophyta—seaweed cultivation.

Gracilaria is a marine red alga which has been studied extensively because of its commercial value as a source of agar, its importance in diet, and its increasing demand in the cultivation of the sea abalone (CHIANG 1981, Edward et al. 1982, Cordero 1984). Previous studies have shown that the growth, agar content and its quality of this alga may be limited by the amount of available nitrogen and the rate of nitrogen uptake also can be limited by a variety of environmental conditions (DEBOER et al. 1978, DEBOER 1979, WANG and YANG 1980, BIRD et al. 1981, 1982, Bird 1988, Lapointe 1981, Lapointe et al. 1984a, b, FUJITA and GOLDMAN 1985, ROTEM et al. 1986). Those kinds of information are most useful for purpose of Gracilaria Accordingly, we initiated the cultivation. present study to examine the effects of salinity, temperature and light on the uptake of NO₃ of Gracilaria tenuistipitata var. liui ZHANG and XIA (formerly called Gracilaria vertucosa) which has been cultivated extensively in

Taiwan (CHIANG 1981).

Materials and Methods

Vegetative plants of G. *tenuistipitata* var. *liui* were collected from an aquaculture pond at Anpin, Tainan, Taiwan.

Plants of about 5 kg (wet weight) were grown in a flat-bottom concrete tank $(2.0 \text{ m} \times 4.0 \text{ m} \times 1.0 \text{ m})$ for 3-4 weeks in unenriched running seawater (about 1.5 volumes of seawater were exchanged per day) until the plants became pale straw-yellow in color, which is indicative of a nitrogen deficiency of the plants (RYTHER *et al.* 1981).

Epiphytes removed

Before each experiment, nitrogen-deficient Gracilaria were cleaned to ensure that all of the nitrogen from the medium had been assimilated by the Gracilaria plants only. The procedure used for cleaning the plants was based on the technique of BIRD (1976). Hav-

ing removed sand and epiphytic algae, the plants were immersed for 30 seconds in a sodium dodecyl sulfonate seawater solution. The fronds were then transferred to a 0.001% (v/v) formaldehyde solution for 30 seconds, whereupon they were rinsed twice in sterilized seawater.

Apparatus

Experiments were carried out in a growth chamber at 10°C. For cultivation of the fronds, 500 ml Pyrex flasks were used and they were kept in glass-made aquaria (60 cm \times 30 cm \times 36 cm) with water of required temperature which was controlled with LAMYCON 500 DX IC Controller thermostat. Water in the aquaria was well mixed by bubbling with compressed air. Irradiance was provided by cool-white 40-W fluorescent lamps at 120 μ E m⁻²s⁻¹.

Preconditioning thallus

Prior to each experiment, cleaned thalli of 5.0 ± 0.2 g wet weight were preconditioned by incubation in 500 ml flasks containing sterilized seawater at the required salinity and temperature under an $11 : \overline{13}$ hr photoperiod and a light intensity of $120 \ \mu \text{E m}^{-2}\text{s}^{-1}$ for 7 days. Each experimental condition was run in duplicate and all experiments were repeated once.

Nitrate was measured according to STRICKLAND and PARSONS (1972). C/N values of the plants before and after each experiment were determined with a Perkin-Elmer 240 elemental analyzer.

A modified growth medium SWM (McLACHLAN 1973) (lacking soil and liver extract, S-3 vitamins and NaNO₃) was used. Salinity was modified by dilutions with distilled water or by concentration of seawater by heating and was corrected for evaporation every other day during the experiments. The pH of the medium was adjusted to 7.5.

Experiment I: Effects of temperature and salinity on NO_3^- uptake

Combinations of temperature (10, 15, 20, 25 and 30°C) and salinity (10, 20 30, 40 and

50%) were used.

Preconditioned thalli of 5.0 ± 0.2 g (wet weight) were inoculated into each flask containing 300 ml medium which had 200 μ M NO₃⁻ and were grown at the required conditions. Every 24 hr, over a 6-day period, water samples of 1 ml each were withdrawn from all cultures and analyzed for NO₃⁻ concentration. In addition, water samples were also taken from a flask without seaweed to determine any other loss of NO₃⁻ occurring.

Experiment II: Effects of light and darkness on NO_3^- uptake

The thalli which had been preconditioned for 7 days under conditions of 15°C, 20%, 11: $\overline{13}$ hr photoperiod and 120 μ E m⁻²s⁻¹ were incubated in four flasks each containing 300 ml medium with a level of 200 μ M NO₃⁻. Each flask contained thalli of 5.0±0.2 g (wet weight).

Two of the four flasks were wrapped with aluminum foil and then enclosed in a lighttight container. Then both sets of cultures were returned to the same conditions as those of the precondition, except that 24 hr illumination was provided, instead of $11:\overline{13}$ hr photoperiod. Water samples were taken from each culture every 2 hr over the initial 24 hr to determine the level of residual NO₃⁻.

After 24 hr, the medium of all cultures was replaced with fresh medium, and the experiment was continued for additional 6 days. Every 24 hr, water samples were taken from each culture to determine the NO_3^- concentration.

Experiment III: Uptake of NO_3^- by the apical and basal segments

Thalli were treated for 7 days under the same conditions as those in Exp. II and were cut into two portions (apical and basal) of segments, each measuring 3.0 cm and weighing 5.0 ± 0.2 g (wet weight). Then the segments were inoculated into 300 ml medium with 200 μ M NO₃⁻ and were grown under the same conditons as in the previous culture. Every 2 hr, the concentration of NO₃⁻ in the culture media was measured.

Results

Experiment I

No measurable amount of NO_3^- was lost from the flasks without plant. Thus any loss from the flasks containing the *Gracilaria* could be assumed to have been due to assimilation by the algae.

As shown in Table 1, the thalli grown in the combinations of 15°C, 20°C, 10% and 20% assimilated all of NO_3^- in the medium within 24 hr. In general, plants grown in lower salinities (10-30%) assimilated $NO_3^$ more rapidly than those grown in higher salinities (40 and 50%). Those grown at 1525°C absorbed 85-100% of the NO_3^- within 4 days. However, plants grown at 10 and 30°C assimilated NO_3^- more slowly than those grown at other temperatures regardless of the salinity.

Experiment II

The results (Fig. 1) of this experiment showed that NO_3^- uptake in the "light" and in the "dark" was essentially the same within 7 hr after the initiation of the experiment. After 7 hr, however, the plants grown in the "light" began to assimilate more NO_3^- than those in the "dark". For example, after 20 hr the "light" plants had assimilated all NO_3^- in the

Table 1. Uptake (% of initial concentration, 200 μ M NO₃⁻) of nitrate-nitrogen by nitrogenstarved Gracilaria tenuistipitata var. liui at different temperatures and salinities.

Temp. (°C)	Sal.	Uptake				
	(‰)	Day 0	Day 1	Day 2	Day 3	Day 4
10	10	0.0	16.2	30.1	64.9	75.9
	20	0.0	26.3	37.3	72.5	83.5
	30	0.0	30.9	47.5	62.0	71.9
	40	0.0	8.6	26.6	44.2	58.7
	50	0.0	1.8	18.9	32.6	42.8
	10	0.0	100.0	_	_	_
	20	0.0	100.0	_	—	_
15	30	0.0	54.2	87.0	92.5	100.0
	40	0.0	40.0	79.3	88.5	100.0
	50	0.0	26.2	48.4	49.6	71.2
	10	0.0	100.0	_	_	_
	20	0.0	100.0	—	—	—
20	30	0.0	38.7	53.2	74.0	85.8
	40	0.0	24.2	42.9	58.7	62.8
	50	0.0	18.3	31.0	45.5	58.4
	10	0.0	72.8	86.9	100.0	_
	20	0.0	64.3	79.3	89.6	100.0
25	30	0.0	34.4	43.5	63.5	84.9
	40	0.0	16.5	23.7	46.5	60.2
	50	0.0	10.8	22.0	40.8	58.1
	10	0.0	18.2	34.6	44.0	78.0
	20	0.0	29.8	40.5	63.8	87.9
30	30	0.0	24.8	36.5	49.4	69.4
	40	0.0	11.6	20.6	32.6	54.8
	50	0.0	10.4	18.7	31.1	49.4



Fig. 1. Decrease of nitrate-nitrogen in the medium due to the uptake by nitrogen-starved *Gracilaria tenuistipitata* var. *liui* in the light (--) and in the dark (---).



Fig. 2. Changes of nitrate-nitrogen in the medium due to the uptake (or release) by *Gracilaria tenuistipitata*. var. *liui* in the light (—) and in the dark (---) after the materials experienced the same conditions as shown in Fig. 1.

medium, whereas the "dark" plant had assimilated only 65%. In addition, Fig. 2 shows that plants in the light continued to assimilate NO_3^- from the fresh medium while those in the dark actually lost some of the previously assimilated NO_3^- to the medium.

Experiment III

The results of this experiment shown in Fig. 3 indicate that segments of the basal portion assimilated about 80% of NO_3^- in the



Fig. 3. Uptake of nitrate-nitrogen by the apical (--) and basal (---) segments of nitrogenstarved *Gracilaria tenuistipitata* var. *liui*.

medium within 24 hr, whereas those of the apical one assimilated less than 40% of the original concentration. However, segments of the apical portion increased their wet weight and produced more new branches than the basal segments after 7-day cultivation (unpublished data).

Discussion

Earlier studies (LAPOINTE and RYTHER 1979, RYTHER and HANISAK 1981) on the culture of *Gracilaria* have shown that healthy plants can lose their dark reddish-brown color and become pale-yellow when they are held under very low NO_3^- concentrations. The change in color is indicative of nitrogen deficiency, with C/N values changing from about 6 to nearly 30, after stocking in the tank with unenriched running seawater. Plants used in this study indicated a change in color from dark reddish-brown to pale-yellow, while C/N values increased from about 5 to 15, indicating nitrogen deficiency.

Rapid N-assimilation by N-starved

Gracilaria depends upon carbohydrate reserves (RYTHER et al. 1981), which in turn are affected by temperature and salinity. EHRKE (in Gessner 1970) found that photosynthetic rates of Fucus serratus. Plocamium cocconeum and Enteromorpha compressa were higher than respiration at lower temperatures ($\leq 20^{\circ}$ C). In this experiment, the Nstarved Gracilaria growing at 15 and 20°C assimilated NO₃⁻ more quickly than those growing at 30°C. This could be due to the rate of photosynthesis of these plants exceeding that of respiration, thereby increasing their carbohydrate reserves during the preconditioning period. Therefore they may have been able to assimilate NO_3^- more rapidly at the expense of carbohydrate reserves. On the other hand, as temperature increases beyond the optimum range for growth of the plants, the rate of respiration exceeds that of photosynthesis (EHRKE in GESSNER 1970), thereby reducing the carbohydrate reserves. This may explain the slower assimilation of NO_3^- at 25 and 30°C than at 15 and 20°C. The low uptake rate of NO₃⁻ at 10°C might be due to the slow metabolic rate of the plants at this temperature.

HUANG (1980) found that G. tenuistipitata var. liui showed the highest photosynthetic rate at 25°C in salinities of 10-20‰ and that the rate decreased as the salinity increased from 20 to 50‰. These findings agree with our present results that plants can assimilate more NO_3^- in lower salinities (10-30‰) than in higher ones (40-50‰). These results support the observation of GESSENER and SCHRAMM (1971) that although both photosynthesis and respiration decrease with increased salinity, salinity affects more photosynthesis than respiration.

RYTHER et al. (1981) found that N-starved Gracilaria assimilated more ammoniumnitrogen following exposure to daylight than did plants held in the dark, and showed that N-starved macroscopic algae can assimilate nitrate in the darkness, as can microalgae (cf. SYRETT 1962). The same phenomenon is also shown in our study on the assimilation of nitrate-nitrogen by N-starved Gracilaria (Fig.

2). The plants in the "light" and in the 'dark" showed no substantial difference in the uptake of nitrate-nitrogen during the first six hours of the experiment. This observation suggests that the carbohydrate reserves in both plants were almost equal at first. However, the "light" plants were able to maintain or increase their carbohydrate content due to photosynthesis and hence were able to continue NO_3^- assimilation under light condition. On the other hand, the "dark" plants continued to deplete their carbohydrate reserves and ultimately began to lose the ability to assimilate NO_3^- . Rapid Nassimilation by starved algae depends upon carbohydrate reserves and ceases when those reserves are depleted (SYRETT 1962). In their study on two red macroalgae, D'ELIA and DEBOER (1978) found that decreases in nitrogen uptake rates occur in response to nitrogen satiation of the seaweeds. This was also true for G. tenuistipitata var. liui when the medium of both the "light" and the "dark" was replaced with fresh one after 24 hr. The plants in the "light" continued to assimilate NO_3^- but at a slower rate, and only 72% of NO_3^- added was assimilated after 6 days in contrast to 100% in the first 24 hr. Plants in the "dark" did not assimilate any NO_3^- , but actually lost some.

The color of the basal portions of the plants used in this study was generally slightly darker than that of the apical ones, suggesting that the basal region had more pigment available for photosynthesis than the apical This appeared to be the case as the ones. photosynthetic rate of the basal portion was almost 1.5 times higher than that of the apical one (unplished data). ROSENBERG and RAMUS (1982) found that N-starved plants use pigment-protein as a nitrogen source for cell division, and since cell divisions are usually more active in the apical part than in the basal part of a plant, the apical parts would tend to lose their pigments more quickly than the basal ones. This was confirmed when the apical segments produced more branches than the basal ones after 7-day cultivation.

In conclusion, our findings on the condi-

tions for nitrogen uptake by nitrogen starved Gracilaria could be helpful in choosing time for adding fertilizers to Gracilaria ponds.

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江 永 棉・林 俊 亮: 窒素欠乏条件下に置かれた紅藻 Gracilaria tenuistipitata var. liui の硝酸塩吸収

紅藻 Gracilaria tenuistipitata var. liui (従来 Gracilaria verrucosa と呼ばれたもの)を窒素欠乏海水中に置いた後,温度5段階 (10, 15, 20, 25, 30°C)と塩分5段階 (10, 20, 30, 40, 50%)を組合わせた25の条件下で硝酸態窒素の吸収を調べた。15°C及び20°Cと10%及び20%の組合わせでは24時間以内に培地中のNO₃⁻ (200 μ M)は全て吸収されたが,低温 (10°C)高塩分 (40及び50%)下では吸収は遅かった。硝酸態窒素の吸収は初めの6時間は明条件下でも暗条件下でも変りはなかったが,その後は、明条件下の藻体の方が暗条件下の藻体より急速な吸収を示した。明条件下の藻体は20時間以内に培地中のNO₃⁻ (200 μ M)を全て吸収し、新しい培地に移すとさらに吸収を続けた。これに対し、暗条件下の藻体は初めの24時間はNO₃⁻ をゆっくり吸収し、新しい培地に移すとならに吸収を停止した。窒素欠乏藻体の基部片は培地中のNO₃⁻ (200 μ M)の80%以上を24時間以内に吸収したが,先端部片はわずか40%を吸収しただけであった。(台湾台北市 国立台湾大学海洋研究所)

Regeneration process of *Ecklonia* marine forest in the coastal area of Shima Peninsula, central Japan

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MAEGAWA, M. and KIDA, W. 1989. Regeneration process of *Ecklonia* marine forest in the coastal area of Shima Peninsula, central Japan. Jpn. J. Phycol. 37: 194–200.

A regeneration process of the *Ecklonia* marine forest was studied with methods of permanent quadrat and mapping for 6 years. The regeneration process and turnover time were revealed as compared with those of terrestrial climax forests. Three phases of gap, building and maturation were distinguished with reference to structural and dynamic features of the population in the regeneration process. The turnover time (regeneration cycle) of the canopy layer was 3 years. The regeneration process of the *Ecklonia* marine forest was controlled by intraspecific competition for getting light.

Key Index Words: building phase—Ecklonia cava—gap phase—mature phase—Phaeophyceae—population dynamics—regeneration—seaweed.

It is considered that the marine climax forest is maintained by dynamic equilibrium, i.e. partial destruction and construction of the canopy. Consequently, the structure and function are stable for many years beyond the life expectancy of the major component individuals. The mechanisms of regeneration (secondary succession) of the marine climax forest are the subject of study attracting ecological interest of some researchers in recent years. However, only a little knowledge was accumulated for the change in population structure of marine forests throughout a long period of study for more than 5 years (TANIGUCHI and KATO 1984, DAYTON et al. 1984, KIDA and MAEGAWA 1985). The recent studies of stability and succession emphasize the need for the recognition of appropriate scales in time and space (SUTHERLAND 1981, CONNELL and SOUSA 1983). Particularly, the time scale should be longer than the maximum life span of the major component individuals in the study of population dynamics.

Recently, the regeneration processes of terrestrial climax forests in many countries have been studied intensively. Many authors have emphasized that tree fall and opening in the canopy play an important role in terrestrial forest regeneration (BRAY 1956, BARDEN 1981, RUNKLE 1981). BRAY (1956) called such an opening the "gap", and the regeneration of terrestrial climax forests takes place mainly in such gaps. The process is named the "gap phase regeneration".

In this study, the regeneration process of marine *Ecklonia* forest was traced with methods similar to the ecological analysis used in terrestrial forests, such as permanent quadrat and mapping. The fundamental properties of structure and regeneration of marine *Ecklonia* forest are comparable well to those of terrestrial forests, in spite of notable differences in the scale of population and the turnover time of the regeneration cycle between them. This kind of information will be useful not only in evolving and examining the theory of succession and stability of marine forest but also in forest conservation and afforestation for its probability of application.

Materials and Methods

Permanent quadrat experiment for analyz-



Fig. 1. Maps showing the location of study area.

ing the regeneration process of the Ecklonia cava population was carried out offshore at Hamajima (Fig. 1). In May 1982, 2 quadrats of $1 \text{ m} \times 3 \text{ m}$ constructed with ropes were set on a flat rocky substratum within a population at a depth of 8 m at Stns. 1 and 2. Each quadrat was divided into 6 small subquadrats $(0.5 \text{ m} \times 1 \text{ m})$ for convenience of measuring and mapping. All individuals in 2 quadrats were marked by tagging sequentially numbered plastic plates $(1 \text{ cm} \times 2 \text{ cm})$ around the holdfast for adult plants and plotting the position of individuals on a distribution map for young and small ones. The smallest juveniles marked in this study were 1-3 cm long which could be distinguished from ones of other species.

From the month when the plants were marked through June 1987, presence or absence of individuals and plant size (stipe length) were measured by means of SCUBA diving. The census in the quadrats was carried out 19 times at two- or three-month intervals from 1982 to 1984, and at six-month intervals from 1984 to 1987. Total plants marked in 2 quadrats for 6 years reached 1000 individuals. Such numerous data enabled us to conduct a comprehensive study of the changes in population structure.

Results

Yearly changes of frequency distribution of the stipe length in 2 quadrats in June from 1982 to 1987 are shown in Fig. 2. Shaded parts show the number of plants lost during a period till the following year. The yearly changes in frequency distribution of stipe length in both quadrats showed a similar tendency. In 1982 large fronds with stipe length of more than 20 cm occupied greater parts, but in 1983 most of large fronds in the canopy disappeared and many recruits were produced. In 1984 and 1985 large fronds which developed from recruits in 1982 and 1983 occupied a large part of the population, forming the canopy again. In 1986 most of canopy fronds disappeared and many recruits were produced, showing a similar frequency distribution as in 1983. Frequency distribution in 1987 showed a similar trend as that in 1984. Thus, the number of recruits was con-



Fig. 2. Yearly changes in frequency distribution of stipe length of *Ecklonia cava* population at Stns. 1 and 2 from 1982 to 1987. Shaded portions show the loss during a subsequent year.



Fig. 3. Changes in the population density of total fronds $(-\Box-)$, fronds with stipes shorter than 20 cm $(-\odot-)$, fronds with stipes longer than 20 cm $(-\odot-)$, average stipe length $(-\odot-)$, and standing stock $(-\odot-)$ of *Ecklonia cava* at Stns. 1 and 2 from 1982 to 1987.

trolled by the density of large fronds. After most of large fronds forming the canopy were lost or drifted out, many recruits were produced and grew to the canopy 1-2 years later. Consequently, the turnover time (regeneration cycle) of the canopy layer of the *Ecklonia* marine forest was 3 years. A large number of adult fronds were lost from 1982 to 1983 and from 1985 to 1986, i.e. during the third and the fourth year from germination. Fig. 3 shows seasonal and yearly changes in the density, standing stock and mean stipe length with advancement of the regeneration process in both populations at Stns. 1 and 2. Standing stock was calculated from the allometric relation between stipe length and total frond weight as indicated in a previous paper (MAEGAWA and KIDA 1984). Mean stipe length is the average for total fronds in the quadrat at every census. Therefore, it is



Fig. 4. Schematic diagram of the regeneration process in *Ecklonia cava* population, and changes in the population density and standing stock with advancement of the regeneration process.

a parameter representing the height of the population.

The number of young fronds exhibited periodic changes at intervals of 3 years. The density of young fronds was high in 1983 and 1986 when the density of adult fronds was low, and it was low in 1982, 1984, 1985 and 1987 when adult fronds formed a dense canopy. The maximum density of adult fronds (larger than 20 cm in stipe length) was about 14 individuals/m² which was similar in both quadrats. The changes of standing stock and mean stipe length showed a similar trend: i.e. both were at the peak in 1982, 1984, 1985 and 1987 when the adult fronds formed a dense canopy, and were low in 1983 and 1986 when most of the adult fronds were lost and many recruits were produced in the population. Maximum standing stock and mean stipe length were 0.8 kg/m² and 30-40 cm, respectively.

From the results mentioned above, a schematic diagram of the regeneration process in Ecklonia forest was drawn as illustrated in Fig. 4 with summarizing the changes in density, standing stock and regeneration pro-Three phases could be distinguished cess. with reference to structural and dynamic feature of the population in the regeneration process. In the first place, the gap is opened by the loss of many large fronds which form the canopy. During the initial 3 to 6 months from gap formation, the density of recruits increases rapidly from winter to spring (gap phase). After the population density reaches the maximum in nearly half a year from gap formation, it decreases rapidly. During this period plants grow rapidly and the standing stock also increases greatly (building phase). Thereafter, the standing stock approaches the maximum (steady state) within 1-1.5 years after gap formation, although it shows winter depression because of decaying old bladelets after the release of zoospores from late autumn to winter. In addition, the population density decreases gradually (mature phase). The mature phase is maintained for about one year. The regeneration process of the Ecklonia forest corresponds well to the

typical "gap regeneration" in terrestrial climax forests

Discussion

Recently, long-term ecological researches of seaweeds have been carried out to examine the distribution of species and to analyze the structure of populations or communities. As the result of these studies, the most important factor controlling algal structure was thought to be wave action (Sousa 1979, DAYTON and TEGNER 1984) and/or grazing by herbivores (EBELING et al. 1985, Novaczek and McLACHLAN 1986) which act as external factors. Thus, until now it has been considered that the density and standing stock of marine forests varied irregularly depending on the number of herbivores and the sudden occurrence of storms. In this study, we propose another factor which might be the most important one controlling the population structure of marine forests. It is an intraspecific competition like self-thinning which acts as an internal factor with advancement of the regeneration process. Consequently, structures such as population density and standing stock change periodically at a given interval of the turnover time. The self-thinning is caused originally by the process of getting space and light. Particularly in a dense marine forest, light is the most important limiting factor for growth, and there is a clear advantage to be gained by having light collecting apparatus above that of neighborhood. In our previous papers (MAEGAWA and KIDA 1987, MAEGAWA et al. 1987, 1988), it was clear that germination and growth of young fronds were controlled by light intensity on the population floor. The number of young fronds on the population floor play an important role for the regeneration process as major constituents of coming generation.

In the *E. cava* population many recruits, the density of which was 45-60 fronds/m² at Stn. 1 and 25-35 fronds/m² at Stn. 2, were produced in the gap during the period of 3-6 months after the opening was made in the canopy. Difference in the number of recruits was

thought to be caused by the difference of space on the substratum available for germination and growth of young fronds. A large number of recruits as mentioned above decreased rapidly to 10-15 fronds/m² in one This decrease in the density supports vear. an evidence of self-thinning which is caused by the changes in the light condition in a population. A large number of recruits germinated too late or grown under dim light beneath neighboring superior recruits are destined to die or lose selectively because they cannot have enough light to grow in the On the other hand, several population. recruits germinated earlier or grown rapidly have a possibility to survive to canopy fronds. Recruits produced densely in the gap tend to increase skewness in size frequency distributions, which is caused for strong in-Recruits are comtraspecific competition. petitively inferior to the established individuals; they may remain small for a long period and be subjected to high mortality. As the result, self-thinning is more active in a dense population with extreme skewness of size distributions, and is one of the most important factors in regulating the structure and density of a plant population developed naturally.

Regeneration of marine climax forests such as E. cava populations is usually initiated by the formation of the gap due to death or loss of large canopy fronds. A very small opening formed by loss of one large frond is soon closed by adjacent canopy fronds. Consequently, the regeneration process starts when the assemblage of canopy fronds is lost at the same time and a relatively large opening is formed. In this study, the regeneration process started when the density of canopy fronds with stipes of more than 20 cm long decreased to 2-4 individuals/m². IWAHASHI (1971) also observed that a lot of recruits of E. cava occurred when the density of adult plant decreased to 1-2 fronds/m² in the coastal water of Izu Peninsula.

WATT (1947) suggested that terrestrial forest communities have mosaics of patches in which various phases of the regeneration process are arranged spatially, and the age of plants in the patch becomes almost even. This phenomenon is called "cyclic succession" or "regeneration complex". WATT's mosaic theory was applicable to various terrestrial forest types (WILLIAMSON 1975, Ohsawa 1981, Runckle 1981, Kanzaki 1984) and is a valuable concept for understanding terrestrial forest structures and regeneration. WATT (1947) distinguished four phases (gap, building, mature, and degeneration) in the course of regeneration. WHITMORE (1982)recognized three phases (gap, building, and mature) in the regeneration process of many terrestrial forests. In this study, three phases (gap, building, and matrue) were verified in the regeneration process in E. cava forest which is the same as those of terrestrial forests. It is quite interesting that such phases can be distinguished by similar structures and dynamic features of the regeneration process in both terrestrial and marine forests, although there are considerable differences in the scale of a population and/or community and in biological and physiological characteristics of the component species between the two. The most important difference is the turnover time of regeneration, which is 100-200 years or more for terrestrial forests (NAKA 1982, NAKA-SHIZUKA 1984) while only 3 years for marine E. cava forest. Such a short turnover time of E. cava forest offers great advantage for this kind of population study as compared with terrestrial forests.

It has been generally observed that there was considerable skewness of age distribution in the *E. cava* population (IWAHASHI 1971, OHNO and ISHIKAWA 1982, KIDA and MAEGAWA 1983). Specifically, young fronds can scarcely grow in a fully developed population in the mature phase. A quadrat sampling method has generally been employed for analyzing the age distribution and for estimating the standing stock of algal populations. When a quadrat is placed within a particular fully developed population which is in the mature phase, large and old canopy fronds may occupy most parts of the population, and the mean standing stock in the area may be overestimated. It is considered that many and large scale quadrat methods and/or a long-term observation over the life span of individuals are necessary to estimate a mean size- or age-distribution, standing stock, and regeneration process of marine forests.

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前川行幸・喜田和四郎:三重県志摩半島沿岸域におけるカジメ海中林の更新過程

三重県志摩半島沿岸域のカジメ群落内に、2つの永久コドラートを設置し、1982-1987年の約6年間にわたる 個体群動態の調査・解析から,群落の更新過程を明らかにした。永久コドラート内の群落の茎長組成,密度,平 均茎長,及び現存量などの規則的な年変化から,更新の周期は3年と考えられた。また、更新のプロセスは典型 的なギャップ更新であった。カジメ群落の更新過程は,その構造や機能の面から、3相に分けて考えることがで きた。林冠を形成する大型個体のまとまった流失により、ギャップが形成され、ギャップ形成後の3-6ヶ月は、 幼体の加入量が多く,死亡率もそれほど高くはなく、また、現存量は密度の増加とともに高くなる(ギャップ相)。 ギャップ形成後1-1.5年で群落は最大密度となり、幼体の加入量は止まり、その後、密度は急激に減少する。し かし、この時期の現存量の増加は著しい(建設相)。ギャップ形成後1-1.5年で現存量は飽和し、密度減少も緩 やかになり、林冠が形成される(成熟相)。カジメ群落の更新過程は、基本的には陸上の森林群落と同じであっ た。このようなカジメ群落の更新を規制する要因として、群落内の光環境の変化とそれにともなう種内競争が考 えられた。(514 三重県津市江戸橋2-80 三重大学生物資源学部藻類増殖学研究室)
Karyology and nuclear DNA content of *Gelidium pusillum* (Gelidiales, Rhodophyta) from North Carolina, USA

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Gelidium pusillum (STACKHOUSE) LE JOLIS from coastal North Carolina was found to have 10 bivalents during diakinesis of tetraspore mother cells, indicating a chromosome complement of 2N=20. The DNA-localizing fluorochrome hydroethidine with epi (incident) UV illumination was used to determine relative nuclear DNA in tetrasporophyte cortical cells and tetraspore mother cells, and in gametophyte germling cortical cells. Results from microspectrophotometry provide evidence of nuclear DNA fluctuations correlated with the alternation of haploid and diploid chromosome complements observed in this species' life history.

Key Index Words: chromosomes-DNA quantification-epifluorescence-Gelidium-Rhodophyta.

As presently circumscribed, the Gelidiales comprise one of the smallest orders of Florideophycidae (HOMMERSAND and FREDE-RICQ 1988), consisting of a single family, the Gelidiaceae (MAGGS and GUIRY 1987) with nine genera (SANTELICES and STEWART 1985). Five of these genera are monotypic, or are represented by a few species with relatively restricted distributions. Much of the attention devoted to this order has centered on the numerous species of Gelidium and Pterocladia as they are often conspicuous members of temperate and tropical floras (SANTELICES and STEWART 1985) as well as commercially important sources of agar (GUZMÁN DE PRÓO and DE LA CAMPA DE GUZMÁN 1978, SANTELICES et al. 1981, McLachlan 1985).

The most reliable taxonomic feature for distinguishing *Gelidium* from *Pterocladia* is based on cystocarpic structure with *Pterocladia* having a single locule (or two unequally developed locules), while *Gelidium* is bilocular (FAN 1961, KRAFT 1981, AKATSUKA 1986a, HOMMERSAND and FREDERICQ 1988). Unfortunately, female reproductive structures are uncommon or unknown for many of these species (WEST and HOMMERSAND 1981, SANTELICES and STEWART 1985). Consequently, morphological characters of noncystocarpic plants are routinely used for taxonomic delineations at both the genus and species levels (STEWART 1986, 1974, STEWART and NORRIS 1981, AKATSUKA 1986b, MAGGS and GUIRY 1987).

Need for additional means of delimiting species has been prompted by emerging information that Gelidium and Pterocladia species produce characteristic agars with distinct commercial applications, as well as the desire to efficiently manage and utilize this natural resource (SANTELICES and STEWART 1985). Elsewhere, cytogenetic studies have provided criteria to distinguish closely related species of red algae including Porphyra (MUMFORD 1975, MUMFORD and COLE 1977, KAPRAUN and FRESHWATER 1987), Gracilaria (BIRD et al. 1982) and Polysiphonia (KAPRAUN 1977, 1978). Unfortunately, no karyological information is available for any species of Pterocladia, and published data for Gelidium is restricted to imprecise chromosome numbers for three species (DIXON 1954, BOILLOT 1963, MAGNE 1964, KANEKO 1966). In contrast, karyological studies of two other Gelidiaceae, Acanthopeltis japonica OKAMURA (KANEKO 1968) and Gelidiella acerosa (FORSSKÅL) J. FELDMANN et HAMEL (RAO 1974), have shown that careful selection of material and use of appropriate technique can result in precise chromosome numbers as well as evidence of Consequently, recently developed meiosis. methods (KAPRAUN and cytogenetics GARGIULO 1987a, b, KAPRAUN and FRESHWATER 1987) were modified for use with Gelidium busillum (Stackhouse) Le Jolis (=G. crinale (TURN.) LAMOUR.), a common member of the local flora in coastal North Carolina (KAPRAUN 1980).

In addition, the DNA-localizing fluorochrome hydroethidine with epi-(incident) UV illumination (KAPRAUN *et al.* 1988) was used to demonstrate fluctuations in nuclear DNA levels associated with meiosis by comparing the C levels of tetrasporophytes, tetraspore mother cells and gametophyte germlings.

Materials and Methods

Gelidium pusillum plants were collected in June 1988 from intertidal rocks at Kure Beach, North Carolina (see KAPRAUN 1980 for habitat description and location map). Fertile branch tips bearing tetrasporangia were excised, cleaned of epiphytes and debris, and placed in petri dishes with 20 ml enriched seawater medium (VSE) (FRESHWATER and KAPRAUN 1986). Mature tetraspores were released within 6 hr after which the fertile branches were removed and fixed at 24:00 in 3:1absolute ethanol-glacial acetic acid (AUSTIN 1959). Tetraspores were incubated at 22°C, 100 $\mu E \cdot m^{-2}s^{-1}$ photon flux density and 12:12 LD for 14 days. Resultant germlings were fixed as above. Material fixed for chromosome counts was treated and stained in 2% aceto-orcein (KAPRAUN and MARTIN 1987). Documentation was made by microphotographs and by viewing 35 mm Kodak Plus-X film with a 48X microfiche reader and tracing the projected images (KAPRAUN and FRESHWATER 1987).

Fixed material for measurement of nuclear DNA was stained with the DNA-localizing

fluorochrome hydroethidine for 10 min and then destained in phosphate buffer (PBS) for 48 hr prior to examination (KAPRAUN 1989). Epi-fluorescence data were standardized to the average intensities (I_f) of telophase (2C) nuclei in tetrasporophyte cortical cells (KAPRAUN et al. 1988) and the results analyzed and presented in histograms (GOFF and COLEMAN 1984). Observations and photomicrographic documentation were made with brightfield and epi-(incident) UV illumination using an Olympus BH2-RFK microscope and exciter filter BP-545, dichroic mirror DM-580 and barrier filter 0-590 which are specific for hydroethidine emissions (KAPRAUN et al. 1988).

Results and Discussion

Chromosome numbers for seven taxa of Gelidiales in the present and previously published investigations are given in Table 1. In Gelidium pusillum, 10 bivalents were observed in meiotic metaphase (diakinesis) of tetraspore mother cells (Fig. 1). The haploid chromosome complement of 1 N=10 appears to include six chromosomes which are conspicuously larger than the other four (Fig. 1). Tetrasporophyte cortical and medullary cell preparations inlcuded many late prophase and metaphase mitotic nuclei in which 17-18 of the 20 chromosomes present could be observed (Fig. 2). Unfortunately, the tendency for the nuclear envelope to remain intact and confine chromosomes during mitosis precluded accurate counts in these cells.

The basic chromosome complement for the Gelidiales appears to be 1X=5 (KANEKO 1968), with diploid (2 N) numbers of 10, 20 and 30 (Table 1) representing a polyploid series. The reported aneuploid number of N=4 in Gelidiella acerosa (RAO 1974), if correct, suggests that this taxon may be distinct from Gelidium species. It would be a matter of great interest to confirm this report and to obtain karyological details for additional Gelidiella species in light of recent evidence that questions the validity of the criteria used to delimit Gelidiella from Gelidium (MAGGS and

Karyology and nuclear DNA of Gelidium

2	Chromosor	D		
Species	1 N	2 N	Kelerence	
Acanthopeltis japonica Okamura	15	30	Канеко 1968	
Gelidiella acerosa (Forsskal) J. Feldmann et Hamel	4 8		Rao 1974	
Gelidium latifolium (GREV.) BORNET et THURET	5 (4-5)	10 (9-10)	Dixon 1954	
Gelidium latifolium (GREV.) BORNET ET THURET		20 (c.18)	Boillot 1963	
Gelidium latifolium (GREV.) BORNET et THURET VAR. luxurians (CROUAN)		30 (25-30)	Magne 1964	
Hamel et Feldmann				
Gelidium pusillum (Stackh.) Le Jolis	10	20	Present study	
Gelidium sesquipedale (CLEMENTE) THURET (as G. corneum	5 (4-5)	10 (9-10)	Dixon 1954	
(Huds.) Lamour.)				
Gelidium vagum Okamura	10 (7-10)		Kaneko 1966	

Table 1. Chromosome numbers in species of Gelidiaceae.

* Ploidy levels were not indicated in all references.

Guiry 1987).

Microspectrophotometry with DNA-localizing fluorochromes has been used extensively for quantitative determination of nuclear DNA in algae (Al-Kubaisy *et al.* 1981, Cole-MAN 1982, GOFF and Coleman 1984, 1986,



Figs. 1 & 2. Tetrasporophyte nuclei following aceto-orcein staining. Fig. 1. Meiotic metaphase (diakinesis) with 10 bivalents in a tetraspore mother cell. Arrow indicates additional chromosome below focal plane. Fig. 2. Cortical cell showing early mitotic prophase with 17–18 of the 20 chromosomes present.

Figs. 3 & 4. Tetrasporophyte nuclei following hydroethidine staining. Fig. 3. Cortical cell nuclei visualized with episcopic UV illumination. Fig. 4. Tetraspore mother cell with meiotic prophase II nuclei (arrows) visualized with bright field illumination.

	n	1 C	2 C	4 C
Tetrasporophyte cortical cells	20		50 ± 5	
	20		51 ± 4	
	7		53 ± 4	
	20			101 ± 4
	20			98 ± 6
	20			96±8
Mature tetraspores	10		51 ± 7	
Germinating tetraspores and gametophyte germlings	30		49±8	
	14	27 ± 4		
	20	32 ± 4		
Mean I _f		29	51	98

Table 2. Fluorescence intensity (I_f) mean \pm SD for *Gelidium pusillum* phases.

SCHNETTER et al. 1984, KAPRAUN et al. 1988). In the present study, hydroethidine staining for periods as brief as 10 min followed by destaining in PBS buffer for 2-3 days at 4°C resulted in intense nuclear fluorescence with only slight cytoplasmic interference (Fig. 3). Surprisingly, individual chromosomes could be observed in dividing nuclei following hydroethidine staining under bright field (Fig. 4) as well as episcopic UV illumination.

Results of the microspectrophotometry investigation of *G. pusillum* are summarized in Table 2. Mean DNA values for germinating tetraspores and gametophyte germlings had DNA content levels corresponding to 1 C and 2 C values of 1N nuclei, while DNA values for tetrasporophyte cortical and medullary cells had 2 C and 4 C levels (Fig. 5). I_f values were not obtained for tetraspore mother cells and their meiotic nuclear divisions as dense starch granules and background fluorescence prevented precise nuclear readings.

Mean DNA values for 2 C nuclei closely approximate 50% of the 4 C values in this study (Table 2). I_f values for 1 C nuclei which were consistently higher than the predicted 50% of 2 C nuclei indicate that initiation of replication rapidly followed karyokinesis in these cultured germlings.

The assumption that members of the Gelidiales possess a *Polysiphonia*-type life history is based primarily on reports of isomorphic gametophytes and tetrasporophytes in

nature (WEST and HOMMERSAND 1981), and has been demonstrated in culture for only one species, Gelidium coulteri HARVEY (MACLER and WEST 1987). Cytogenetic investigations reported haploid and diploid which chromosome complements for gametophytes and tetrasporophytes, respectively, have provided additional evidence for an alternation of haploid and diploid phases in the Gelidiales (KANEKO 1968, RAO 1974). Results of the present study indicate that nuclear DNA content fluctuations corresponding to 1 N and 2 N phases as well as chromosome counts can be useful in confirming a sexual cycle for species of Gelidiales.

The present study indicates that the Gelidiales amenable are to improved cytogenetic techniques and microspectrophotometry. Consequently, it is concievable that these procedures could be used to determine if an alternation of haploid and diploid phases occurs in the many species for which gametophytes are rare or unknown (WEST and HOMMERSAND 1981). In addition, information for chromosome numbers and relative DNA content per basic genome may provide additional criteria for delineating morphologically similar taxa. For example, a previous investigation of Codium (Chlorophyta) in the North Atlantic demonstrated that four superficially similar erect species could be distinguished by a combination of chromosome numbers and interspecific



Fig. 5. Frequency distribution of relative DNA values for tetrasporophyte and gametophyte nuclei following hydroethidine staining. n=number of nuclei, I_f =fluorescence intensity mean ± SD.

DNA contents (KAPRAUN et al. 1988).

Finally, preliminary studies of genetic modifications in the agar-producing red alga Gracilaria tikvahiae MCLACHLAN suggest that autopolyploidization can result in improved mariculture stock (van der Meer 1983, van DER MEER and PATWARY 1983). However, karyological criteria for successful autopolyploidization include a suboptimal (or low) number of small chromosomes (LEVAN 1945). Consequently, Gracilaria species which have N=24 or N=32 (MAGNE 1964, McLachlan *et al.* 1977. Bird and McLACHLAN 1982, BIRD et al. 1982) are only marginally suited for this form of genetic modification (VAN DER MEER and PATWARY In contrast, haploid chromosome 1983).

complements of 1 N=5 and 10 in *Gelidium* species (Table 1) suggest that these taxa may be more likely candidates for genetic improvement by autopolyploidization.

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Donald F. KAPRAUN・J. Craig BAILEY:米国ノースカロライナ沿岸より得た 紅藻テングサ目の一種 *Gelidium pusillum* の核学並びに核 DNA 含有量

米国ノースカロライナ沿岸より得た紅藻テングサ目の一種 Gelidium pusillum について核学的研究を行ない,四 分胞子母細胞のディアキネシス期では10個の二価染色体を有することを認めた。また,フロロクロム・ハイドロ エチディンで染色し,紫外線を投射し,蛍光顕微分析を行って,四分胞子体の皮層細胞と四分胞子母細胞並びに 配偶体の皮層細胞について相対的な DNA 量を調べた。その結果から,本種が複相と単相の世代を有しているこ とが示唆された。(Department of Biological Sciences, University of North Carolina, Wilmington, North Carolina 28403, U.S.A.) Jpn. J. Phycol. (Sôrui) 37: 208-212, September 20, 1989

日本産オモテソゾはミツデソゾと同一物

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SAITO, Y. 1989. Conspecificity of two Japanese Laurencia species: L. okamurae and L. japonica. Jpn. J. Phycol. 37: 208-212.

Laurencia japonica YAMADA from Chiba Prefecture on the Pacific coast is here shown to be taxonomically synonymous with *L. okamurae* YAMADA. *L. japonica* seems to be an early seasonal form, with a thicker and tougher frond than the late-seasonal form, typical of *L. okamurae*. Thus, the writer makes the following proposal.

Laurencia okamurae YAMADA, 1931, p. 206, pl. 7, text-figs. J & K.

Syn. Laurencia japonica YAMADA, l. c., p. 211, pl. 11, figs. a & b; text-fig. L.

My erroneous identifications of some of Dr. M. S. DOTY's collection as L. japonica were previously corrected to L. papillosa.

Key Index Words: conspecificity—Laurencia japonica—Laurencia okamurae. Yuzuru Saito, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido, 041 Japan

Laurencia japonica YAMADA オモテソゾは山田 (YAMADA, 1931)によって,千葉県で4月に採集され た材料にもとづいて設けられた。同県江見(えみ)で 採集された基準標本は成熟した四分胞子体で,普通の L. okamurae YAMADA ミッデソゾより太くて頑丈そうで あり,体色は黒ずんでいる。筆者も1963年5月に神奈 川県で,オモテソゾに同定出来ようか,という四分胞 子体を採集しているが,体は太くて黒っぽいとはいえ, ミッデソゾ類似の形態をしていた。この様な個体にも 髄細胞膜の半月形肥厚部の存在が明らかだったので, ミッデソゾとの類縁は感じ始めていた。

能登谷ほか (1978)は L. pinnata YAMADA ハネソゾの 胞子を培養すると,高さ2mm内外という小型なうち に成熟することを報告した。工藤・斎藤 (1985)は, 野外でも生育季節の後期には,培養のもの程ではない にしても小さい成熟個体が目につくこと,同じ属のミ ッデソゾや L. intermedia YAMADA クロソゾでもその様 に小さい成熟個体が見出されること,等を報告した。 そこで,オモテソゾ,ミッデソゾの標本について,と くに成実枝の太さを計測して見たところ,季節の進む につれて細くなり,その太さの点で両種の境界を明ら かにすることは不可能であった。そこで,両種は同一 であること,学名は L. okamurae を使用すべきこと, L. japonica は異名となること,等が明らかになったの で、ここに報告する。

Laurencia japonica YAMADA オモテソゾと考えられた 標本の観察

筆者が Laurencia japonica オモテソゾに同定してもよ い,と考えた標本を採集したのはただ一度,1963年5 月26日、神奈川県三浦市の初声(はっせ)でのことで あった。個体数は 6-7 個と少なかったが、どれも黒 みがかった紫色で,ほとんど緑色を帯びることはない。 それらのうち,最大の個体 (Fig. 1) は約 14 cm 高く, 主軸の根元付近で約 2mm まで太く,外形は L. okamurae ミッデソゾに類似するとはいえ,全体に頑 丈そらな印象を受ける。髄細胞の膜には半月形肥厚部 の存在が明らかで、採集した個体全部が四分胞子体で あった。四分胞子嚢を持つ成実枝は、太いもので直径 が約 560 µm あった。筆者 (SAITO, 1967, p. 29) の計測 した北海道の L. okamurae ミツデソゾでは 450-550 µm と記録されているので、それよりいくぶん太いことが 明らかであった。この採集は、筆者のソゾ属植物の形 態研究の材料を集めていた頃のことで、当然その研究 に取り入れられる筈であったが、材料が L. okamurae ミッデソゾにかなり類似していることや,L. japonica オモテソゾとして記載するには個体数が不足であっ た、等の理由で結局は保留されてしまった。



Figs. 1 & 2. Laurencia okamurae YAMADA. Fig. 1. Dried habit of specimen from Hasse, Kanagawa Pref. (May 26, 1963, leg. Y. SAITO), first identified as *L. japonica* YAMADA. Fig. 2. Lectotype of *L. japonica* YAMADA (Emi, Chiba Pref., April 1923. SAP 13879. This specimen is designated as "lectotype" in the present paper, since Dr. YAMADA noted as "the type specimen" in his 1931 paper, however, there is no such kind of writing on the specimen).

ところで, *L. japonica* YAMADA オモテソゾの選定基 準標本* (YAMADA, 1931, pl. 11, Fig. b; 本報告の Fig. 2)は,千葉県の江見で1923年4月に採集されたもので, 根元の最も太い部分を計測すると直径約 1.2 mm あ り, 神奈川県初声の標本よりかなり細いが, この点を 重視するのは適当ではなかろう。また,四分胞子囊を つけた成実枝は直径約 570 μ m まで太く,上記した初 声のものよりいくぶん太い。しかし,これらの点だけ から前者と区別するのは困難というべきであろうし, 両者の髄細胞の細胞膜には,ともに明らかな半月形の 肥厚部が存在することを見ても,互いによく似かよっ ている,というべきなのではなかろうか。なおこの標 本には,山田によると思われる「天津ノモノト同ジ」 との鉛筆による書き込みが見られる。この天津(あま つ)のもの,とは従基準標本(YAMADA,1931, pl. 11, a;本報告の Fig. 3)のことで,選定基準標本と同じく 千葉県の天津で1923年4月に採集されたもので,明ら かに緑色を帯びる。かなり若い,と思われるこの標本 に関して山田は「通常は羽状分岐する」と記しておら れる(YAMADA,1931, p. 212)。この標本の若い成実枝 には,直径 500 µm を越えるものもあった。また,髄

^{*} YAMADA, 1931, pl. 11, fig. b. の説明には, 明らか に "L. japonica sp. nov. The type specimen. xl." と記し てあるので、筆者はそれを山田幸男先生の確かなご意 見と推察する。しかしながら、その標本 (SAP. 13879) 上にその旨の記入は無い。今後の混乱を避けるため, との吉田忠生博士のご意見もあり, 筆者はここで "SAP. 13879" を L. japonica YAMADA の選定基準標本: lectotype に指定するのが妥当と考えた。



Figs. 3 & 4. Laurencia okamurae YAMADA. Fig. 3. Paratype of L. japonica YAMADA (Amatsu, Chiba Pref., April 1923. SAP 13881). Fig. 4. Dried habit of specimen from Nou, Niigata Pref. (July 23, 1960, leg. Y. SAITO).



July 1923. SAP 13875).

Figs. 5 & 6. Laurencia okamurae YAMADA. Fig. 5. Dried habit of specimen from Moheji, near Hakodate, Hokkaido (September 13, 1963, leg. Y. SAITO). Fig. 6. Holotype of L. okamurae YAMADA (Bou, Kagoshima Pref.,

細胞の膜には半月形肥厚部の存在も明確であった。

Laurencia okamurae YAMADA ミツデソゾ標本の観察

筆者は1962年から数年間, 函館の北海道大学水産学 部から函館湾をまたいだ西方約 10 km の茂辺地(4) へじ)で、頻繁にソゾ属植物を採集したことがある。 そこで採れた Laurencia okamurae ミツデソゾ標本の観察 によると、8月10日頃の標本の最も太い成実枝の直径 は 550 µm に近いものもあったが, 多くは 470 µm 以 下であった。しかしながら、季節が進んで9月末とな れば,最も太いもので直径 380 µm 位になり,その途 中の8月中旬から9月中旬(Fig.5は茂辺地で1963年 9月13日採集の材料による)あたりに採集された個体 の成実枝は、最大のもので直径が 450 µm から 380 µm であって,ほぼ中間的な寸法といえるが,一般的 には,季節の進んだところで採集されたものほど細い, という傾向は明らかであった。L. okamurae ミッデソゾ の正基準標本 (YAMADA, 1931, pl. 7; 本報告の Fig. 6) は、鹿児島県の坊(ぼう)で1923年7月に採集された ものであるが、その季節はこのミツデソゾにとっては、 函館辺の9月頃に相当するのであろうか,最も太い成 実枝の直径は約 400 µm である。

その他,筆者が新潟県の能生で1960年7月23日に採 集した標本 (Fig. 4)では,主軸の最も太い部分の直径 が 1.2 mm に近く,成実枝の太いものは直径 540 µm にもなっていたが,体の色彩が緑色を帯びていたから か,何のためらいもなく L. okamurae ミッデソゾに同 定していた。また,同じく筆者が1964年6月21日,島 根県の七類(しちるい)で採集した材料は,主軸の根 元付近で直径 1.3 mm 近いものもあったが,前者と同 様に緑色を示していたからか,あっさりと L. okamurae ミッデソゾに同定された。未熟の末端枝,稀に見られ た成実枝とも,直径は 360 µm とかなり細い。

ここで取り扱った L. okamurae ミツデソゾにも,老 若にかかわりなく, 髄細胞膜に半月形肥厚部の存在は 明らかであった。

論 議

山田は, 選定基準標本の台紙上に「天津ノモノト同 ジ」との記入をして居るが, 天津のもの, とは若い方 の個体で, Laurencia japonica の従基準標本 (Fig. 3) であ る。その標本は,彼の意見によれば「通常は羽状分岐 する」とされた (YAMADA, 1931, p. 212)。しかし筆者 は,その標本が羽状分岐する様に見えるのは,若くて 比較的柔軟な藻体が強く圧されたため、と考えて居る。 とすれば、髄細胞膜の半月形肥厚部の存在や、若い成 実枝の寸法その他、どの性質を当たって見ても L. okamurae YAMADA ミッデソゾに同定して良いものと考 える。

さて, L. japonica オモテソゾと考えられた標本の成 実枝は, 筆者が神奈川県初声で採集したもの (Fig. 1), 選定基準標本 (Fig. 2), ともに太く, 直径は 560-570 µm になる。しかしながら, その他の明らかに L. okamurae ミッデソゾと考えられた標本の成実枝の直 径は, 一般に季節の進むにつれて細くなることが知ら れ, 560 µm 以下 360 µm までほぼ連続していて, ど こかに両種の境界を見いだすことさえむつかしい様で ある。

能登谷ほか(1978)は、函館産の L. pinnata YAMADA ハネソゾの両性胞子を培養して生活史を完結させた 際,発生体はほぼ一か月前後で,思いもかけない小型 なうちに成熟したことを見て、環境如何では、早期, 小型で成熟できること、一生育季節に多数回の世代交 代をかさねている可能性、等を考察した。その後、工 藤・斎藤(1985)は、函館西方の日本海沿岸の太田や、 対岸の青森県下北半島の下風呂で,8月末や9月のは じめに採集された非常に小形なハネソゾは早急に成熟 して小型で終わったもので,秋型と見るのが良かろう, と考えた。その報文の末尾には、「L. okamurae YAMADA ミッデソゾや L. intermedia YAMADA クロソゾ等も秋の 材料は一般に枝も細く小型であるが、それらも今回の ハネソゾと同様な形態的変異といえるのではなかろう か」という考察も記述されている。これらの事実と考 察を、前記した筆者の「オモテソゾの太い成実枝も季 節の推移につれて細くなり、ミツデソゾの成実枝と区 別出来なくなる」とした考えと併せ、ここで次の様に 結論したい。

1) L. japonica オモテソゾは L. okamurae ミツデソゾ に併合されるべきものである(前者は YAMADA, 1931 の p. 211で,後者は同 p. 206)。

2) オモテソゾ型個体は,一般に生育初期の 4-5 月 に本邦中部で見られ(基準標本は千葉県で1923年 4 月 に,筆者のものは神奈川県で1963年 5 月に採集),ミ ッデソゾ型個体より太くて頑丈そうに見える。

3)6月以降はオモテソゾ型個体は見られなくなり、 ミッデソゾ型だけになって、体は末端の成実枝を含め て順次細くなり、多くは緑色を帯びる(ミッデソゾの 基準標本は鹿児島県の坊で1923年7月採集。函館付近 の材料でそれに最も類似したのは、茂辺地で1963年9 月採集のもの)。

謝 辞

この研究に観察が必要だった Laurencia japonica YAMADA オモテソゾの選定基準標本と従基準標本, L. okamurae YAMADA ミッデソゾの正基準標本,等の観 察に当たっては、北海道大学理学部の吉田忠生教授に ご便宜を戴いた。さらに、同教授からはこの原稿に関 する有益なご意見も賜わった。記して謝意を表す。

付 記

筆者は以前, ハワイ大学の Dr. M. S. Dorv 採集に よるハワイとフィリピンのソゾ属植物の研究 (Saito, 1969) を実施し, そこで Laurencia papillosa (FORSKÅL) GREVILLE の他に L. japonica YAMADA も記載した。後者 は L. papillosa のうち, 枝の分岐した部分などに半月形 肥厚部らしいものを認めた場合で山田幸男先生 (YAMADA, 1931, p. 212)の「老成した L. japonica は外形 が L. papillosa に似る事がある」を参考にしてのことで あった。しかし後に,筆者のその同定が誤りであるこ とを知ったので,筆者は 2 回目のハワイ大学訪問のお り, Dr. M. S. Dory の該種に同定された標本の学名 を L. papillosa に訂正を済ましてある。

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Photosynthetic characteristics of several species of Rhodophyceae from different depths in the coastal area of Shima Peninsula, central Japan

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In order to elucidate vertical distribution of Rhodophyceae with reference to the photosynthetic characteristics and photosynthetic pigments, several species of Rhodophyceae were collected from shallow water (near the low water level) and deep water (about 25 m depth) in the coastal area of Shima Peninsula, Mie Prefecture, and used for measuring photosynthesis and respiration as well as for analyzing photosynthetic pigments. Photosynthesis measurements were carried out under white light similar to sunlight and under green light close to the light condition in coastal deep waters. Shallow-water species (*Gracilaria incurvata* and *Pachymeniopsis elliptica*) had higher photosynthetic efficiency for white light than for green light, whereas deep-water species (*Meristotheca papulosa, Beckerella subcostata* and *Peyssonnelia caulifera*) had higher photosynthetic efficiency for white light. The amounts of chlorophyll *a* and phycoerythrin were measured in nine shallow-water species and five deep-water species. The ratio of phycoerythrin to chlorophyll *a* contents was clearly higher in deep-water species (4.2-9.3, average 6.4) than in shallow-water species for green light is due to a high ratio of phycoerythrin to chlorophyll *a* contents, and that shallow-water species for green light is due to a high ratio of phycoerythrin to chlorophyll *a* contents, and that shallow-water species have adapted to white light and deep-water species to green light. This is a kind of chromatic adaptation of Rhodophyceae by changing phycoerythrin content under natural conditions.

Key Index Words: chlorophyll a—photosynthesis—photosynthetic pigments—phycoerythrin—Rhodophyceae seaweed.

Photosynthesis of algae is an important basis of the production in the coastal ecosystem. Thus, much attention has been focused on studies of photosynthesis of algae from the viewpoint of production ecology (ARUGA 1986). In general, the depth to which seaweeds grow is determined by the amount of available light for photosynthesis (DUNCAN and LOBBAN 1985). Thus, the photosynthetic study with reference to photosynthetic pigments is of great importance not only for production ecology but also for physiological ecology.

YOKOHAMA (1973a, b) and KAGEYAMA and YOKOHAMA (1974) reported that photosynthetic properties of seaweeds from different depths depended on light quantity and quality. Photosynthesis-light curves of seaweeds from shallow water were of the sun type, and those of seaweeds from deep water were of the shade type. Moreover, photosynthesis-light curves under white light and green light showed a remarkable difference in Chlorophyceae and Rhodophyceae. As for Rhodophyceae, YOKOHAMA (1973b) suggested that the ratio of phycoerythrin to chlorophyll a had an important role in characterizing the photosynthetic properties of the species growing in shallow and deep water. Rhodophyceae containing phycobilin pigments would be expected to have a greater vertical range of growth in the Furthermore, YOKOHAMA and his sea. reported that most of the coworkers Chlorophyceae in deep water or shade sites have siphonaxanthin as a photosynthetic pigment for collecting green light (YOKOHAMA et al. 1977, KAGEYAMA et al. 1977, KAGEYAMA and YOKOHAMA 1978). MAEGAWA et al. (1987, 1988) reported that the difference in daily compensation point between young fronds of *Eisenia bicyclis* and *Ecklonia cava* is one of the most important factors in determining the difference in their vertical distribution. Thus, photosynthetic characteristics and pigment contents are the most important factors determining vertical distribution of seaweeds.

The present study deals with the factors governing the difference in vertical distribution of several species of Rhodophyceae with reference to photosynthesis and photosynthetic pigments. The aim of the present study is to measure accurately photosynthetic rates under various light conditions and conduct quantitative analysis of phycoerythrin to obtain the phycoerythrin/chlorophyll *a* ratio in relation to the vertical distribution of Rhodophyceae.

Materials and Methods

Photosynthesis study

Several species of Rhodophyceae were collected from different depths around the coast of Shima Peninsula, Mie Prefecture, from May to September 1987 (Fig. 1). These species were classified into two groups, 'shallow-water species" and "deep-water species", according to the sampling depth. As shallow-water species, Gracilaria incurvata OKAMURA was collected just below the sea surface from floating buoy used for pearl oyster cultivation near Zaga Island in Ago Bay, and Pachymeniopsis elliptica (HOLMES) YAMADA was collected from near the low water level at the coast of Iwaizaki. Deep-water species, Meristotheca papulosa (MONTAGNE) J. AGARDH, Beckerella subcostata (OKAMURA) KYLIN and Peyssonnelia caulifera OKAMURA, were collected from a depth of about 25 m off Iwaizaki by SCUBA diving.

Fig. 2 shows the seasonal variations of seawater temperature at the depths of 0, 20 and 30 m (average for 8 years, 1981–1988) near the sampling area (solid circle in Fig.



Fig. 1. Maps showing the location of study area at Shima Peninsula, central Japan. sampling area; • station for measuring water temperature.

1). During the period of measuring photosynthesis and respiration (May to September), the seawater temperature varied from 18.3°C in May to 26.3°C in September in surface water, from 17.8°C in May to 23.4°C in August at a depth of 20 m, and from 17.7°C in May to 20.8°C in August at a depth of 30 m.

Collected samples were transported to the Fisheries Research Laboratory of Mie University in Zaga Island and were rinsed with filtered seawater to make them free of obvious epiphytes with careful handling not to wound the fronds and were protected from direct sunlight. Sample pieces of 10–20 cm² were cut out from fronds, and were kept in running seawater overnight to avoid abnormal results caused by cutting (SAKANISHI *et al.* 1988). Photosynthesis and respiration were measured with Productmeter, an improved differential gas-volumeter (YOKOHAMA *et al.*



Fig. 2. Seasonal changes of seawater temperature at the depths of 0 m (—), 20 m (----) and 30 m (----) off Iwaizaki $(34^{\circ}14'N, 136^{\circ}43'E)$. Average of 8 years (1981-1988).

1986, YOKOHAMA and MAEGAWA 1988). Measurements of photosynthesis and respiration were carried out at 8 different light intensities from 0 to $400\mu E/m^2/s$ under white light and green light. A projector lamp (Kondo 100 V-300 W) was used as the white light source, and the green light was obtained by penetrating the white light through a 0.4 M nickel sulfate solution 10 mm thick. Spectral distributions of white light and green light were measured with a Techtum Quantaspectrometer OSM-2500 as shown in Fig. 3. White light from the projector lamp is similar to the sunlight, although quanta of short wave band from 400 to 500 nm are slightly less than those of the sunlight. Green light is approximated to the light condition at a depth of around 20 m in coastal waters. The light intensity was controlled with neutral density filters (Toshiba TND-50, -25, -12.5). Photon flux density was measured with a quantum meter system (LI-COR LI-192SB, LI-1000).

Culture flasks of about 100 ml capacity were used as the reaction and reference vessels of Productmeter, and filtered seawater (30 ml) was poured into both vessels, with a cut frond in the reaction vessel. After pre-incubation for 30 minutes at 400 μ E/m²/s, the seawater in both vessels was renewed, and the measurement was carried out from high to low light intensity with the same frond. Respiration was measured after the photosynthesis measurement. Each measurement took about 25 minutes and the seawater was renewed each time. It took 5-6 h for a series

of measurements starting from 09:00 h. Photosynthesis and respiration were measured at 20°C which was nearly the same as in situ seawater temperature of sampling area (cf. Fig. 2). After the measurements, fronds were rinsed with freshwater and used for area measurement. At the same time, small frond discs (0.332 cm²) were taken for photosynthetic quantitative analysis of pigments.

Absorption spectra

Fronds used for measuring photosynthesis and respiration were transported to the Laboratory of Phycology, Faculty of Bioresources, Mie University. *In vivo* absorption spectra of the fronds were measured with a Hitachi 330 Spectrophotometer equipped with an end-on type photomultiplier.

Measurement of photosynthetic pigments

Nine species collected from intertidal zone



Fig. 3. Spectral distributions of white light and green light used for the measurements of photosynthesis.

to a depth of 2 m, and five species from a depth of about 25 m were used for quantitative measurement of photosynthetic pigments. A disc of 0.332 cm^2 or a piece of 0.1-0.2 g were cut out of samples. Fresh or frozen (-20° C) samples were used for extraction of photosynthetic pigments.

Fresh samples were used for the measurement of chlorophyll a content. Chlorophyll awas extracted in 90% acetone in a mortar. The extract was centrifuged for 5 minutes at 3000 rpm, and absorbances at 750, 663, 645 and 630 nm were measured with a Hitachi 101-01 Spectrophotometer. The amount of chlorophyll a was calculated by the equation of SCOR-UNESCO (1966).

Frozen samples were transported to the Phycology, Faculty Laboratory of of Bioresources, Mie University and were used for measurement of phycobilin content. Phycobilins were extracted in phosphate buffer solution (pH 6.5) with 0.2 g of quartz sand in a mortar. The extract was centrifuged for 30 minutes at 3000 rpm, and the supernatant was ultracentrifuged for 30 minutes at 35000 rpm. Absorbances of the supernatant at 750, 650, 620 and 565 nm were measured with a Hitachi 100-20 Spectrophotometer, and the amount of phycoerythrin was calculated by the equation of FUJITA (1979).

Results

Photosynthesis-light curves

Fig. 4 shows photosynthesis-light curves of two shallow-water species, *Gracilaria incurvata* and *Pacymeniopsis elliptica*, under white light and green light. Relative gross photosynthetic rates on a frond area basis are illustrated in the figure. In both species, the photosynthetic rate increased linearly with increase in light intensity in the range lower than $50 \ \mu E/m^2/s$, and it increased slowly with further increase in light intensity. The photosynthetic rate was almost saturated at $200 \ \mu E/m^2/s$ under both green light and white light. In the light intensity range lower than $200 \ \mu E/m^2/s$, the relative photosynthesis of



Fig. 4. Photosynthesis-light curves of two shallow-water species under white light (\bigcirc) and green light (\bullet) at 20°C.

both species was higher under white light than under green light.

Fig. 5 shows the relative photosynthesislight curves of three deep-water species, Meristotheca papulosa, Beckerella subcostata and Peyssonnelia caulifera, under white light and green light. In all the three species, the photosynthetic rate increased linearly with increase in light intensity in the range lower than 50 μ E/m²/s, and it increased slowly with further increase in light intensity. Light saturation points of Meristotheca papulosa and Beckerella subcostata were 200 μ E/m²/s under white light and 100 μ E/m²/s under green light. As for Peyssonnelia caulifera, light saturation point was 100 μ E/m²/s under white light and 70 μ E/m²/s under green light. The relative photosynthesis was higher under green light than under white light in the light intensity range lower than 200 μ E/m²/s in Meristotheca papulosa and Beckerella subcostata, and in the light intensity range lower than 100 μ E/m²/s in Peyssonnelia caulifera.

Absorption spectra

In vivo absorption spectra of two shallow-



Fig. 5. Photosynthesis-light curves of three deep-water species under white light (\bigcirc) and green light (\bigcirc) at 20°C.

water species and two deep-water species, which were used for measuring photosynthesis and respiration, are shown in Fig. 6. For comparisons the spectra are normalized at 680 nm where the absorption bv chlorophyll *a* dominates. There were considerable differences of absorbance in green region of 490-580 nm between shallow-water species and deep-water species. Absorbances were higher in deep-water species than in shallow-water species at the wave lengths from 490 to 580 nm, where the absorption by phycoerythrin predominates. Thus, it is expected that deep-water species are relatively rich in phycoerythrin, suggesting to have higher phycoerythrin/chlorophyll a ratio, as



Fig. 6. In vivo absorption spectra normalized at 680 nm of shallow-water species, Gracilaria incurvata (—) and Pachymeniopsis elliptica (––), and deepwater species, Meristotheca papulosa (----) and Beckerella subcostata (.....), used for measurements of photosynthesis.

compared with shallow-water species.

Photosynthetic pigments

Chlorophyll *a* and phycoerythrin contents of nine shallow-water species and five deepwater species were estimated. Chlorophyll *a* contents were $4.2-19.4 \ \mu g/cm^2$ in shallowwater species and $9.4-16.3 \ \mu g/cm^2$ in deepwater species. Phycoerythrin contents were $10.4-63.5 \ \mu g/cm^2$ in shallow-water species, and $49.5-90.8 \ \mu g/cm^2$ in deep-water species. The level of chlorophyll *a* contents in shallowwater species was almost the same as that in deep-water species. However, the level of phycoerythrin contents in deep-water species was higher than that in shallow-water species.

Fig. 7 shows the ratio of phycoerythrin (PE) to chlorophyll a (Chl.a) contents in nine shallow-water species and five deep-water species. The PE/Chl.a ratios in deep-water species (4.2-9.3, average 6.4) were clearly higher than those in shallow-water species (0.5-4.3, average 2.6)

Discussion

The present study was attempted to elucidate vertical distribution of Rhodophyceae with reference to the photosynthetic characteristic and the amount of photosynthetic pigments. Several samples collected from shallow water (near the low water level) and from deep water (about 25 m)



Fig. 7. The ratio of phycoerythrin to chlorophyll *a* contents of shallow-water species and deep-water species. Average (\bigcirc) and the range for 4–15 samples are illustrated in each species.

near the lower limit of algal vegetation in a coastal region were compared with respect to their photosynthetic rates under white light (similar to sunlight) and green light (similar to the light condition in coastal deep water) and to their PE/Chl.a ratios.

Shallow-water species (Gracilaria incurvata and Pachymeniopsis elliptica) had higher photosynthetic efficiency for white light than for green light (Fig. 4). Conversely, deepwater species (Meristotheca papulosa, Beckerella subcostata and Peyssonnelia caulifera) had higher photosynthetic efficiency for green light than for white light (Fig. 5). These results are almost similar to those by YOKOHAMA (1973b). As for shallow-water species, the difference of photosynthetic efficiency between white light and green light obtained in the present study was well in agreement with that reported by Yоконама (1973b). As for deep-water species, however, there were remarkable differences between the present result and Yokohama's (1973b) result. This discordance may be due to the difference in

the depth of sampling; 8-10 m in YOKOHAMA (1973b) and 25 m in the present study.

In *in vivo* absorption spectra (Fig. 6), it is clear that the deep-water species absorb green light (490-580 nm) more effectively than the shallow-water species do. The wavelengths of green region corresponds to the absorption band of phycoerythrin, a photosynthetic accessory pigment in Rhodophyceae. Therefore, the difference of absorption spectra green region between shallow-water in species and deep-water species is due to the difference of phycoerythrin content. Higher content of phycoerythrin in deep-water species is quite convenient for utilizing green light which occupies a greater part of irradiance at depths around 20 m in the coastal water.

Chlorophyll *a* contents were not so greatly different between shallow-water species and deep-water species. Phycoerythrin contents were appreciably higher in deep-water species than in shallow-water species. As a result, PE/Chl.*a* ratios were clearly higher in deepwater species than in shallow-water species (Fig. 7) as expected from the difference in absorption spectra in Fig. 6. Thus, the high photosynthetic efficiency of deep-water species for green light is due to their high ratio of phycoerythrin to chlorophyll *a* contents.

It was reported that there is a considerable change in phycoerythrin content of Rhodophyceae under natural conditions depending on the depth of water (RAMUS et al. 1976a, b, MOON and DAWES 1976) and under culture conditions depending on the light quality (BRODY and EMERSON 1959). There was a clear difference in phycoerythrin content between shallow-water species and deepwater species, even though the range of variation was not small in several species (Fig. 7).

In the present study, it is clearly shown that the difference of photosynthetic characteristics between shallow-water species and deep-water species is dependent on phycoerythrin content which is closely related to the light conditions in growing sites, and that the shallow-water species have adapted to white light and the deep-water species to green light. They are examples of chromatic adaptation of Rhodophyceae by changing their phycoerythrin contents according to the light conditions at growing depths.

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村瀬 昇・前川行幸・喜田和四郎・三重県志摩半島沿岸における生育水深の異なる 紅藻数種の光合成特性

三重県志摩半島沿岸の低潮線付近の浅所および水深 25 m 付近の深所から採取した紅藻数種について光合成測定と色素分析を行い,得られた光合成活性および色素組成から,紅藻の垂直分布特性を解明しようと試みた。

太陽光に近い白色光と水深 20 m 付近の光の波長組成に近似させた緑色光の下で,光合成-光曲線を求めたと ころ,浅所産のものは白色光を,深所産のものは緑色光を効率よく光合成に利用することが明らかになった。そ こで、クロロフィル a と緑色域の光を吸収する紅藻特有の光合成色素フィコエリスリンを定量し,クロロフィル a に対するフィコエリスリンの含有比 (PE/Chl. a)を求めた。その結果, PE/Chl. a は浅所産のものでは 1~4 であ るのに対し,深所産のものでは 4~9 と高かった。これらのことから,深所産紅藻は,浅所産のものに比べてフ ィコエリスリンの含有比が高いために,緑色域の光を中心とする沿岸深所の光環境下で効率よく光合成を行って いることが明らかとなった。

以上のことから,浅所産および深所産紅藻は,それぞれの生育水深の光環境によく適応した光合成特性と色素 組成をもっていることが明らかとなった。これは,紅藻類におけるフィコエリスリン含有比を生育水深によって 変えることによる色適応の結果である。(514 三重県津市江戸橋2-80 三重大学生物資源学部藻類増殖学研究室)

Taxonomic and distributional notes on northeast Pacific Antithamnieae (Ceramiales, Rhodophyta)

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Lindstrom, S.C. and GABRIELSON, P.W. 1989. Taxonomic and distributional notes on northeast Pacific Antithamnieae (Ceramiales, Rhodophyta). Jpn. J. Phycol. 37: 221-235.

The number of species of antithamnioid algae recognized as occurring along the Pacific coast of North America from Alaska to Oregon is reduced from 17 to 12. Antithamnion alternans and A. asymmetricum are conspecific with Antithamnionella pacifica, and Antithamnion simulans is conspecific with Scagelia pylaisaei. Antithamnion dendroideum does not appear to be present in the area; the single record from southeast Alaska remains unconfirmed. Antithamnion gardneri and Antithamnionella glandulifera are conspecific with Antithamnionella spirographidis, which is recorded from Prince William Sound, Alaska to Baja California, Mexico in the northeast Pacific; A. miharae from Japan is also considered a synonym of A. spirographidis. Antithamnionella shimamurana comb. nov. has not been confirmed to occur east of the Aleutian Islands. New northern distribution records are established for Hollenbergia subulata, Platythamnion reversum, and P. villosum. The recognized northern distribution limit of Antithamnion kylinii is southern British Columbia, not southeast Alaska, and that of Hollenbergia nigricans is central British Columbia, not southwest Alaska.

Key Index Words: Antithamnieae—Antithamnion—Antithamnionella—biogeography—Ceramiaceae— Ceramiales—Hollenbergia—northeast Pacific—Platythamnion—Rhodophyta—Scagelia—taxonomy.

At present count 17 species of antithamnioid algae are recorded as occurring on the Pacific coast of North America from Alaska to Oregon (LINDSTROM 1977, PHINNEY 1977, SCAGEL et al. 1986). These include eight species of Antithamnion, four of Platythamnion, two of Antithamnionella, two of Hollenbergia and one Scagelia. Among these are the three remaining species of the 13 species of Antithamnion, first described by GARDNER (1927a, 1927b), that have not been investigated since their original description.

In order to ascertain the identities of these taxa and to confirm their distributions in the area from Oregon to Alaska, we have examined type specimens for most of the species and have checked records of all the species present in *UBC* (herbarium abbreviations after HOLMGREN *et al.* 1981; an exclamation mark after a specimen designation indicates that the specimen has been examined by us).

Our research indicates that only 12 species of antithamnioid algae should be recognized as occurring from Alaska to Oregon: two species of Antithamnion (A. defectum and A. kylinii), three Antithamnionella (A. pacifica, A. shimamurana, and A. spirographidis), two Hollenbergia (H. nigricans and H. subulata), one Scagelia (S. pylaisaei), and four Platythamnion (P. heteromorphum, P. pectinatum, P. reversum, and P. villosum). We follow MOE and SILVA (1980) in not recognizing the tribe Heterothamnieae; we therefore attribute these species to the Antithamnieae sensu lato.

Materials and Methods

Herbarium specimens were identified by direct observation, using a Zeiss dissecting microscope, or slides were prepared by cutting out a small portion of a specimen along with the mounting paper, staining with acetic acid and aniline blue (HANSEN and SCAGEL 1981), and mounting in 20-50% corn syrup. Microscope slides were examined with a Leitz Dialux compound microscope. Photographs are of liquid preserved specimens stained as above, or of unstained material mounted on slides in corn syrup. Photographs were taken on the Zeiss dissecting microscope or on the Leitz compound microscope.

Results

ANTITHAMNION NAEGELI 1847

Following WOLLASTON (1972b), Antithamnion is circumscribed by these features: 1) erect or prostrate thalli lacking rhizoidal cortication and with equal and opposite whorlbranches, the basal cells of which bear no branches and are distinctly smaller (usually quadrate in shape) than the more distal whorl-branch cells, 2) gland cells on special branches, 2-5 cells in length, borne abaxially or adaxially on whorl-branches or their ramuli, 3) tetrasporangia cruciately divided and usually ovoid when mature, 4) procarps numbering 2-20 and borne on basal cells of whorl-branches or whorl-branch ramuli and 5) only one carposporophyte matures at each fertile branch apex. WOLLASTON pointed out that there appear to be two clusters of species, those from southern Australia that closely resemble the type species, A. cruciatum, and those from the northeast Pacific. Representatives of both of these groups occur in the northwest Pacific (Japan).

Antithamnion defectum Kylin 1925

Antithamnion defectum is a common and widespread taxon in the local area. It is distributed from Prince William Sound. Alaska (HANSEN et al. 1982) to Baja California, Mexico (WOLLASTON 1976). The species has a thallus consisting of erect branches from a prostrate base. It is readily identified by its opposite whorl-branches that are pectinately branched adaxially and by the absence of a whorl-branch opposite each indeterminate branch (Fig. 1). Basal cells of whorl-branches are conspicuously smaller than more distal cells (Fig. 1) and gland cells are present on reduced whorl-branch ramuli. Other distinguishing features are listed in Table 1.

WOLLASTON (1972a) apparently did not see

the type specimen of Antithamnion defectum when she reviewed the species of Antithamnion and related genera on the Pacific coast of North America. For this and other species for which she did not see the type specimen, she queried the herbarium (LD? for A. defectum and Antithamnionella glandulifera and TCD? Antithamnionella pacifica). for Moreover, WOLLASTON appears to have selected one of the localities from the original protologue of each species and designated it as the type locality. By indicating type locality and herbarium, WOLLASTON has effectively lectotypified those species with a single specimen from that locality in the designated herbarium. For Antithamnion defectum, however, the indication of Friday Harbor does not clearly select a single specimen as there are three in LD! with this locale written on them in KYLIN's hand. Although WOLLASTON included "growing on piles on the dock" as part of the type locality description, none of the LD specimens indicates where it was growing. Because one of the specimens already has been designated "Typus" by an unknown person (Per Lassen, pers. comm.), we recognize this specimen as the lectotype. This specimen is labeled "Canoe Island, Friday Harbor, 24 June 1924", by H. KYLIN. Two other specimens on the same sheet, labeled "Friday Harbor, 30 June 1924", and "Canoe Island, Friday Harbor, 22 July 1924", would be paralectotypes.

Antithamnion dendroideum Smith et Hollenberg 1943

Antithamnion dendroideum (type locality: near Monterey, California) has been recorded by ROSENTHAL and BARILOTTI (1974) from Khaz Bay in southeast Alaska. We have not been able to locate any specimens from their collections, and we have found no other material referable to this taxon in the study area. We therefore reinterpret the distribution of *A. dendroideum* as central California to Baja California, Mexico (WOLLASTON 1972a, 1976).

Antithamnion kylinii GARDNER 1972b

Antithamnion kylinii (type locality: Victoria,

	Antithamnion		Hollenbergia		Scagelia	Antithamnionella		
	defectum	kylinii	nigricans	subulata	pylaisaei	pacifica	spirographidis	
Usual number of whorl-branches	2	2	2(3)	3	3	2	2(3)	
Placement of whorl- branches on axial cell	Distal	Distal	Medial	Distal	Distal	Distal	Distal	
Branching of whorl- branches	Adaxial	Adaxial	Distichous	Distichous to Distichous to Unbran pseudodichot- omous to 3 omous to 3 orders orders		Unbranched	Unbranched	
Size of basal cell of whorl-branch relative to more distal cells	Smaller	Smaller	Same size	Same size	Same size	Smaller	Same size	
Ramulus on basal cell of whorl-branch	No	No	No	Yes/no	Yes/no	No	No	
Maximum diameter of axial cells	120 <i>µ</i> m	120 µm	300 µm	300 µm	400 µm	100 µm	50 µm	
Position of gland cells	Short, small- celled ramuli	Short, small- celled ramuli	Lateral	Terminal	Lateral, near base of branch	None	Lateral, near base of branch	
Position of tetrasporangia	Mostly one- celled pedicels, adaxial on proximal cells of whorl-branches	One-celled pedicels	1-several celled pedicels	On adaxial ramuli	Sessile, adaxial on proximal cells of whorl- branches	Pedicellate, adaxial on whorl-branches or in place of whorl-branches	Sessile, adaxial on proximal cells of whorl- branches	

Table 1. Comparison of features of species of Antithamnion, Hollenbergia, Scagelia, and Antithamnionella occurring in British Columbia and adjacent waters.



British Columbia) is distinguished from A. defectum by its totally erect habit and by the presence of a whorl-branch opposite each indeterminate lateral branch (Fig. 2). Other features are listed in Table 1. This taxon has been reported north of southern British Columbia only once (ROSENTHAL and BARILOTTI 1974). Since no voucher specimens could be located for this record from Khaz Bay, southeast Alaska, and since there are no other reports of this taxon from northern British Columbia or southeast Alaska (SCAGEL et al. 1986), the distribution of this taxon is emended to southern British Columbia to Baja California, Mexico (WOLLASTON, 1976). In British Columbia this taxon is very uncommon, there being only four collections in UBC in addition to an isolectotype specimen (UBC A2246!). These records are from Ladysmith Harbour, Vancouver I. (UBC A64975!), from Grappler and Bamfield Inlets, Bamfield, Vancouver I. (UBC A41880! A47739!) and from Tribune Bay, Hornby I., Strait of Georgia (UBC A68732!).

ANTITHAMNIONELLA Lyle 1922

WOLLASTON (1968, 1972b) supported recognition of Antithamnionella as distinct from Antithamnion and circumscribed the genus as follows: 1) distinct form of apical development of branches (i.e. a sinusoidal apex with one of a pair of whorl-branch initials cut off in a series from successive axial cells, first on one

side of the axis, then on the other, with the apex flexing away from the side where the most recent series of initials has been produced), 2) inconsistency in number and branching of whorl-branches, 3) gland cells adaxial on whorl-branch cells, 4) tetrasporangia often tetrahedrally divided and nearly spherical in shape, 5) spermatangia (as spermatangial mother cells") cut off laterally rather than terminally and 6) only 1-3 procarps produced per branch apex, each borne on a reduced whorl-branch. MOE and SILVA (1980) pointed out that only in certain species of Antithamnionella [i.e. A. floccosa (O.F. MUELLER) WHITTICK (as Antithamnion floccosum), Antithamnionella spirographidis (SCHIFF-NER) WOLLASTON, A. glandulifera (Kylin) WOLLASTON and A. pacifica (HARVEY) WOLLASTON, and we would add A. miharae (TOKIDA) ITONO and A. shimamurana (NAGAI) comb. nov.] does whorl-branch initiation proceed as described above and illustrated by WOLLASTON (1972b and Table 2 therein). This pattern does not appear to occur in A. sarniensis Lyle, the lectotype species of Antithamnionella (L'HARDY-HALOS 1986, Figs. 9, 10). SUNDENE (1964) suggested that A. samiensis and A. spirographidis are conspecific, but L'HARDY-HALOS (1986) demonstrated that the two species do not hybridize and that there are several characters by which they can be distinguished. In light of L'HARDY-HALOS' results, MOE and SILVA's (1980) sug-

Fig. 1. Habit of Antithamnion defectum showing absence of whorl-branches on axial cells that bear indeterminate branches (arrows). Lindstrom 5620, Cape Suspiro, Alaska. Scale bar=135 μ m.

Fig. 2. Habit of Antithamnion kylinii showing whorl-branches present on axial cells that bear indeterminate branches (arrow). UBC A64975, Ladysmith, Vancouver I., B.C. Scale bar= $385 \mu m$.

Fig. 3. Sinusoidal apex of male plant of Antithamnionella pacifica showing unequal development of opposite pairs of whorl-branches and basal cells (arrow) of mature whorl-branches that are smaller than more distal cells. Gabrielson 364, Whiskey Pt., Quadra I., B.C. Scale bar=90 μ m.

Fig. 4. Habit of Antithamnionella spirographidis. Note sinusoidal apices of indeterminate branches, lateral gland cells on whorl-branches (small arrows) and oblong, immature tetrasporangia (large arrows) also borne on whorl-branches. Gabrielson 242, Deep Cove, B.C. Scale bar=135 μ m.

Fig. 5. Apex of female plant of *Scagelia pylaisaei* with lateral gland cells (arrows). *Gabrielson 300*, Pt. Atkinson, B.C. Scale bar=135 μ m.

Fig. 6. Hollenbergia subulata apex showing subterminal gland cells (arrows) on whorl-branches. UBC A54962, Lasqueti I., B.C. Scale bar=135 μ m.

Fig. 7. Unequal development of three whorl-branches per mature axial cell of *Scagelia pylaisaei*. Note conspicuous dark-staining gland cells on whorl-branches. *Gabrielson 300*, Pt. Atkinson, B.C. Scale bar=135 μ m.

Fig. 8. Portion of rehydrated isotype specimen (No. 944) of *Hollenbergia nigricans* from UBC copy of *Phycotheca Boreali-Americana*. Note pairs of whorl-branches (arrows) borne mid-way along axial cells. Scale bar=135 μ m.

gestion, that species of *Antithamnionella* with sinusoidal indeterminate apices should be placed in a segregate genus, merits consideration.

Antithamnionella pacifica (HARVEY) WOLLASTON 1972a

Antithamnionella pacifica originally was described by HARVEY (1862) as Callithamnion floccosum var. pacificum, a variety of an Atlantic species. KYLIN (1925) raised the variety to specific status. WOLLASTON (1972a) made the combination Antithamnionella pacifica, and she included Antithamnion uncinatum GARDNER 1927b as a variety, making the new combination A. pacifica var. uncinata. The distinctness of this northeast Pacific species has made it an easily identifiable taxon in the local flora (Table 1; Fig. 4). It is common and widely distributed, from Baja California (WOLLASTON 1976) to the Aleutian Is. (HANSEN et al. 1982).

WOLLASTON (1972a) indicated Esquimalt to be the type locality of Antithamnionella pacifica and included "on stems of larger algae" as part of the type locality description. However, she queried the location of the type in TCD. HARVEY (1862) originally had referred to specimens from both Orcas I. [Washington] and Esquimalt, and KYLIN (1925) followed Harvey in mentioning type specimens from both localities. Only specimens from Orcas I. can be found in TCD!. All were collected in April 1858 One of the specimens by David Lyall. also has "found covering the stem of larger algae" in HARVEY's hand; it is the only specimen to have "var. ß. pacificum" in HARVEY's hand. It is this specimen that should be considered the lectotype. In addition to the specimens in TCD, three HARVEY specimens are in K-BM! Two of these are also from Orcas I. and were found on stems of larger algae. The third, collected by DAVID LYALL, Feb. 1859, at Esquimalt, does not include information on where it was growing.

During our examination of some of GARD-NER's species of Antithamnion, we came across two that clearly belong to this species. Antithamnion alternans GARDNER (1927a, type locality: Cook Inlet, Alaska) is represented by UC 296622! (G.B. RIGG & R.J. GRIGGS No. 61). The basal cells of the simple, usually opposite whorl-branches are smaller than more distal cells and nearly quadrate; branch tips are acute, and "tetrahedral" tetrasporangia $(55-60 \times 68-75 \ \mu m)$ are pedicellate, branched or unbranched, and adaxial on whorlbranches. An unusual feature of this specimen is the occurrence of tetrasporangial branches in place of whorl-branches along the main axis or abaxially on the basal cell of a whorlbranch rather than adaxially on the basal or suprabasal cells. Such a disposition of tetrasporangia has been observed on several relatively coarse Antithamnionella pacifica specimens from Alaska (UBC A23065!, Lituja Bay, and A20853!, Coronation I.). Gland cells are absent. Antithamnion alternans has the habit of a robust Antithamnionella pacifica, and we consider the former to be a synonym of the latter.

Antithamnion asymmetricum GARDNER 1927b (type locality: Sitka, Alaska) is represented by UC 296633! (NLG No. 3937). It also has the habit of Antithamnionella pacifica, with slightly recurved, simple, opposite whorl-branches whose basal cells are slightly to distinctly smaller than more distal cells. Gland cells are absent, and branch tips may or may not be acute. Near the apex, branches are arranged in alternate secund series of three's. Tetrasporangia are pedicellate. Based on the features listed above, we consider Antithamnion asymmetricum a synonym of Antithamnionella pacifica. In summary, then, we list below the synonyms of this species:

Antithamnionella pacifica (HARVEY) WOLLASTON 1972a, p. 87

BASIONYM: Callithamnion floccosum var. pacificum HARVEY 1862, p. 176

- =Antithamnion floccosum var. pacificum (HARvey) Setchell et Gardner 1903, p. 341
- =Antithamnion pacificum (HARVEY) KYLIN 1925, p. 47, Figs. 28a-d?, 29a-f, 30f?
- =Antithamnion alternans GARDNER 1927a, p. 377, Pl. 78 (Figs. 1, 2)

- =Antithamnion asymmetricum GARDNER 1927b, p. 411
- =Antithamnion uncinatum GARDNER 1927b, p. 408 Pl. 89 (Fig. 2), Pl. 90

We would like to reiterate (LINDSTROM 1987) the need for experimental work to determine just how closely related Pacific Antithamnionella pacifica is to Atlantic A. floccosa. Morphologically, these two species have failed to diverge in any significant features. Whorlbranches are paired, simple, subequal, subulate, and taper to an acute tip; they are arranged distichously. Indeterminate branches replace whorl-branches usually every third axial cell and alternate from one side of the rachis to the other. Gland cells are rare if not entirely absent (never seen by us in A. pacifica; reported not to occur in A. floccosa by WHITTICK 1980). Tetrasporangial, male, and female reproductive structures and postfertilization development also are identical.

Antithamnionella spirographidis (SCHIFFNER) WOLLASTON 1968

SCHIFFNER (1916, p. 137) described Antithamnion spirographidis based on specimens that he collected from the harbor at Trieste on August 12 and 14, 1914 growing in 0.5-3 m on the tube worm Spirographidis. He provided a detailed description and figures of the habit (erect axes to 10 mm from creeping filaments with rhizoids formed from the basal cells of opposite whorl-branches), branch initiation (in unilateral alternating series from the high side of subapical cells such that the major axis has a sinusoidal appearance), gland cells (sparsely present and not welldeveloped to abundant and well-developed on the second and third cells of whorl-branches), tetrasporangia (adaxial and sessile on basal and second cells of whorl-branches to 50 μ m diameter and tetrahedrally, although appearing cruciately, divided) and spermatangia in series on whorl-branches). (adaxial WESTBROOK (1934) first described cystocarpic plants collected at the Davenport Dockyard and Plymouth Sound in England. Her observations on the habit, gland cells, tetrasporangia and spermatangia corroborated those of SCHIFFNER, as did FELDMANN-MAZOYER'S (1941, pp. 265-267) based on Mediterranean Sea collections and WOLLASTON'S (1968, pp. 345-347) based on Australian collections. WOLLASTON (1968) transferred A. spirographidis to Antithamnionella Lyle (1922).

GARDNER (1927a) described Antithamnion tenuissimum based on material collected in the drift from La Jolla, California and grown in an aquarium (WOLLASTON 1972a). Antithamnion tenuissimum GARDNER is antedated by A. tenuissimum (HAUCK) SCHIFFNER (1916) based on type material from the Adriatic Sea, and therefore DE TONI (1936) proposed the substitute name A. gardneri for GARDNER's specimen. GARDNER described his plant as erect to 30-60 mm with opposite whorl-branches that produce rhizoids from their basal cells, gland cells sparse and tetrasporangia adaxial in series of 3-6 on whorl-branches, sessile and nearly tetrahedrally divided. DAWSON (1962) stated that Antithamnion gardneri was equivalent to Antithamnion spirographidis, but he gave no reason for his opinion. UMEZAKI (1963) reported A. gardneri from Osaka, Japan and for the first time described and illustrated spermatangia in this species. His illustrations of habit, rhizoid formation and tetrasporangial position agree with those of GARDNER, but axial cell diameters are smaller than those reported by GARDNER, and tetrasporangia are larger (Table 2).

WOLLASTON (1972a) included A. gardneri under "doubtful species or records". Although she agreed with DAWSON's suggestion regarding the identity of GARDNER's specimen, she did not propose A. gardneri as a synonym of Antithamnionella spirographidis. We have re-examined GARDNER's original glycerine slides of Antithamnion tenuissimum (UC 296692!=Gardner (=A)gardneri) 5085a, the holotype), and although in poor condition, they clearly represent a species of Antithamnionella based on vegetative features, including a sinusoidally curved apex with whorl-branch initials developing in a series first on one side of the main axis and then on

	A. gardneri	A. glandulifera			A. miharae	A. spirographidis				A. tenuissimum
Source	Umezaki (1963)	Kylin* (1925)	Dawson* (1962)	Wollaston (1971)	Токіда* (1942)	Schiffner [*] (1916)	Westbrook* (1934)	Feldmann- Mazoyer* (1940)	Wollaston (1968)	Gardner (1927a)
Axial cell diameter	32–50 μm	60–100 μm	30–40 μm	30–35 µm	70–112 μm	60 µm	20–45 µm	$30{-}40~\mu{ m m}$	$30{-}50~\mu{ m m}$	60–75 μm
Axial cell length/width ratio	5-8	3—5	1.5-2	8	3–6	1.5-3	3-7	8-10	3–6	n.g.
Pattern of whorl- branch initiation at apex	unilateral in alternating series	n.g.	n.g.	unilateral in alternating series	unilateral in alternating series	unilateral in alterna- ting series	unilateral in alterna- ting series	unilateral in alterna- ting series	unilateral in alterna- ting series	unilateral in alterna- ting series
Number of whorl-branches	2	2	2(3)	2(3-4)	2(3)	2	2	2	2	2
Origin of rhizoids	Basal cells of whorl- branches	n.g.	n.g.	n.g.	Basal cells of whorl- branches	Axial cells at base	Basal cells of whorl- branches	Basal cells of whorl- branches	Basal and occas. 2nd cell of whorl-branch	Basal cells of whorl- branches
Presence of gland cells	Present	Abundant	Absent, occasional, or abundant	Present	Sparse	Sparse to abundant	Sparse	Absent to sparse	Sparse	Sparse
Position of gland cells	Adaxial	Adaxial on inner cells of whorl- branches	Inner & cen- tral cells of whorl- branches	Adaxial on inner to cen- tral cells of whorl- branches	Adaxial on 2nd cell of whorl-branches	Adaxial on inner cells of whorl- branches	Adaxial on inner cells of whorl- branches	Adaxial on inner cells of whorl- branches, esp. 2nd cell	Adaxial on 2nd or 3rd cell of whorl-branches	On cells of whorl-branches
Position of tetrasporangia	Adaxial on whorl- branches	Sessile on 2nd and more distal cells of whorl- branches	Sessile on lower 2 cells of whorl- branches	Sessile, adaxial on inner to central cells of whorl-braches	Sessile, adaxial on inner 2–3 cells of whorl-branches	Adaxial on inner cells of whorl- branches	Sessile, adaxial on inner one or two cells of whorl-branches	Sessile, esp. 1st cell	Sessile, basal and occas. 2nd cell of whorl-branches	Adaxial on cells of whorl-branches
Size and shape of tetrasporangia	24–45 μm× 40–75 μm, orbicular- ovate	n.g., ovoid	35–50 μm, ellipsoidal, ovoid	>60 µm long ovoid- subspherical	32–48 μ m × 48–66 μ m, ellipsoid- ovoid	50 μ m long, ovate	30×50 μm, ellipsoidal	35×60 μm, ovoid	30–35 μm× 40–48 μm, ovoid	18–22 μ m × 34–38 μ m, broadly ellipsoidal
Division pattern of tetrasporangia	Most cruciate, some tetra- hedral	Cruciate	Tetrahedral	Cruciate or tetrahedral	Tetrahedral	Tetrahedral	Tetrahedral toward cruciate	Cruciate or tetrahedral	Tetrahedral	Almost tetrahedral

Table 2. Comparison of features of Antithamnion gardneri, Antithamnionella glandulifera, Antithamnionella miharae, Antithamnionella spirographidis, and Antithamnion tenuissimum GARDNER non SCHIFFNER.

* As Antithamnion

n.g.=not given

the other. Tetrasporangia are sessile, a feature characteristic of A. spirographidis, and gland cells are sparse. GARDNER's tetrasporangia have smaller dimensions than any others reported for A. gardneri or Antithamnionella spirographidis, but in all other vegetative and reproductive features that have been observed, there is close agreement (Table 2). Thus, we consider Antithamnion gardneri DE TONI a synonym of Antithamnionella spirographidis (SCHIFFNER) WOLLASTON.

In the area from northern Washington to southeast Alaska, there are only two reported collections of Antithamnion gardneri, both from northern Puget Sound (PHILLIPS and VADAS 1967, PHILLIPS and FLEENOR 1970). We were able to examine only one of PHILLIPS and VADAS' collections, that from Smith I. (48°19'30"N, 122°50'33"W). The specimens (UBC WS1487!), including both tetrasporic and male thalli, are typical of Antithamnionella in their vegetative structure, and the pedicellate tetrasporangia are characteristic of A. pacifica. No other locally recorded species of Antithamnionella, including A. spirographidis, bears pedicellate tetrasporangia. We therefore suspect that all records of Antithamnion gardneri reported by PHILLIPS and VADAS (1967) and PHILLIPS and FLEENOR (1970) are Antithamnionella pacifica.

The only other report of Antithamnion gardneri (as A. tenuissimum sensu GARDNER) in the northeast Pacific is that of DOTY (1947), based on a specimen collected on floating timber in Coos Bay near Marshfield, Oregon. We have examined DOTY's original collection (MD 2359 in UC!). It also belongs in Antithamnionella and is A. spirographidis. As noted by DOTY on the herbarium sheet and observed by us, branching is opposite; a branch occurs opposite each indeterminate axis; apices of cells are blunt to broadly rounded; gland cells are absent, and tetrasporangia are sessile. In his description, DOTY noted that "branching, cells and general proportions are quite like GARDNER's description and figures; however no gland cells were found and the largest tetrasporangia were about 50 \times 70 μ m." In a notation on the herbarium sheet, however, Dory stated that most tetrasporangia are smaller.

While comparing the local species of Antithamnionella to Antithamnion gardneri, we discovered that Antithamnionella glandulifera (KYLIN) WOLLASTON, based on Antithamnion glanduliferum KYLIN (1925), also strongly resembles Antithamnionella spirographidis. KYLIN provided only a brief description of Antithamnion gladuliferum, citing only general habit features such as height, branching, presence of gland cells, size of axial cells and occurrence of sessile tetrasporangia (Table 2).

We have examined the only specimen of KYLIN'S Antithamnion glanduliferum in LD! This specimen, epiphytic on a kelp, was collected at Friday Harbor, Washington, 18 July 1924. It conforms to KYLIN'S original protologue and should be considered the lectotype.

During our investigations, we recognized that another North Pacific Antithamnion, A. miharae (TOKIDA 1942, type locality: Tomari Bay, Kunashiri I., Kurile Is.), also bore a striking resemblance to Antithamnionella spirographidis. When TOKIDA described A. miharae, he noted its similarity to both A. glanduliferum and A. gardneri (as A. tenuissimum), separating it from the former in having tetrahedrally divided tetrasporangia, fewer gland cells and the occasional presence of branched whorl-branches, and from the latter in less sparse branching more markedly tapered whorl-branches, shorter rhizoidal filaments without gland cells and somewhat larger axial cells and sessile tetrasporangia.

DAWSON (1962) stated that Antithamnion miharae " \cdots is apparently exceedingly like, if not identical with A. glanduliferum." He noted that SMITH (1944) had pointed out that tetrasporangia of A. glanduliferum are cruciate, but often appear as if tetrahedrally divided. DAWSON, in his key to North Pacific species of Antithamnion, segregated A. gardneri, which he believed to be conspecific with A. spirographidis, from A. miharae and A. glanduliferum based upon the common supression of one member of a pair of whorlbranches in the former, whereas whorlbranch supression was said to occur only rarely in the latter two species. Our observations of numerous specimens of Antithamnionella glandulifera in UBC indicate, however, that one whorl-branch of a pair commonly is supressed (Fig. 3), as in A. spirographidis.

WOLLASTON (1972a) repeated DAWSON'S and TOKIDA'S observations that Antithamnionella glandulifera closely resembles Antithamnion miharae. She stated, however, that A. glandulifera most closely resembles A. pacifica, but was distinguished by having conspicuous gland cells and sessile tetrasporangia. She made no comparison between A. glandulifera and A. spirographidis.

YOSHIDA (1981), in observing the vegetative and reproductive morphology of *A. miharae*, also noted the similarity of this species to *A. glandulifera*.

Antithamnion scrippsiana (DAWSON 1949), a minute species with unbranched whorlbranches, no gland cells, and sessile, adaxial tetrasporangia has been synonymized with A. glandulifera DAWSON (1962).

Table 2 compares vegetative and reproductive features of Antithamnion gardneri, Antithamnionella glandulifera, A. miharae and A. spirographidis discussed above. It is evident that there are no consistent discontinuities that can be used to segregate these taxa. Size of thalli depends upon age of the plant, with reported sizes ranging from 3-5 mm to 80 mm. Likewise, diameter of axial cells and length to width ratios depend upon the location of the axial cells measured. Consistent among all the taxa is the pattern of whorlbranch initiation at the apex, number of whorl-branches per whorl, branching of whorl-branches, origin of rhizoids from the basal or second cell of whorl-branches, and the position of tetrasporangia, gland cells and spermatangia on whorl-branches. Gland cells range from abundant to rare to absent. The pattern of division of tetrasporangia varies from cruciate to tetrahedral, with both patterns being observed by some workers. Reports of sizes of tetrasporangia vary because sporangia continue to increase in size following cleavage into four spores. Based on the foregoing observations we propose the following synonymies:

Antithamnionella spirographidis (SCHIFFNER) WOLLASTON 1968, p. 345.

- BASIONYM: Antithamnion spirographidis SCHIFFNER 1916, p. 137, Figs. 19-27.
- =Antithamnion gardneri G. DE TONI 1936, p. 1
- =Antithamnion glanduliferum Kylin 1925, p. 47, Figs. 28e-g
 - =Antithamnionella glandulifera (Kylin) Wollaston 1972a, p. 86
- =Antithamnion miharae Токида 1942, р. 90, Figs. 5, 6
 - =Antithamnionella miharae (Токіда) Ітоно 1977, р. 24
- =Antithamnion scrippsiana DAWSON 1949, p. 15, Figs. 26, 27, 58
- =Antithamnion tenuissimum GARDNER 1927a, p. 377, Pl. 77 non Antithamnion tenuissimum (HAUCK) SCHIFFNER 1916

Most reports of Antithamnionella spirographidis (SCHIFFER 1916, WESTBROOK 1934, WOLLASTON 1968) have been from harbors or dockyards, except in the north Pacific, where, based on the above synonymies, the taxon is widespread, occurring from Prince William Sound, Alaska (HANSEN et al. 1982) to Baja California, Mexico (WOLLASTON 1976), in the southern Kurile Is. (TOKIDA 1942), and in eastern Hokkaido (YOSHIDA 1981). Antithamnionella spirographidis may have been introduced to localities outside the north Pacific by man.

Antithamnionella spirographidis is compared to other antithamnioid algae in the local area in Table 1.

Antithamnion shimamuranum NAGAI 1941

Antithamnion shimamuranum NAGAI (type locality: Minamishima, Ushishiru I., Kurile Is.) looks like an extreme form of Antithamnionella floccosa-A. pacifica in habit. Like the latter, Antithamnion shimamuranum cuts off a series of three to six whorl-branches along one side of the apex before switching to the other side. The basal cell of a whorl-branch tends

to be quadrate, and branch tips are acute. Gland cells are lacking. In contrast to Antithamnionella floccosa-A. pacifica, Antithamnion shimamuranum has its "tetrahedral" tetrasporangia borne on a single-celled pedicel; we saw no evidence of a multicellular pedicel, as is typical of Antithamnionella floccosa-A. pacifica, in the isotype material, SAP 021972!, that we examined. Moreover, the whorl-branches of Antithamnion shimamuranum are branched whereas they are unbranched in Antithamnionella floccosa-A. pacifica. These differences suggest that Antithamnion shimamuranum is a species distinct from Antithamnionella floccosa-A. pacifica although, as noted by NAGAI (1941), no doubt closely related to them. We therefore propose the new combination:

Antithamnionella shimamurana (NAGAI) LIND-STROM et GABRIELSON

BASIONYM: Antithamnion shimamuranum NAGAI 1941 p. 207 Pl. VI (Figs. 8-11)

PHILLIPS and VADAS (1967) reported Antithamnionella shimamurana (as Antithamnion shimamuranum) from two localities, Deception (UBC Pass WS1485!) and Ebev's Landing (UBC WS1486!), Whidbey I., Washington. We have examined both of these collections and observed that whorlbranches are opposite and unbranched, and tetrasporangia are on one to several-celled pedicels. These features correspond to A. pacifica and not to A. shimamurana.

Antithamnionella shimamurana also has been reported from the Aleutian Is. (NAKATANI and BURGNER 1974, as Antithamnion shimamuranum). We have been unable to locate any material of this species from there, but we believe it is likely that the species is present in the Aleutian Is. as well as in intermediate areas between there and the middle Kurile Is., where NAGAI (1941) recorded it.

HOLLENBERGIA WOLLASTON 1972a

Hollenbergia, another segregate genus of Antithamnion, was established by WOLLASTON (1972a) to include Hollenbergia subulata (HARVEY) WOLLASTON, the type species (type locality: Esquimalt, Vancouver I.), and H. nigricans (GARDNER) WOLLASTON (type locality: Botanical Beach, Port Renfrew, Vancouver I.). The genus was characterized as having 1-4 whorl-branches of which the basal cell is of similar length to other branch cells. Gland cells are terminal on whorl-branch ramuli in H. subulata and lateral near apices of whorl-branches in H. nigricans. Location and development of reproductive structures are similar to Antithamnion.

Hollenbergia subulata (HARVEY) WOLLASTON 1972a

Although present throughout the year, Hollenbergia subulata is most conspicuous in the local flora during winter and spring in habitats ranging from exposed to protected. The distinctive terminal position of its gland cells (Fig. 6) prevents it from being confused with any other local taxon. Other features are listed in Table 1. Hollenbergia subulata has been recorded from British Columbia to Monterey, California (WOLLASTON 1972a, 1976). We have confirmed its occurrence in Alaska (SCAGEL et al. 1986) and extend its range northwesterly to Chugach I., Kenai Peninsula (UBC A59909!). Additional Alaskan records in UBC are A20941! (Kayak I.) and A59911! (Port Etches).

Hollenbergia nigricans (GARDNER) WOLLASTON 1972a

In contrast, Hollenbergia nigricans has been collected only rarely and then only from exposed habitats. In addition to the type collection from Botanical Beach (P.B.-A. No. 944 in UC! and an isotype in the UBC P.B.-A.!), we have observed one other collection from there (UBC A69639!) and one from Hedley I. (50°54.5'N 127°35.2'W-UBC A17048!). Hollenbergia nigricans has been reported to occur from Vancouver I., B.C., to northern California (WOLLASTON 1972a, 1976). A specimen identified as this species from Cold Bay, Alaska (in ALA!; McRoy et al. 1971) has been identified by M.J. WYNNE as Scagelia pylaisaei.

As indicated by Table 1, Hollenbergia

nigricans also has a distinctive set of features. It is most easily identified by its relatively short, broad cells and by the placement of whorl-branches near the middle of mature axial cells (Fig. 8) rather than subapically, a characteristic of the other taxa considered here.

SCAGELIA WOLLASTON 1972a

Scagelia, a monotypic genus segregated from Antithamnion by WOLLASTON (1972a), is circumscribed as follows: erect thallus with 2-4 whorl-branches per cell, often unequal in length (Figs. 5, 7); branch apices curved with irregular initiation of whorl-branches [as in northeast Pacific species of Antithamnionella (see above)]; gland cells lateral on cells of whorl-branches (Figs. 5, 7); procarps on basal cells of whorl-branches; branch apex and fertile whorl-branch continuing to grow during carposporophyte development, so that several carposporophytes may be borne on a single fertile axis; spermatangia on short ramuli of whorl-branches; tetrasporangia sessile on whorl-branches, cruciately or occasionally appearing tetrahedrally divided.

Scagelia pylaisaei (MONTAGNE) WYNNE 1985

Along with Antithamnionella pacifica, Scagelia pylaisaei (type locality: Newfoundland) is the most common antithamnioid alga in the local flora. Although distinctive from all other locally occurring antithamnioid algae based on vegetative and reproductive features (see above; Table 1), the taxon is highly variable with regard to size and robustness of the thallus, as well as the abundance of its laterally disposed gland cells. Recently, WHITTICK (1988) has demonstrated that in northwest Atlantic populations the abundance of gland cells is controlled to some extent by temperature and salinity. Scagelia pylaisaei occurs in the Arctic Ocean, North Atlantic Ocean, Bering Sea (HANSEN and SCAGEL 1981), the northeast Pacific Ocean from the Aleutian Is. to southern California (SCAGEL et al. 1986), and has been reported from the Galapagos Is. in the southeast Pacific (TAYLOR 1945, as Antithamnion occidentale KYLIN).

Antithamnion simulans GARDNER (1927a, type locality: Sitka, Alaska) is represented by UC 276134! (NLG 3938). It has the habit, both macroscopic and microscopic, of Scagelia pylaisaei. Two or three whorl-branches, of different lengths, occur on each axial cell, and whorl-branches are lax and taper to an acute tip. The lateral gland cells are typical of S. pylaisaei and occur mostly near the base of whorl-branches and their ramuli. Basal cells of branches are of similar shape and size to more distal branch cells. We therefore consider Antithamnion simulans GARDNER (1927a) a synonym of Scagelia pylaisaei (MONTAGNE) WYNNE. [See Note added in proof.]

PLATYTHAMNION J. AGARDH 1892

The genus *Platythamnion* is distinguished by its four whorl-branches, two longer lateral ones and two shorter transverse ones, and by a pattern of indeterminate branch initiation before whorl-branches are formed and a subsequent deflection of the apex away from these alternately formed indeterminate branches (WOLLASTON 1968, 1972c). Moreover, gland cells are sessile and adaxial on central cells of whorl-branches. Of these features, only the regular occurrence of four whorl-branches distinguishes Platythamnion from the sometimes-recognized Pterothamnion NAEGELI, which also can possess whorls of four branches in robust specimens (ATHANASIADIS 1985, MOE and SILVA 1980, WOLLASTON 1979); these two genera have types however, from widely separated geographic areas [Platythamnion heteromorphum (J. AGARDH) J. AGARDH-Santa Cruz, California; Pterothamnion plumula (ELLIS) NAEGELI-Brighton, No one has yet proposed England]. synonymy although it has been hinted at. In reproductive features, Platythamnion resembles Antithamnion although the cruciate tetrasporangia of Northeast Pacific Platythamnion spp. are significantly smaller than those of local Antithamnion spp.: 36-45 µm maximum length versus 70-80 μ m.

Four species of *Platythamnion* occur in the study area. They are most easily distinguished

on the pattern of branching of lateral whorl-branches: lateral whorl-branches with four ramuli (two long and two short) with the longer ramuli branched on both sides of their axes (P. heteromorphum); lateral whorlbranches usually with four ramuli (two long and two short) but with longer ramuli pectinately branched adaxially [P. reversum (SETCHELL et GARDNER) KYLIN; type locality: Whidbey Island (west coast), Washington]; lateral whorl-branches pectinately branched adaxially with two ramuli and sometimes with an abaxial ramulus from the basal cell of the whorl-branch (P. pectinatum Kylin); whorlbranches usually with two adaxial and 0-1 abaxial ramuli (P. villosum Kylin).

WOLLASTON (1972c) did not see the type specimens of Platythamnion villosum and P. *bectinatum*, but she quoted their type localities from part of KYLIN's (1925) original descriptions and queried the specimens as being in LD. A specimen of P. villosum in LD!, collected at Friday Harbor, 15 July 1924, by H. Kylin, has been marked "Typus" by an unknown person. This specimen can be considered the lectotype based on WOLLASTON's selection of "Friday Harbor" as type locality. In the case of P. pectinatum, a Peavine Passage specimen in LD!, collected 10 July 1924 by H. KYLIN, has been designated "Typus" by an unknown person, but WOLLASTON selected "Friday Harbor" as the type locality for this species. A lectotype of this species has yet to be defined.

Among the species occurring in British Columbia, two (P. pectinatum and P. villosum) are common and widespread; one (P. reversum) is uncommon but widely distributed, and one (P. heteromorphum) is rare and narrowly distributed. Both P. pectinatum and P. villosum are known from Mexico (WOLLASTON 1972c, 1976) to Prince William Sound, Alaska (P. pectinatum to Bass Harbor, Alaska—HANSEN et al. 1982 and UBC A60548! A61351! A61353! A61373! A61385! and A61386!, and P. villosum to Little Smith *A61326*!—a Alaska-UBC northern Ι., Platythamnion reversum distribution record). has been recorded from southern British Columbia to Charleston, Oregon (WOLLASTON 1972c), but we have not confirmed its occurrence in Oregon. Specimens in UBC are from the San Juan Is. (Lopez Pass-UBC A1142!), the Strait of Georgia (Lasqueti I.-UBC A56100! and Pt. Atkinson-UBC A56631!), and the Oueen Charlotte Is. (off Robber Inlet, Maude, I., at Haina-UBC A64619!), a northern range extension. Platythamnion heteromorphum is known locally only from Salmon Bank, off San Juan I., Washington (UBC A69638!), southern Vancouver I. (Edward King I.-UBC A40982! and between Fleming and Tzartus Is., Barkley Sound-UBCA47726!), and the north end of the Strait of Georgia (Waiatt Bay-UBC A58611!). Outside the area, it has been recorded from Oregon, California, and Baja California. Mexico (Wollaston 1972c, 1976).

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Sandra C. LINDSTROM・Paul W. GABRIELSON:北東太平洋岸産フタツガサネ族 (紅藻イギス目)の分類と分布上の知見

アラスカからオレゴンまでの北アメリカ太平洋岸から知られているフタツガサネ族の種数は17から12に減らされた。Antithamnion alternans と A. asymmetricum は Antithamnionella pacifica と同種であり, Antithamnion simulans は Scagelia pylaisaei と同種である。Antithamnion dendroideum はこの地域には分布しないようであり, アラスカ南東部からの唯一の記録は確認されていない。Antithamnion gardneri と Antithamnionella glandulifera は, 北東太平洋岸ではアラスカの Prince William Sound からメキショの Baja California にかけて報告されている Antithamnionella spirographidis と同種であり、日本から報告されている A. miharae も A. spirographidis の異名と考えられる。Antithamnionella shimamurana comb. nov. の分布はアリューシャン列島の東ではまだ確認されていない。Hollenbergia subulata, Platythmnion reversum および P. villosum の北部での新しい分布が明らかにされた。Antithamnion kylinii の分布の確認 された北限はアラスカ南東部ではなくブリティッシュコロンビア南部であり,Hollenbergia nigricans の確認された 北限はアラスカ南西部ではなくブリティッシュコロンビア中部である。(Department of Botany, University of British Columbia, Vancouver, B.C., V6T 2B1 Canada)

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Hiroshi YABU and Hirotoshi YAMAMOTO: Chromosome number of Gracilaria chorda and G. vermiculophylla

Key Index Words: chromosome number—Gracilaria chorda—Gracilaria vermiculophylla— Gracilariaceae—Rhodophyta.

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In the Gracilariaceae (Rhodophyta), the chromosome numbers have been recorded for two species as shown in Table 1. This communication gives the chromosome count on two Japanese *Gracilaria* species from Hokkaido.

The tetrasporophytes of G. chorda HOLMES obtained on the shore at Kamiiso near Hakodate in September 1987 and those of G. vermiculophylla (OHMI) PAPENFUSS obtained in the lagoon of Akkeshi near Kushiro in July 1987 were employed as materials. Fixing was made immediately after collection for *G. vermiculophylla*, but made after half-day preservation in the filtered seawater with aeration in the laboratory for *G. chorda*. Acetic alcohol (1:3) was used for fixing. Staining was done with aceto-iron-haematoxylinchloral hydrate solution recommended by WITTMANN (1965).

The chromosome counts were possible at late prophase I in the tetrasporangia, and



Fig. 1. Late prophase I in the tetrasporangium of Gracilaria chorda Holmes. $\times 2,800$. Fig. 1'. Drawing of Fig. 1.


Fig. 2. Late prophase I in the tetrasporangium of *Gracilaria vermiculophylla* (Онмі) PAPENFUSS. ×2,800. Fig. 2'. Drawing of Fig. 2.

Table 1. Chromosome counts in Gracilariaceae.

Species	Locality	Chromosome number	Investigator
Gracilaria multipartita	not cited	n = 6 - 7	Greig-Smith 1954
G. verrucosa	Roscoff (France)	n = 32	Magne 1964
G. verrucosa	South Devon (England)	n = 32	BIRD et al. 1982
G. verrucosa	Barkley Sound (Vancouver Is, Canada)	n = 24	BIRD et al. 1982
G. verrucosa	Vicinity of Hakodate (Japan)	n = 24	Үави and Үамамото 1988

both species showed to have n=24 chromosomes (Figs. 1 & 2), being the same as the count for the materials of *G. verrucosa* in the Vancouver Island by BIRD *et al.* (1982) and in the vicinity of Hakodate, Japan by YABU and YAMAMOTO (1988).

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籔 熈*・山本弘敏**:ツルシラモとオゴモドキの染色体数

北海道産のオゴノリ属植物2種(ツルシラモとオゴモドキ)の四分胞子体を酢酸・アルコール(1:3)で固定 し,酢酸・鉄・ヘマトキシリン・抱水クロラール液で染色して染色体数を調べた。両種共に四分胞子嚢内第一核 分裂前期の末期で n=24 の染色体数が得られた。(*041 函館市港町3-1-1 北海道大学水産学部;**041-16 北 海道茅部郡南茅部町 北海道大学水産学部付属臼尻水産実験所)

Hiroshi KAWAI : First report of *Phaeosaccion collinsii* FARLOW (Chrysophyceae, Sarcinochrysidales) from Japan

Key Index Words: Chrysophyceae—Phacosaccion collinsii—Sarcinochrysidales. Hiroshi Kawai, Department of Botany, Faculty of Science, Hokkaido University, Sapporo, 060 Japan

An alga referable to Phaeosaccion collinsii FARLOW (Chrysophyceae, Sarcinochrysidales, Phaeosaccionaceae) was collected in March 1987 at Isoya, Hokkaido, facing to the Sea of Japan (leg. Mr. Y. Sumita). It occurred as tuft on subtidal rocks at a depth of about 4 m below Mean Low Water Level. The thallus was olive-brown, saccate, to 20 mm in length (Fig. 1). It resembled young thallus of some brown alga such as Punctaria or Petalonia but was distinguished by the hollow habit (Fig. 2), brighter colour and soft texture. The holdfast was small and disc-shaped, composed of several cells (Fig. 3). Rhizoidal filaments were not observed. The thallus was polystichous (Figs. 4 and 5), becoming saccate and monostromatic with increased size (Fig. 2). The cells of the thallus showed no morphological differentiations and, in surface view, arranged in packets of two to four cells. These cells are $6-8 \times 6-9 \mu m$, each of which contained a parietal chloroplast with a prominent pyrenoid (Figs. 6 and 7). An inner lamella was observed in the pyrenoid (Fig. 6). When mature, all cells of the thallus were transformed into zoospores. After the release of the zoospores, only a gelatinous membrane remained (Figs. 8 and 9). Zoospores were pyriform and typically flagellated with a longer anterior flagellum and a shorter posterior one (Fig. 10). They contained a chloroplast provided with an eyespot and a pyrenoid (Figs. 11 and 12). Transitional helices were observed in the transitional region distal to the basal plate (Fig. 13). [For TEM observations, material was

3% fixed in glutaraldehyde in 0.1 M cacodylate buffer, postfixed in 2% OsO4 in 0.1 M cacodylate buffer, dehydrated in a acetone series and embedded in Spurr's epoxy resin (Spure 1969), sectioned with a diamond knife, and stained with uranyl acetate and lead citrate. Observations were made using Hitachi H-300 TEM at the Institute for Algological Research, Faculty of Hokkaido Science, University]. The posterior flagellum of this alga showed the greenish autofluorescence as seen in many phaeophycean zoospores (KAWAI 1988). My specimens agree well with the original description and previous reports of Phaeosaccion collinsii FARLOW (FARLOW 1882, MCLACHLAN et al. 1971), and with the specimen of this species in Phycotheca Boreali-Americana (COLLINS et al. 1895) in the general habit and the morphology. Accordingly, it was identified as Phaeosaccion collinsii.

Although *Phaeosaccion collinsii* has been reported from various localities in cold-water areas of the North Atlantic Ocean, this is the first report for the Pacific Ocean. The species was first described as a brown alga and included in the Punctariaceae (FARLOW 1882). Later, PARKE and DIXON (1964) suggested that it be transferred to the Chrysophyceae, which was supported by the studies of McLACHLAN *et al.* (1971), CRAIGIE *et al.* (1971), and CHEN *et al.* (1974) on the life history, morphology, chemical composition and fine structure of the species.

Cultures were started from zoospores, released from the field-collected thalli, by the pipetting method. They were cultured in polystyrene petri-dishes, 90 mm in diameter, using PESI medium (TATEWAKI 1966).

A part of this work was supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture of Japan (No. 63740387).

Culture conditions were 5°C SD (short day; 8:16hLD), 5°C LD (long day; 16:8hLD), 10°C SD, 10°C LD, 15°C SD, 15°C LD, 20°C SD and 20°C LD, under white fluorescent light of about $28 \,\mu Mm^{-2}s^{-1}$ (5°C) or 46 μ Mm⁻²s⁻¹ (10°C, 15°C, 20°C). (Lux values were measured using a photocell illuminometer and converted to quantum irradiance by the following relation: 250 lux =4.6 μ Mm⁻²s⁻¹.) The zoospores became rounded and formed walls after settlement on They germinated in a the substratum. unipolar, direct type of germination and developed into prostrate branched filaments (Fig. 15) or directly into erect thalli (Fig. 14). Erect thalli were first uniseriate, then formed longitudinal walls (Fig. 14) and became saccate (Fig. 16). Well-developed erect thalli attained a length of 5 mm. At 5°C, erect thalli developed into saccate thalli similar to the plant in nature. However, they only formed filamentous thalli at 10°C. At 15°C and 20°C, they did not grow well. Mature thalli formed zoospores at 5°C and 10°C. There were no obvious effects of photoperiod on morphogenesis or maturation of the thalli. The results of my culture experiments agree with those of McLACHLAN et al. (1971) on the life history pattern in response to the temperature.

Acknowledgments

I am grateful to Mr. Y. SUMITA, Ocean Research & Systemworks Co., Ltd, for collecting the specimen. I am also grateful to Dr. J. McLachlan, National Research Council of Canada for his critical reading and improving the English of the manuscript.

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Figs. 1–9. *Phaeosaccion collinsii* FARLOW in nature. Fig. 1. Habit of the thallus (arrowhead shows mature part of the thallus). Fig. 2. Cross section of the saccate thallus (embedded in Spurr's epoxy resin and stained with toluidine blue). Fig. 3. Basal part of the thallus (asterisk) and young uniseriate erect filamentous thallus. Fig. 4. Young polystichous filament. Fig. 5. Young saccate thallus. Fig. 6. TEM micrograph of a vegetative cell (C, chloroplast; Nu, nucleus; P, pyrenoid; arrowheads, inner lamella). Fig. 7. Surface view of vegetative part of thallus. Fig. 8. Surface view of mature part of thallus (arrowheads show emptied area). Fig. 9. Surface view of almost emptied thallus after releases of zoospores.





Figs. 10–16. *Phaeosaccion collinsii* FARLOW in nature and in culture. Fig. 10. Released typically flagellated zoospore. Fig. 11. TEM micrograph of mature part of the thallus (asterisk shows gelatinous membrane, and arrowhead shows pyrenoid). Fig. 12. TEM micrograph of a zoospore before release (arrowhead shows basal part of flagella, and asterisk shows eyespot). Fig. 13. TEM micrograph of a flagellum in longitudinal section (arrow shows basal plate, and arrowhead shows transitional helices). Fig. 14. Young erect filamentous thallus in culture without prostrate filaments (arrow shows longitudinal wall, and arrowhead shows basal part). Fig. 15. Young erect filamentous thallus with prostrate filaments (arrowhead). Fig. 16. Saccate thallus in culture.

川井浩史:日本新産黄金色藻 Phaeosaccion collinsii FARLOW (フクロコガネモ:新称)

北海道磯谷において採集された比較的大型の葉状体を形成する黄金色藻を Phaeosaccion collinsii FARLOW (サルシ ノクリシス目,フクロコガネモ科;新称)と同定した。藻体は袋状で1層の細胞層からなり,細胞は表面観で 6-8×6-9 µm で,1個のピレノイドを伴った色素体を含む。成熟すると藻体の全体の細胞がそれぞれ1個の遊走 子に変成する。遊走子は涙滴形で,典型的な褐藻型の側生する2鞭毛,1個の色素体と眼点を有する。透過型電 顕による観察の結果ピレノイドには内膜構造が,また鞭毛基部にはらせん構造が見られた。本種は北大西洋の冷 水域の広い範囲から報告されているが太平洋沿岸からの報告はこれが初めてである。本種の遊走子を5-20°Cの 長日,短日条件で培養した結果,直接型の発芽の後,分枝した糸状体を経て,直立体を生じた。直立体は初め単 列で,次いで縦の隔壁を生じ,袋状の藻体に発達した。5°C,10°C で藻体は成長,成熟し自然藻体と同様の遊走 子を生じた。(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

ABRAMOV, I. I. (編) :下等植物分類学の最新の知見 (Novitates Systematicae Plantarum Nonvascularium) 第25巻.183 pp. ナウカ出版社(レニングラード支部). 1988. (ロシア語)

ソ連邦科学アカデミーコマロフ植物学研究所の,下 等植物一般(藻類,菌類,地衣類およびコケ類)に関 する最新の知見を集めた論文集の25巻。それぞれの論 文タイトルにはラテン語の併記がある。藻類関係の掲 載論文12篇は,以下の通り。

Beljakova, R. N.: 数種の海産ラン藻の形態と生物 学。p. 3-9. ソ連新産種とされたラン藻 5種: Phormidium submembtanaceum, Yonedaella lithophila, Plectonema calothirichoides, Microchaete vitiensis, Kyrtuthrix maculans に 関する形態および分布。

Beljakova, R. N.: ソ連新産種 Solentia paulocellularis (Erceg.) Le Campion-Alsumard et Golubic (Cyanophyta). p. 9–12. 日本海の Furugel'ma 島沿岸で採集された表 題種について。

Beljakova, R. N.: ベーリング海北西沿岸のラン藻。 p. 12-27.52種(ソ連新産3種を含む)の記述。

Bondarczuk, L. L. & Kuznetsov, L. L. : バレンツ海 沿岸表層のケイ藻フロラの季節変動。p. 27-31。3 深 度でのフロラの変動を調査した。

Vinogradova, K. L.: ソ連北極海の Cladophora Kütz. p. 31-38. ソ連の北極海に見られる 2種 C. rupestris と C. sericea についての詳しい記述。

Efimova, I.B.: ムルマン(バレンツ海)の藻類フ ロラ.p. 38-42。Epiphyte と endophyte のうち,新た に Entocladia maculans, Pylaella nana, Mikrosyphar polysiphoniae, Stictyosiphon curta の4種が記録された。後 の2種はソ連新産種。

Konstantinova, I. A.: 数種の Chlorococcum Menegh. (Chlorococcophyceae) の特異的な細胞内構造。p. 43-44. R. Starr のコレクションより得た表題属の type strain 18種についての電顕による観察。

Makarova, I. V. & Achmetova, N. I.: バルハシ湖の 新産ケイ藻 IV。p. 45–50. 20種が新産種とされた。

Okolodkov, Yu. B.: チュコト海の parasitic および epiphytic なプランクトン。p. 50-53. 新たに parasites 2種 (*Dissodinium pseudolunula, Paulsenella chaetoceratis*), epiphyte 1種 (*Characiopsis* sp.), と未同定 2種 (おそら く parasites) が記録された。

Okolodkov, Yu. B.: 東シベリア海のプランクトン フロラ。p. 53-54. 32種 (Dinophyta 4; Chrysophyta 1: Bacillariophyta 27) が記録された。

Perestenko, L. P.: ベーリング海の紅藻フロラ補遺。 p. 54-57. 新たに41種が記録された。また, Velatocarpus Perest. のタイプ種 V. ochotensis Perest. は Iridaea pustulosa P. et R. のシノニムであることが明らかになったので, Velatocarpus pustulosus (P. et R.) Perest. comb. nov. が記載された。

Selivanova O.N.: カムチャツカ南東部の海藻フロ ラ補遺。p. 57-63. 10種のカムチャツカ新産(ソ連邦 新産 2 種を含む)の大型藻類が記録された。

日本ではあまり知られていないソ連の藻類学の一端 である。ソ連ではおもに、多数ある国内誌にさまざま な論文がロシア語で掲載される。情報の国際化も望ま れるのだが。

(山梨大学教育学部生物学教室 御園生拓)

日本藻類学会第4回ワークショップ:藻類分類基礎 講座参加記

1989年4月1日(土)9:00~17:00, 東京女子体育 大学において藻類分類基礎講座と題して, 第4回ワー クショップが開催された。午前中は高橋永治先生によ り, 黄金色藻類の分類についてスライドと参考資料を 用いた講義が行われた。先ず, Chrysophyta の現在の 分類体系の説明がなされ、その中で、Lagynion, Chrysococcus, Kephyrion, Chrysocapsa, Hydrurus, Ochromonas, Didymochrysis, Synchrypta, Uroglena, Anthophysa, Dinobryon, Chrysolykos, Spiniferomonas, Chrysosphaerella, Polylepidomonas, Phaeothamnion, Tetraparma, Triparma, Synura, Mallomonas といった,現存の日本産の属名が示 された。次に Chrysophyta の分類の歴史,全体的な形 態,色素・貯蔵物質・細胞壁の成分の他の門との比較, 鞭毛や鞭毛装置構造の比較, Mallomonas, Synura, Paraphysomonas, Spiniferomonas, Chrysosphaerella \mathcal{O} scale \mathcal{O} 構造や, scale によるグルーピングについてなどの講 義があり、最後にスライドで、主に Mallomonas の scale の構造が示された。また, SEM による scale の 簡単な観察法も紹介された。

昼食後,地球温暖化の影響か一週間近くも早く満開 に咲き誇った桜の花の下で参加者及び関係者による記 念撮影が行われた。撮影場所の横のトラックでは陸上 競技の記録会が行われており,若い歓声を気にしなが らの記念撮影となった。シャッターは記録会に参加す る学生によるもので,一同,彼女の「はい,チーズ!」 の声にいっそう顔をほころばせた。

午後からは加崎英男先生により車軸藻類の分類につ



第4回ワークショップ参加者

いて、参考資料とスライドを用いた講義と4種の車軸 藻の観察が行われた。先ず, Charophyta の分類体系 及び分類基準の説明があり, 先端生長の仕方, 雌器・ 雄器のでき方,つき方,各部位の名称等の説明の後, Chara braunii, C. corallina, C. zeylanica, C. sejuncta, C. fibrosa, Nitellopsis obtusa, Nitella flexilis, N. pulchella, N, hyalina, N. fallosa 等, 各々の種の説明がなされた。講 義の後,加崎先生が用意して下さった4種を実体顕微 鏡を用いて観察し, 講義で聞いたばかりの様々な形質 を実際に確認した。それらはシャジクモ、カタシャジ クモ,クサシャジクモ、オトメフラスコモであり、こ の内, クサシャジクモは臭いにおいのためその名が付 いているとのことで、参加者一同バットに鼻を近づけ てにおいを確認しようと試みたが、多くの人の意見は 別の種の方が臭いとのこと、筆者も同意見であった。 更に, 実体顕微鏡だけでは飽き足らず, 高倍の光学顕 微鏡まで出していただき,造精糸や橋細胞等,雄器の 細かい構造まで観察することができた。最後に、4種 をサンプルビンにいただいて帰った。いくつかの研究 室ではこれらが教育材料として使われているかもしれ tel'a

参加者は筆者のように基礎知識を補うために参加し ている者より,実際に実験材料としてこれらの生物を 使用したい人が多かったのではないかと思う。また, 学会には出席しないが個人的に非常によくこれらの生 物を御存じの方もおられたようである。今回は一日の 日程であり,東京という土地柄のせいもあろうと思う が,採集会もなく,スライドと用意された材料を見る にとどまったのが少し心残りであった。最後に,今回 のワークショップ開催の労をとられた東京女子体育大 学の福島博先生はじめ関係者の方々及び,高橋,加崎 両先生に深く感謝いたします。

(国立公害研究所・笠井文絵)



住所変更

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退 会

浜田真美(茨木県),協和醱酵工業(東京都),斉藤岳由(千葉県),稲葉忠明(福井県),中谷まり子(京都府), 山本俊夫(京都府),山本真規子(兵庫県),Smithsonian Institution (U.S.A.)

お詫びと訂正

藻類37巻2号162頁の退会者欄に、本学会会員である今津達夫氏(兵庫県)の氏名が掲載されましたが、その 後、学会事務センターより学会事務局宛に、会員原簿に二重登録されていたものを訂正した際、誤って退会扱い にしたとの連絡がありました。氏に深くお詫びすると共に、これを訂正させていただきます。

お知らせ

Korea-Japan Symposium on Phycology (韓日藻類学シンポジウム)

本年春の評議員会および総会において紹介があり、また持ち回り評議員会において大筋が承認された韓国藻類 学会との合同の研究集会について、その後打合せの結果、標記のシンポジウムが開催される見通しとなりました。 シンポジウムのスケジュールとしては、

- 1989年11月22日(水) 到着,受付
 - 23日(木)) (招待者研究発表(両国各5名)
 - 24日(金) (自由参加者研究発表(両国各10名)
 - 25日(土) 見学(午前),解散
 - (会場はソウルの Lotte Hotel)

が予定されています。

このシンポジウムに自由参加を希望される方は,研究発表(<u>著者名と標題を英文で</u>お知らせください)の有無 を含めて,下記宛にハガキで大至急お申込みください。研究発表の採択は先着順とさせていただきます。なお, 使用語は英語です。(研究発表申込みの締切りは10月16日です。)

[申込先] 〒108 東京都港区港南4-5-7

東京水産大学 有 賀 祐 勝

日本学術会議だより Mo.13

第14期初めての勧告採択される

平成元年5月 日本学術会議広報委員会

日本学術会議第107回総会報告

第107回総会の主な議事概要は次のとおりであった。

第1日(4月19日)の午前。まず、会長からの前回総会 以後の経過報告及び各部・委員会の報告が行われた。次い で、今回総会に提案されている6案件について、それぞれ 提案説明がなされた後、質疑応答が行われた。続いて、こ れらの6案件のうち、「人間の科学特別委員会」を設置す る案件については、直ちに採決が行われ、設置が決定され た。この件は、前回総会(昨年10月)において第14期活動 計画並びにそれに基づく第14期の特別委員会の設置が決定 された際に、その付帯申合せとして、この「人間の科学」 については、その具体的な進め方に関し、予め検討、整理 を行った後に、当特別委員会を設置させることとされたた め、前回総会後に、検討会が設置され、問題点の整理が行 われてきたものである。

第1日の午後。各部会が開催され,午前中に提案説明さ れた総会提案案件の審議及び設置が決定された「人間の科 学特別委員会」の委員の選出等が行われた。

第2日(4月20日)の午前。前日提案された案件の審議 ・採決が順次行われた。

まず,第6部世話担当の2研究連絡委員会の名称変更 (土壌肥料学研連→土壌・肥料・植物栄養学研連,海水理 工学研連→海水科学研連)に伴う,会則及び関係規則の一 部改正が採択された。

次いで,「副会長世話担当研究連絡委員会の運営につい て(申合せ)の一部改正」が採択された。これは,副会長 世話担当研究連絡委員会の在り方についての抜本的な検討 とは別に,当面の措置として,副会長世話担当研究連絡委 員会のより円滑な運営及び担当副会長の世話機能の充実を 図るために,必要な措置を講じたものである。

続いて、「アジア社会科学研究協議会連盟(AASSREC) への加入について」が採択された。これは、平成元年度予 算において、当該団体への分担金の支出が認められたこと に伴い、当該団体への本会議の加入を総会として議決した ものである。

さらに,第4常置委員会の提案による「大学等における 学術研究の推進についてー研究設備等の高度化に関する緊 急提言(勧告)」が採択された。この勧告は,第14期にな って採択された初めての勧告である。なお,この勧告は, 同日午後直ちに内閣総理大臣に提出され,関係機関等に送 付された(この勧告の詳細は,別掲参照)。

第2日の午後。「人間の科学」について、自由討議が行われた(この自由討議の詳細は、別掲参照)。

第3日(4月21日)午前には、今回設置された前述の人間の科学特別委員会の1回目の委員会をはじめとして、各特別委員会が、午後には、各常置委員会が、それぞれ開催された。

大学等における学術研究の推進につ いて-研究設備等の高度化に関する 緊急提言-(勧告)[要旨]

大学等を中心とする学術研究の財政基盤の現状は, 甚だ 憂慮すべき事態におかれており, この事態を見過ごしては 悔いを後世に残すことになる。したがって, 長期的観点に 立って, 特に基礎研究を育成し, 人類の知的共有財産であ る科学・技術の発展に積極的に貢献することは, 経済大国 と呼ばれるようになった我が国の当然の責務であり, 今こ そ, この責務を果たすべき時である。

日本学術会議では,昭和62年4月に「大学等における学 術予算の増額について」の要望書を政府に提出した。大学 等における学術研究予算を一般の予算要求基準の別枠とす ることが肝要である。

特に,早急な対策を検討する必要がある諸点の中で,今 回,緊急に次の措置を取るよう勧告する。

我が国の研究経費において、国費の負担割合を引き上げ つつ、基礎研究を重視してこれを推進する観点から、国立 学校特別会計予算、私大助成及び公立大学補助の各予算に ついて格段の増額を図る必要があり、その際、特に研究設 備の整備充実を図るべきである。

そのためには、国立大学の研究設備費や公立大学、私立 大学等への研究設備費補助金を飛躍的に増額する措置を取 ること、一大学では措置しにくい大型設備については、全 国的規模の共同利用設備や昭和62年4月の「地域型研究機 関(仮称)の設立について」の本会議勧告においても指摘 している共同利用機器センターを、重点的に早急に整備し ていくことが必要である。人文・社会科学系についても、 昭和63年4月の「大学等における学術諸分野の研究情報活 動の推進について(要望)」のとおり、コンピュータや原 資料、文献、図書コレクションとその利用のための機器や ネットワークなどの整備が極めて重要である。

なお,我が国の基礎研究を限られた人的・物的資源のな かで,より一層有効に推進していくためには,大学等と各 省庁の研究機関の基礎研究に関する研究設備の相互利用と それを通しての研究者の相互交流を推奨する方策を採るべ きである。その際,国の手続きを一段と簡素化,迅速化す るなど制度の改善を図る必要がある。

総会中の自由討議ー人間の科学ー

今回総会の第2日目の午後には、1時から3時間にわた って「総会中の自由討議」が行われた。これは、会員のた めの一種の勉強会で、総会行事の一環として、従来から、 行われてきたものである。今回は、第14期活動計画の中で、 第14期の具体的審議課題の一つとして掲げられている「人 間の科学」という課題を取り上げて行われた。

自由討議は、福場博保第6部会員の司会のもとに、まず、 近藤次郎会長から、「世界人口が50億を超え、来世紀には 100億を突破する。人類の繁栄が人類の破滅を招くおそれ がある。今総会での人間の科学特別委員会の設置は、新聞 ・テレビでも報道されたので、早速一般市民や研究者から も好意的な反響があった。人間のため科学のあり方を考え ることは学術会議にふさわしい命題であると考える。」と の開会の辞があり、続いて、下記の4人の会員による意見 発表が行われ、さらにこれらの意見発表に対する質疑応答 等がなされ、最後に、中山和久第2部会員の閉会の辞があ り、終了した。なお、この討議の内容は、後日、日学双書 として出版される予定である。

4 会員による意見発表の要旨は、以下のとおりであった。

人間と「人間の科学」 肥田野 直(第1部会員・心理学)

「人間の科学」を検討する際に考慮すべき二つの点につ いて提言したい。第一は人間が何を意味するかという点で ある。これは、個体(個人)、人間集団(社会)、人類の三 つのレベルが考えられる。個人は身心の統一体であり、心 は知性と感性、あるいは知情意の三つの側面をもち、自我 (自己)を中心とするミクロコスモスとして把えることが できよう。時間の面からは、個人は成長発達、社会は歴史、 人類は進化の観点から把握することができよう。第二は人 間と「人間の科学」との関係である。これは、研究対象と しての人間,研究主体としての人間、及び研究目的として の人間すなわち人間のための科学という三つの立場が考え られるであろう。

2. 「人間の科学」への接近

島袋 嘉昌 (第3部会員・経営学)

「人間の科学」は、諸科学の特性を認識すると同時に相 互の誤解をときほぐし、人文・社会科学と自然科学をベー スとした総体としての科学を醸成し、生命と生活とを総合 して考える科学をねらいとしている。いわゆる生命尊厳を 抽象化して考えるだけに留めないでその内容をより具体的 に解明することである。

さらに,次のような事項を検討していくべきである。 伝統的科学概念,「人間の科学」の必要性,総合科学と しての「人間の科学」,科学哲学の再吟味。

生物の体は本来保守的であり、したがって急激な進化は 起こりにくい。これに対して文明の発展はポジティブ・フ ィードバックの作用により、2次関数曲線を描いて急速に 発展する。とくに最近の科学・技術の発展に伴って環境は 急激な変化をとげたが、生物の進化がそれに伴って進んで いるとは言い難い。ここに文明と生体との間に大きなディ スクレパンシーが生ずる理由がある。

人体について言えば、われわれの体は1万年以上前の旧

石器時代の環境に適応している。しかし現実の環境は旧石 器時代とは著しく異なり、人体の適応の限度を超えている。 これは文明の発展が必ずしも望ましい方向に進んではいな いという一例であろう。

「人間の科学」の背後にあるもの 井口 潔(第7部会員・外科系科学)

科学を真に人類の福祉に役立てようとするときに必要な ことの中には、科学を行う心と科学を活用する心とは区別 しておかなければならないということではなかろうか。で はそのときの判断の基準はどこに求めたらよいのか。私は 「人間存在の理法」とも言うべき概念に據り処をおきたい と思う。

30億年の生命の歴史の中で精神をもつ生物として人間が 出現し,この人間は,ほんの300年位前から科学の道を歩 みはじめたばかりである。しかし宇宙の秩序の本質は,あ る面は知性によって把えられ,ある面は感性によって生得 的に人間の脳に刻みこまれているはずと私は考える。我々 は「人間存在の理法」を沈思して,それとの調和の下に人 類の繁栄の道を探求して行かねばならぬと思う。

平成元年度における学術研究集会等開催予定

本会議では、毎年、本会議の登録学術研究団体及び広報 協力学術団体に依頼して、これらの各団体の翌年度におけ る学術研究集会等の開催予定について調査を行い、その結 果を、「学術研究集会等開催予定一覧」としてとりまとめ ている。平成元年度分については、昨年11月に調査を実施 したが、調査を依頼した学術研究団体数は956 団体で、回 答のあった団体数は、876 団体であった。

このたび、その結果がとりまとめられたが、それによる と、回答のあった団体からもたらされた開催予定の学術研 究集会等の数は、延べ約3,300 に達している。その分野ご との内訳は次のようになっている。

部	別	学術研究集会等数
第1部(文学, 哲 理学・社	「学,教育学・心 と会学,史学)	701
第2部(法律学,	政治学)	111
第3部(経済学,	商学・経営学)	269
第4部 (理学)		463
第5部(工学)		708
第6部(農学)		326
第7部(医学,菌	谢学,薬学)	714
Ē	ł	3,292

注:学術研究団体の関係する部が複数の場合には,当 該集会等を関係する部にそれぞれ計上したので, 延べ数である。

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。 〒106 東京都港区六本木7-22-34 日本学術会議広報委員会 電話 03(403)6291

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日本学術会議だより №14

人間の科学特別委員会設置される

平成元年8月 日本学術会議広報委員会

日本学術会議は、去る4月に開催した第107回総会において、人間の科学特別委員会を追加設置しましたが、今回の日本 学術会議だよりでは、この特別委員会に加えて、最近発表された「委員会報告」等について、お知らせいたします。

人間の科学特別委員会の設置

本会議は、本年4月に開催した第107回総会において、そ れまでにすでに設置していた7特別委員会のほかに、「人間 の科学特別委員会」の追加設置を決定した。

この人間の科学特別委員会は、同総会中に、委員会の構 成(各部2人ずつ計14人)を済ませるとともに、第1回目 の委員会を開催する等,直ちに、その活動を開始した。委 員長には、中山和久第2部会員が就任した。

今回,本会議が,この特別委員会を設置した理由は次の とおりである。

〈人間の科学特別委員会の設置理由〉

ヨーロッパの産業革命に端を発した科学技術の進歩は急速にその度を加え、かつて人類が予想もしなかった程度に物質文明を開花させたが、一方、それによって人類は、過去に見られなかった重大な危機に立たされている。科学技術の進歩は一面において物質偏重の価値観を強め、生命に対する技術介入に係る不安や、地球生態系の激しい変化を招き、社会経済環境にも様々な問題を醸し出している。

人間が創り、人間が発展させてきた科学は、本来、真理 を追求し、人間の幸福に貢献すべきものであるにもかかわ らず、人類の生活や自然・社会環境に混乱を招いている側 面もあるのではないかとの矛盾も感ぜられ、ここに科学者 の苦悩がある。我々は今や、科学の在り方を再考し、早急 に人間と科学技術との不調和を克服する視点を明らかにし なければならない。

このためには、「人間とは何か」を問い直し、「人間存在 の理法」ともいうべき概念を改めて考え、そこに立脚して、 科学技術と自然との調和を求め、人類進歩への展望を模素 するところから始めなければならない。

人間の人間たる特質はその精神であることを思えば、人間を知性、感性の面から広く把え、人間そのものについて のもっと深い知識と理解が強く望まれる。この立場から、 人間を個体としてばかりでなく、生物学的並びに社会的集 団として把握し、人間の総合理解に努める必要がある。

この特別委員会は、このように人間を学際的、総合的に 把握し、人類の危機に対処することを目指すものである。

「委員会報告」2件を発表

このたび、本会議の「生命科学と生命工学特別委員会」 と「化学研究連絡委員会」は、それぞれ、当面の重要問題 に関する審議結果を取りまとめ、本会議運営審議会の承認 を得て、「委員会報告」として発表した。各「報告」の要旨 は次のとおりである。

ヒト・ゲノム・プロジェクトの推進 について-生命科学と生命工学特別 委員会報告-[要旨]

ヒト・ゲノムの全 DNA 配列決定を主たる目標とするヒ ト・ゲノム・プロジェクトは、極めて大きなインパクトを 学術研究に与えると期待され、我が国として早急かつ重点 的に推進すべきである。そのためには推進組織を設け、基 本計画の立案、実施計画の策定、省庁間などの協議、国際 協力、データ・ベースとレポジトリー整備などを総合的に 行うべきである。一方この推進組織と並んでこれと密接に 連携し、研究計画の実施に伴う社会的・法律的・倫理的諸 問題を客観的・公正に判断することを目的とするチェック 機構を設立し、調和のとれた施策を進める必要がある。

大学等における化学の研究環境の整備についてー化学研究連絡委員会報 告ー「要旨]

化学研究連絡委員会は、昭和63年に発表された日本化学 会報告書を参考資料として、大学等における化学分野の研 究環境の現状について検討を行った。その結果、「全国的視 野に立つ化学の新しい研究体制」の実現に向けての努力を 傾注するとともに、現行の研究環境を抜本的に改善するた めに、関係方面に強く訴えるべきであるとの結論に達した。 日本化学会報告書に盛られている数項目の重点施策のうち でも、特に、①先端研究設備の購入・維持予算の大幅増額、 ②研究基盤整備のための大学院関連予算の充実、③化学の 特殊性を配慮した研究室面積の拡充、は緊急に実施すべき ものと考えられる。

²⁵² 平成 2 年度共同主催国際会議

本会議は、昭和28年以降おおむね4件の学術関係国際会 議を関係学術研究団体と共同主催してきたが、平成2年度 には、2件増えて、次の6国際会議を開催することが、6 月20日の閣議で了解された。(カッコ内は、各国際会議の 開催期間と開催地)。

◆第14回国際土壌科学会議 (平成2年8月12日~18日,京都市) 共催団体:(社)日本土壤肥料学会 ◆第22回国際応用心理学会議 (平成2年7月22日~27,京都市) 共催団体:日本心理学会 ◆第15回国際微生物学会議 (平成2年9月13日~22日、大阪市) 共催団体:日本微生物学協会 ◆第11回国際数学連合総会及び第21回国際数学者会議 (平成2年8月18日~29日,神戸市他) 共催団体:(社)日本数学会他6学会 ◆第11回国際神経病理学会議 (平成2年9月2日~8日,京都市) 共催団体:日本神経病理学会 ◆第5回国際生態学会議 (平成2年8月23日~30日、横浜市) 共催団体:日本生態学会

国際社会科学団体連盟(IFSSO)第9回大会・ 総会の日本開催

国際社会科学団体連盟(IFSSO)の第9回大会及び総会 が、本年10月2日(り)~7日(1)、東京六本木の国際文化会館 と日本学術会議で開催される。

国際社会科学団体連盟 (International Federation of Social Science Organizations,略称 IFSSO)は、世界の社会 科学の発展に貢献することを目的とする、世界各国の学士 院や学術会議で構成されている、社会科学分野を代表する 国際学術団体である。現在、35か国の国家会員等で構成さ れており、我が国では、日本学術会議が、我が国を代表し て加入している。また、現在、日本からは本会議の藤井隆 第3部会員がIFSSOの事務総長を務めている。

なお、IFSSOは、社会科学分野の国際学術団体の連合体 (総括機関)である国際社会科学協議会(International Social Science Council, 略称 ISSC)に加入しており、ISSC の中では、国及び地域を代表する機関という位置付けをも っている。

今回の会議には、IFSSOに加入している各国の学士院や 学術会議の代表,並びに関係する国際機関,国際学術団体 の代表など,50を超える国々から約300名(うち,外国人 は約150名)の科学者等が参加する。

この会議では、メインテーマ「変容する世界の学術政策」 の下に、「研究・訓練体制の改革」、「既存領域を超える新分 野」、「社会と科学・技術のインターフェイス」及び「国際 協力のアカデミック・インフラステラクチャー」の4つの サブテーマが設けられ、多方面から世界の学術政策の変化 が論じられる。

また、この会議では、特に、3つの日本セッションが設 けられ、「急激な科学技術の進歩」について、①人間に与え るインパクト、②法律や政治に与えるインパクト、③社会 経済システムに与えるインパクト、という3つの視点から 論じられ、日本の先端研究が広く紹介されることになって いる。

■本件問い合わせ先:〒102 東京都千代田区紀尾井町7-1, 上智大学心理学研究室内,国際社会科学団体連盟第9回 大会日本組織委員会事務局,電話 03-238-3811

日本学術会議主催公開講演会開催のお知らせ

本会議では、毎年、学術の成果を広く国民に還元すると いう日本学術会議法の主旨に沿うための活動の一環として、 公開講演会を開催しています。

このたび、下記の2つの公開講演会を開催することにし ました。多数の方々の御来場をお願いします。

I 公開講演会「人間は地球とともに生きられるか」

●日時:平成元年10月27日(約13時30分~17時
 ●演題と講演者(カッコ内は所属部)
 ①「地球の温暖化とその影響」:吉野正敏(第4部)
 ②「地球環境と農業のかかわり」:久馬一剛(第6部)

③「地球環境の経営と人間社会の発展」:藤井 隆 (第3部)

I 公開講演会「"人権の歩み"から何を学ぶか-フランス 人権宣言100年を記念して一」

●日 時:平成元年11月18日(十)13時30分~17時

- ●演題と講演者(カッコ内は所属部)
 ①「"人権"以前の世界」:弓削 達(第1部)
 ②「近代日本の人権思想 一自由民権運動の人権論を中心 に一」:大石嘉一郎(第3部)
 - ③「科学技術と人権」:杉本大一郎(第4部)
 - ④「人権の進化と創造」:南 博方(第2部)
- ●会場:日本学術会議講堂(両講演会とも) (東京都港区六本木7-22-34) (地下鉄千代田線、乃木坂駅下車1分)

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- ◆申込締切:各開催日の1週間前まで(先着順, 無料)

◆申込先:〒106 東京都港区六本木7-22-34 日本学術会議事務局庶務課講演会係

■ なお、本会議では、本年度には、上記の他に、「日本の 学術動向」に関する公開講演会の開催を計画しています。 開催日、会場、講演者などの詳細については、決定次第、 新聞広告等でお知らせする予定です。

日学双書の刊行案内

本会議の第102回総会と第103回総会で行われた、本会議 会員による各自由討議の記録を中心に編集された次の日学 双書がそれぞれ刊行されました。

- ・日学双書 No.4「21世紀へ向けてのエネルギー問題」
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5. 北海道周辺のコンプ類と最近の増養殖学的研究. 1977. B 5 版, 65頁。昭和49年 9 月に札幌で行なわれ た日本藻類学会主催「コンプに関する講演会」の記録。4 論文と討論の要旨。価格 1,000円。

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

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