

Studies on *Monostroma* (Monostromataceae, Chlorophyta) in British Columbia with emphasis on spore release

Larry GOLDEN* and David GARBARY**

*Bag 3670, Triple Island Lighthouse, Prince Rupert,
British Columbia, V8J 2M3

**Department of Botany, University of British Columbia,
Vancouver, B.C., V6T 2B1

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Field and culture studies of the marine algae of Triple Island and McNichol Creek in northern British Columbia confirm the presence of three species of *Monostroma*: *M. grevillei*, *M. oxyspermum* and *M. undulatum*. *M. undulatum* is recorded for the first time in the eastern Pacific. *M. arcticum* sensu KORNMAN and SAHLING is considered conspecific with *M. grevillei*. Morphology, spore germination and early development in culture for all species were consistent with observations of these taxa from Europe and Japan. Spore release is similar in all species and this is used to argue that *Monostroma* is a natural group. *Ulvopsis*, *Prctomoncstroma* and *Gayralia* are synonymized with *Monostroma*.

Key Index Words: algal systematics; *Monostroma*; British Columbia; Chlorophyta; phytogeography; spore release

Monostroma was classically defined as a genus of green blade-like monostromatic algae (e.g. WITTRICK 1866, ROSENGING 1893). With the advent of culture and developmental studies this generic concept was shown to be inadequate, and with the work of KUNIEDA (1934), KORNMAN and SAHLING (1962), KORNMAN (1964), GAYRAL (1965), BLIDING (1968) and TATEWAKI (1969) new generic concepts have evolved based on characteristics of life history, and ontogeny (see TANNER 1981 for review). The described or redescribed genera are *Ulvaria* RUPRECHT, *Kornmannia* BLIDING, *Ulvopsis* GAYRAL, *Protomonostroma* VINOGRADOVA, *Gayralia* VINOGRADOVA and *Capsosiphon* GOBI.

Early records of monostromatic green algae in the northwestern Pacific were summarized by SETCHELL and GARDNER (1903, 1920) who

described eight taxa from Alaska to northern Washington. SCAGEL (1966) provided a major literature review and included five species: *M. arcticum* WITTRICK, *M. fractum* JAO, *M. fuscum* WITTRICK, *M. oxyspermum* (KUETZING) DOTY and *M. zostericola* TILDEN. ABBOTT and HOLLENBERG (1976) referred to three species from California (*M. grevillei* (THURET) WITTRICK, *M. oxyspermum* and *M. zostericola*). In addition, LINDSTROM (1977) summarized previous records from Alaska and included five species (*M. arcticum*, *M. areolatum* SETCHELL et GARDNER, *M. fuscum*, *M. grevillei* and *M. oxyspermum*). Other than the paper of DUBE (1967) on *Ulvaria obscura* KUETZING GAYRAL (as *Monostroma fuscum*) there are no reports of life history and developmental patterns of monostromatic green algae in western North America. *Ulvaria obscura* is a member of the Ulvaceae (BLIDING 1968) and will not be considered in this paper. *Monostroma areolatum* is conspecific with *Kornmannia zostericola*

** Present address and reprint requests: Department of Biology, St. Francis Xavier University, Antigonish, Nova Scotia, Canada, B2G 1C0.

(TILDEN) BLIDING which will be treated elsewhere. Regarding *M. fractum*, we have no information.

In this paper we present a field and culture study of the remaining monostromatic green algae known from British Columbia. The species treated are *M. grevillei* (including *M. arcticum*), *M. undulatum* WITTRÖCK and *M. oxyspermum*.

Study sites

Triple Island (54°17' N 130°53' W) was the primary study site. It is a small group of exposed granitic islets 40 km west of Prince Rupert, northern British Columbia. Tides are mixed semi-diurnal with an amplitude of 7.5 m. Water temperature varies from 5°C in January to about 13°C in August. Salinity is ca. 32‰ through most of the year with slightly lower values in July/August. McNichol Creek (54°20' N 130°21' W), 2 km northwest of Prince Rupert is a protected, nutrient rich, estuarine habitat. Additional sites included Barkley Sound, Vancouver Island and Vancouver harbour in southern British Columbia.

Materials and methods

From each field sample plants were processed as follows: 1) 25–50 separate blades were placed singly in 300 ml plastic glasses to release spores, 2) samples of spores were subsequently cultured in filtered seawater and/or PES medium (PROVASOLI 1968) in a north facing window during 1983 or in a growth chamber in 1984, at ca. 11°C and 16–8 h, 3) spore release was followed by examining transverse sections and surface views of actively releasing material, and 4) samples were stained with 1% aqueous aniline blue and/or preserved on permanent slides in 30% Karo. Some plants were fixed in 5% formalin/seawater. Populations were sampled sporadically through the growing season (November to June) on a daily, weekly or monthly basis.

Voucher specimens are deposited in the

Herbarium at the University of British Columbia (UBC).

Results

Monostroma grevillei (THURET) WITTRÖCK

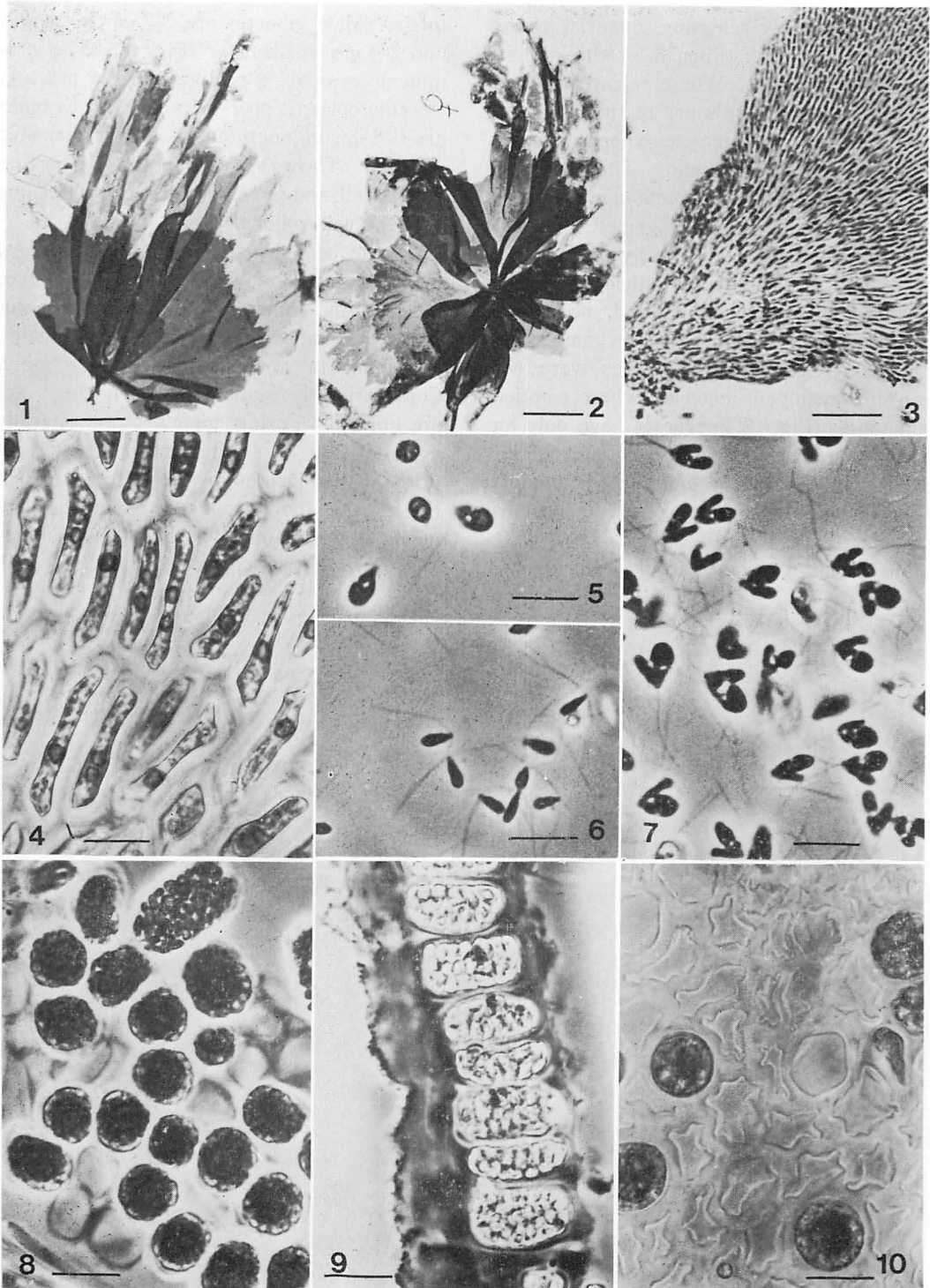
Habitat and seasonality: *Monostroma grevillei* is usually present at Triple Island from late November until mid June. Early in the season populations are limited to shallow, upper intertidal rock pools (ca. 7 m), which become dominated with small plants (ca. 1 cm in height) by January. As days lengthen, deeper and lower pools (at ca. 4–6 m) are colonized. By April, *M. grevillei* is common in the low intertidal zone and attains a size of 15–30 cm. Plants found in June are subtidal at ca. 5 m depth when intertidal plants are rare.

Monostroma grevillei is usually epilithic early in the season but often becomes epiphytic in the late spring. The sac stage is small and transient in intertidal plants, however, subtidal plants may remain sac-like up to 20–30 cm in length. Careful collection and observation of basal portions from most plants will show the remains of the saccate morphology.

Anatomy: Thalli are differentiated into basal, vegetative and reproductive zones, each with its characteristic cell types. Cells near the base are double-ended and have one to several pyrenoids. They are up to 100 μm in length (Fig. 4) and tend to be in linear files. Distally there is a transition zone (Fig. 3) where cell length decreases and cells are more rounded as in typical vegetative portions. Frond thickness varies between individuals and parts of the same thallus. Small, reproductive winter plants may be only 12 μm thick whereas subtidal thalli are >50 μm thick.

Reproduction: *Monostroma grevillei* is dioecious; macroscopically the gametangial zone of the male plant (Fig. 1) is lighter than that of the female plant (Fig. 2). Plants are usually reproductive for several days preceding spring tides.

Gamete release was observed on numerous



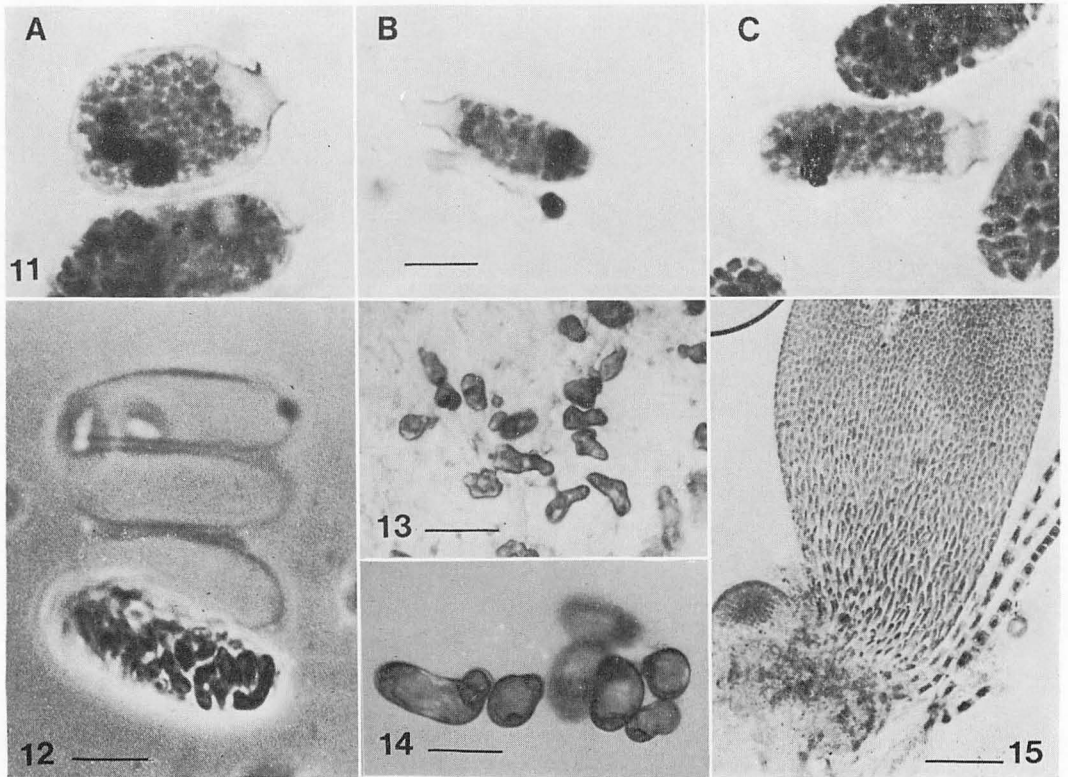
Figs. 1-10. *Monostroma grevillei*. 1. Habit of releasing male plant. Scale=10 mm; 2. Habit of releasing female plant. Scale=10 mm; 3. Lower portion of thallus. Scale=100 μ m; 4. Double-ended cells stained with IKI from lower portion of thallus. Scale=25 μ m; 5. Female gametes. Scale=10 μ m; 6. Male gametes. Scale=10 μ m; 7. Fusing gametes. Scale=10 μ m; 8. Surface view of release area with upper wall absent. Scale=20 μ m; 9. Transverse section through gametangial area of female plant with one wall nearly dissolved. Scale=20 μ m; 10. Surface view of released area showing retained gametangia with apparent irregular openings. Scale=20 μ m.

thalli. In actively releasing material there is no external wall (Figs. 8) or the wall is only locally present. Where release has not yet occurred, both walls are of similar thickness. During release gametes emerge through a pore in the gametangium. They may or may not be enclosed in a common membrane; the latter bursts and the gametes stream though the wall matrix upwardly and laterally until a break in the external cuticle is reached. In aniline blue stained material, occasional flared-necked pores are present on gametangia (Fig. 11 A-C). These structures were not seen in unstained material where emptied gametangia (Fig. 12) appear to have only an unraised circular pore up to $8\mu\text{m}$ in diameter. In surface view of the emptied gametangia in a released thallus, the pores appear as irregular rents (Fig. 10).

The released gametes are positively photo-

tactic. Male gametes are $5-7\mu\text{m}$ in length and $2-4\mu\text{m}$ in diameter (Fig. 6). The prominent eyespot is posterior in the cell and the chloroplast is poorly developed. Females are $6-8\mu\text{m}$ in length and $3-5\mu\text{m}$ in diameter (Fig. 5). The eyespot is in the midportion of the cell and the chloroplast comprises one half the cell volume.

Gamete behaviour differs in the two sexes. Females swim slowly with frequent changes in direction, remaining in a field of view for 20 sec or longer. Males 'flip-flop' rapidly, remaining in a general area indefinitely. Conjugation is immediate when the sexes are mixed. Fusing gametes are laterally apposed (Fig. 7). After fusion the eyespot of the male migrates to the posterior end of the zygote, and flagella are either shed immediately or retained for up to ten minutes. When zygotes are placed in cultures with



Figs. 11-15. *Monostroma grevillei*. 11A-C. Aniline blue stained gametangia with flared-necked exit pore. Scale= $10\mu\text{m}$; 12. Three empty and one nonreleased gametangia. Scale= $10\mu\text{m}$; 13. Codium cells removed from barnacle shell. Scale= $15\mu\text{m}$; 14. Free living codium cells in culture. Scale= $20\mu\text{m}$; 15. Field-collected disc with upheaval and sac stages found on utricle of *Codium fragile*. Scale= $150\mu\text{m}$.

barnacle shell fragments, settlement is random with no apparent substrate preference. Zygotes and unfertilized females developed into codium cells (Figs. 13-14) and no survival of male gametes was observed. One month old codiolums removed from decalcified barnacle shells (Fig. 13) had similar gross morphology to the free living codiolums (Fig. 14).

The above observations were repeated with plants from Barkley Sound in April 1982. Similar results were obtained except that unfertilized male and female gametes were both nonviable.

Discussion: *Monostroma grevillei* has been cultured many times (GAYRAL 1965, KORN-MANN and SAHLING 1962, JÓNSSON 1968, BLIDING 1968, TATEWAKI 1969 (as *M. angicava* KJELLMAN), and this paper) with only slight deviations in results; dioecious gametophytic blades alternate with a shell boring sporophytic codiolum stage. During ontogeny a prostrate disc is produced which forms the sack stage through a central upheaval. The retention of the emptied gametangia on the vegetative thallus after their release was previously noted by GAYRAL (1965) and TATEWAKI (1969) who emphasized spore release as a taxonomic feature. We consider this character diagnostic for *M. grevillei*.

Monostroma grevillei in British Columbia agrees with literature accounts in most aspects; although, it differs in that a sac-like adult form reported in European literature (e.g. BLIDING 1968) is rarely seen. Although we did not observe development of the zoospores in culture, their ontogeny is evident in field material, especially epiphytic plants on *Codium fragile* (SUHR) HARIOT (Fig. 15).

Distribution: *Monostroma grevillei* is a circumboreal species. We consider the Japanese account by TATEWAKI (1969) under the name *M. angicava* to refer to *M. grevillei*. TATEWAKI describes both bi- and quadriflagellate spores being produced by the codiolum stage, whereas other authors only refer to quadriflagellate spores. TATEWAKI (1972) also noted a different chromosome number ($n=ca. 8$) from that given by JÓNSSON

(1968) ($n=6$) for plants from Roscoff. Chromosome numbers are needed from more localities before this feature can be used to segregate species.

Monostroma arcticum WITTRÖCK

Habitat and ecology: *Monostroma arcticum* was found once in April 1983 mixed with intertidal *M. grevillei*. An intensive search in May 1984 located two additional thalli in the subtidal region. These were reproductive several days before the majority of the *M. grevillei* population. Plants were recognized when swimmers became phototactically negative and settled immediately after release.

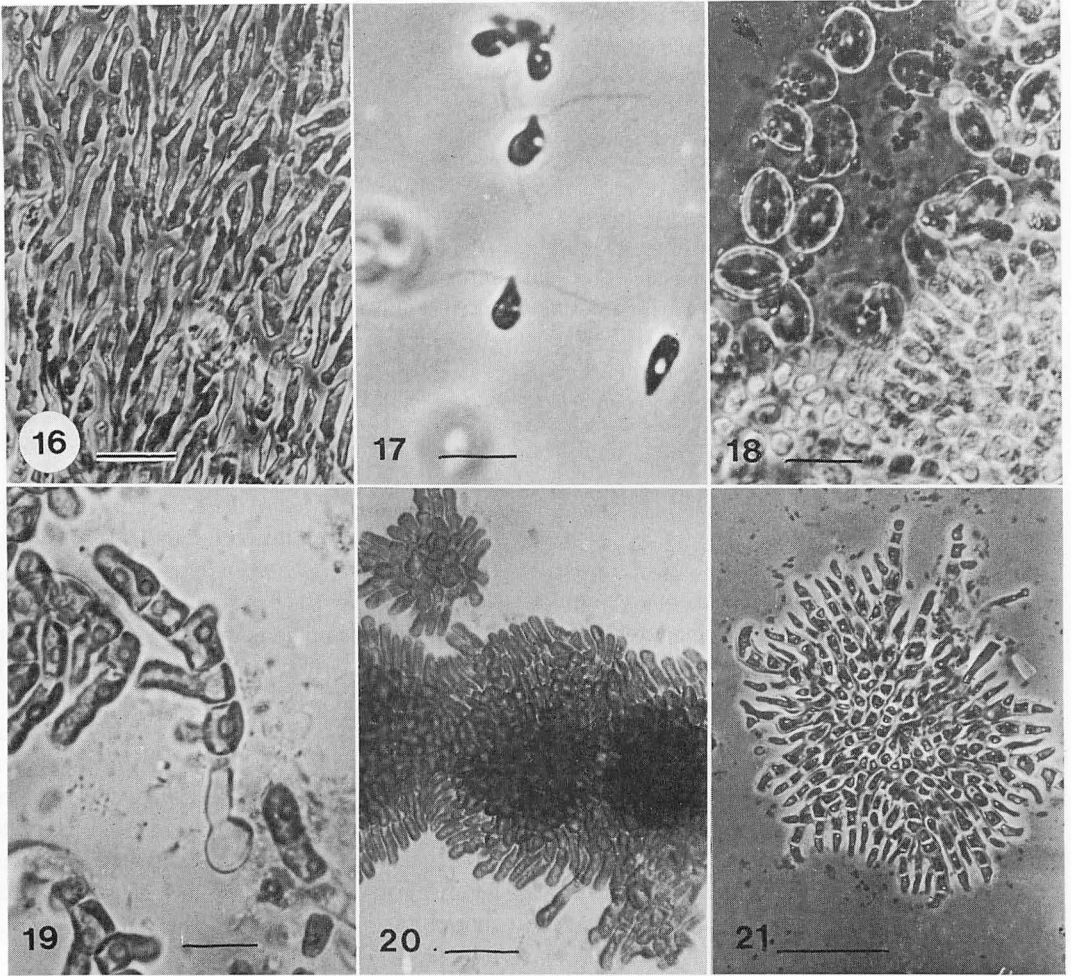
Anatomy: *Monostroma arcticum* from Triple I. is vegetatively indistinguishable from *M. grevillei* (see that species for a description of the vegetative morphology). However, the double-ended cells at the plant bases (Fig. 16) are more irregular than typical *M. grevillei*.

Reproduction: In the two years *Monostroma arcticum* was collected, different mechanisms of spore release were observed. In 1983 a cleared margin was present (Fig. 18), whereas plants collected in 1984 showed spore release identical to *M. grevillei*, i.e. with emptied sporangia remaining on the thallus (Fig. 10).

Released biflagellate swimmers are 8-10 μm in length (Fig. 17) with a prominent eyespot. They are negatively phototactic and settle immediately. No interaction was noted when male gametes of *M. grevillei* were introduced into the release vessels containing active swimmers of *M. arcticum*.

Settled zoospores occasionally showed empty spore germination (Fig. 19). After several weeks prostrate discs were formed (Figs. 20-21) with upheaval occurring in four weeks.

Discussion: Since the culture work of KORN-MANN and SAHLING (1962), *Monostroma arcticum* has come to refer to a *M. grevillei*-like plant that recycles asexually by means of biflagellate swimmers. These germinate directly into a prostrate disc which then becomes saccate. Their plants were not



Figs. 16-21. *Monostroma arcticum*. 16. Irregular pattern of double ended cells from base of plant. Scale=50 μm ; 17. Biflagellate swimmers. Scale=10 μm ; 18. Cleared release area from 1983 thallus indicating wall limit (arrow). Scale=35 μm ; 19. Empty spore germination. Scale=15 μm ; 20. Prostrate discs from 1984 plants beginning upheaval. Scale=50 μm ; 21. Prostrate disc from 1983 plant. Scale=50 μm .

distinguished on vegetative features from *M. grevillei*. This species concept was endorsed by BLIDING (1968) who cultured plants from Sweden and from the type locality in northern Norway. Only six thalli were found by BLIDING in Sweden, all being from the subtidal zone and agreeing "almost completely" with *M. grevillei* from the same location. The Norwegian plants were from the upper intertidal region and differed from *M. grevillei* in having a distinctive layering of the thallus wall observed in transverse section (BLIDING 1968) as previously noted by JAASUND (1965).

In summary, *Monostroma arcticum* differs from *M. grevillei* only in its life history. We question the recognition of any entity at the species level based exclusively on such grounds. In addition, in British Columbia and Sweden only a few individuals have been found with the appropriate life history. JÓNSSON (1968) also notes occasional development of gametes of *M. grevillei* directly into the gametophytic stage without an intervening codiolium. In recognition of the complexities in the life history of *Ulva mutabilis* (see review by FJELD and LØVLIE 1976), we do not consider it suitable to recognize *M.*

arcticum sensu KORNMANN and SAHLING (1962) in British Columbia or elsewhere unless large, self-propagating populations can be found. If such populations can be found then varietal rank would be warranted, as previously suggested by ROSENVINGE (1893).

Monostroma undulatum WITTRÖCK

Habitat and seasonality: Blades of *Monostroma undulatum* are present at Triple I. from late March when thalli are predominantly epilithic, until early June when all surviving plants are epiphytic on *Fucus gardneri* SILVA. In the field this species may be distinguished from *M. grevillei* when either is reproductive.

Habit: The plants are typically smaller (to 10 cm) (Fig. 22) and a lighter green than *M. grevillei*. Many blades arise from a proliferous base. When epiphytic, rhizoids may penetrate deeply into the host (Fig. 23). Blades are lanceolate as juveniles, becoming more ovate with age. Fronds are delicate and fragile.

Anatomy: Thalli of *Monostroma undulatum* are differentiated into rhizoidal, vegetative and marginal cell types (Figs. 23-25). In surface view, the central basal area has long, narrow, more-or-less double-ended cells that may be 100 μm in length (Fig. 25), and usually have one pyrenoid. Distally, cells become more quadrate and in mid-blade cells are ca. 15 \times 15 μm . At apices and in marginal regions near the base cells are much smaller and ca. 5 \times 5 μm . Thallus thickness is also variable with blades being ca. 50 μm thick near the base, ca. 35 μm in mid portions and ca. 20 μm or less at the margins.

The strongly differentiated rhizoidal and marginal cell types at the base of *M. undulatum* (Fig. 24) provide a diagnostic vegetative feature to distinguish it from *M. grevillei*. The juxtaposition of these cell types is absent at the base of *M. grevillei* (see Figs. 3, 24).

Reproduction: At Triple Island *Monostroma undulatum* is reproductive over several days during neap tides. As the tide returns and covers the plants, the apical margin of the blade is covered with small air bubbles which

aggregate into a green froth or scum. This material is comprised of small pieces of thalli and many sporangia which have become dissociated from the plants. From the apices of these sporangia, quadriflagellate swimmers are released one at a time. In blocks of sporangial cells still contained within the thallus wall, the spores move through the mucilaginous wall material to the edge of the fragment where they are liberated.

Swarmers of *Monostroma undulatum* have a distinctive clumping behaviour in which they aggregate with posterior ends touching and flagellated ends free (Fig. 26). This clumping continues for several minutes after which the spores disperse.

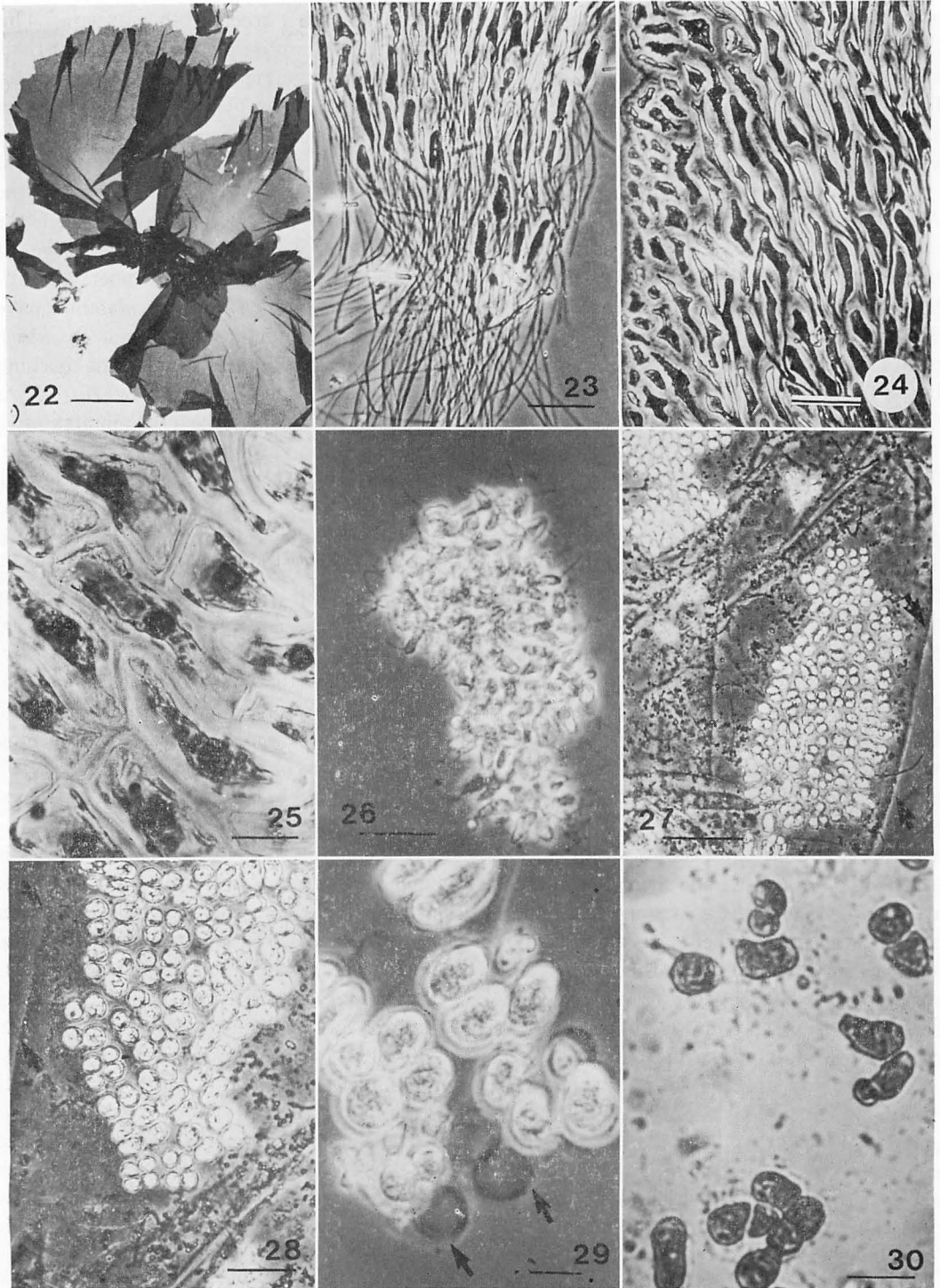
Herbarium sheets of reproductive *Monostroma undulatum* will often show a cleared margin. Examination of formalin preserved material of actively releasing blades shows a thallus wall with geometrically regular blocks of unreleased sporangia intermingled with cleared areas (Figs. 27-28). Cross sections confirm that the external thallus wall is no longer present. Emptied sporangia were infrequent and a small circular pore, opening externally, was observed occasionally (Fig. 29).

Germinated swarmers eventually developed into a squat codium (Fig. 30).

Discussion: *Monostroma undulatum* is unique in the genus in having quadriflagellate swimmers that give rise to a codium stage. The codium also has quadriflagellate swimmers that germinate into a uniseriate filament. This forms a monostromatic blade directly without an intervening saccate phase (YOSHIDA 1964, as *M. pulchrum* FARLOW; TATEWAKI 1969; KORNMANN and SAHLING 1962; BORASO 1977).

The clumping zoospores were first reported by YAMADA and SAITO (1938) and have been consistently reported by subsequent workers. This behaviour may be considered diagnostic for *Monostroma undulatum*.

Adult plants from Triple Island lack the lanceolate blades with undulating margins typical of the species. However, the characteristic shape is usually present in juvenile plants.



Figs. 22-30. *Monostroma undulatum*. 22. Habit. Scale=10 mm; 23. Basal portion of plant with extensive penetrating rhizoids. Scale=70 μ m; 24. Margin of plant near base with small cells juxtaposed to rhizoidal cells. Scale=50 μ m; 25. Double-ended cells in lower thallus stained with IKI. Scale=15 μ m; 26. Large cluster of quadriflagellate swarmer. Scale=15 μ m; 27. Partially released area of thallus. Note straight margins of remaining sporangia. Arrows indicate margin of thallus. Scale=50 μ m; 28. Detail of sporangial area with one wall absent. Arrows indicate thallus margin. Scale=20 μ m; 29. Group of freed sporangia. Note empty sporangia with pores (arrows). Scale=10 μ m; 30. Codiolums resulting from germination of quadriflagellate spores. Scale=20 μ m.

Distribution: *Monostroma undulatum* is present on both sides of the Atlantic Ocean from Newfoundland (SOUTH and HOOPER 1980) and Helgoland (KORNMANN and SAHLING 1962 1977). It is also known from Japan (YOSHIDA 1964, TATEWAKI 1969) and Saghalien (TOKIDA 1954) in the western Pacific and from Argentina (BORASO 1977) in the south Atlantic. In western North America we have identified specimens from the Pribilof and Aleutian Islands in Alaska and northern British Columbia. These are the first records of *M. undulatum* from the eastern Pacific.

Monostroma oxyspermum (KUETZING) DOTY

Habitat and seasonality: *Monostroma oxyspermum* is a brackish water species not found at Triple Island, although it is common in the Prince Rupert area. This species shows a wide variety of habits from small, *Prasiola*-like plants on high intertidal pilings (Fig. 31) to saltmarsh plants that may exceed a meter in length. At McNichol Creek on the northwest side of Prince Rupert harbour, a large, dense population extends about 30 m up the stream. The species is present throughout the year.

Anatomy: The thallus is differentiated into two regions, an upper blade portion and a lower rhizoidal zone (Figs. 31-35). Rhizoidal cells (ca. 40 μm) have an irregular arrangement (Figs. 34, 35), rounded apices and an extended, narrow process (Figs. 34, 35). In some cases thalli produced secondary rhizoidal regions at the blade margins (Fig. 32). Usually there is an abrupt transition between rhizoidal and vegetative cells (Fig. 34). In living material vegetative cells are closely adpressed, polygonal to rounded, and 10-20 μm in diameter. In dried material, cells may become plasmolyzed and appear in groups of 2-4 (Fig. 33). In transverse section plants vary from 10 μm in winter juveniles to about 50 μm in large plants.

Reproduction: *Monostroma oxyspermum* is reproductive for several days prior to spring tides. Sporangial areas have a slight orange tint which facilitates recognition of reproductive plants in the field.

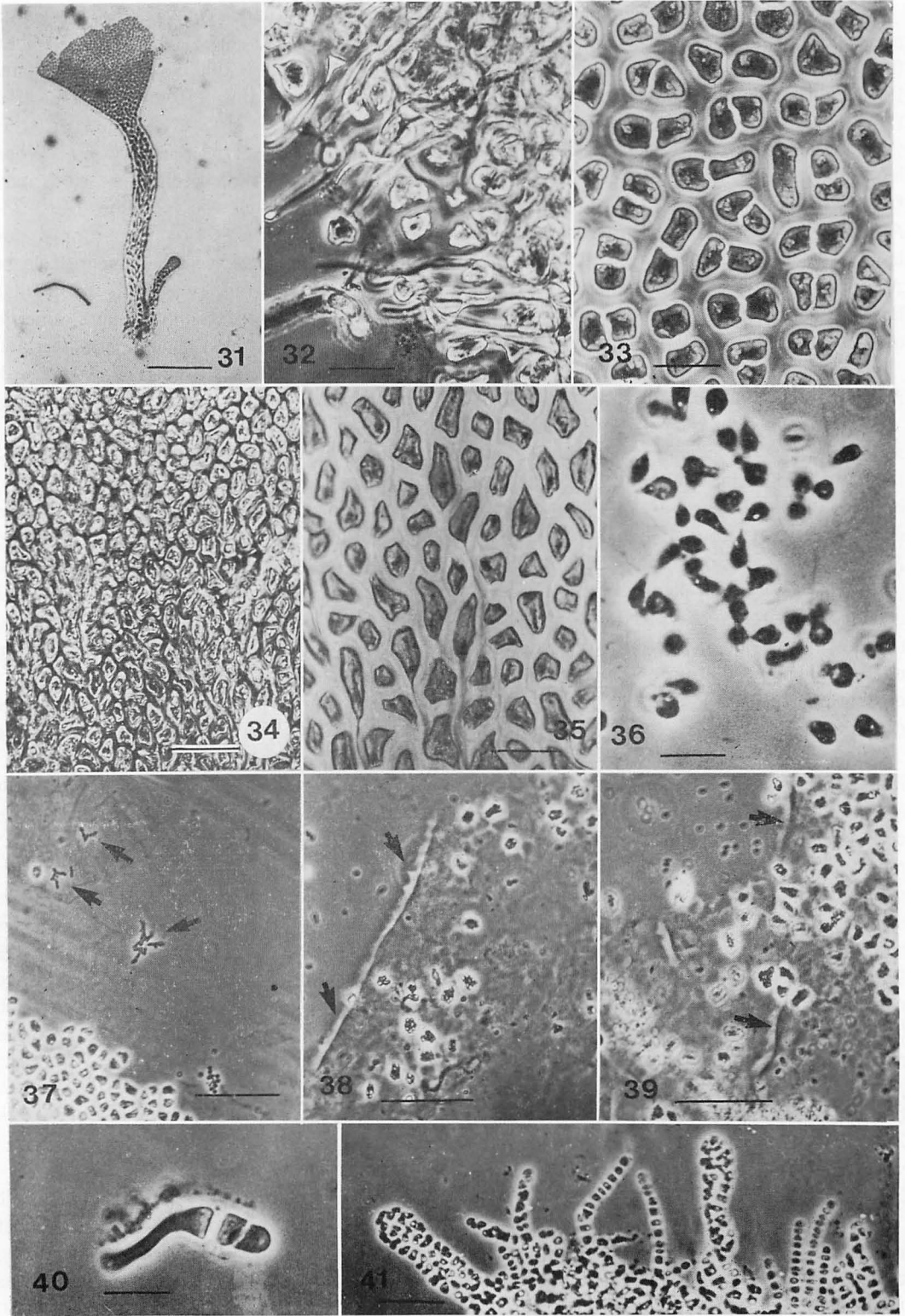
A released thallus may show a cleared margin up to 250 μm wide (Fig. 37). When fresh, the cleared thallus wall has cell impressions remaining from the released sporangia (as in Fig. 8). However, this feature diminishes with preservation. When thalli are folded, jagged cell impressions may be discerned along the fold line (Figs. 38-39). In released areas of plants only one thallus wall is present; where spore release has not yet occurred, two walls of similar thickness are present. Swimmers emerge rapidly from sporangia through a pore, and move through the wall matrix until a break in the cuticle is found. Emptied sporangia were not observed.

The biflagellate swimmers (Fig. 36) are 8-10 μm in length and have prominent eyespots. They are negatively phototactic and swim for up to 60 min, after which they settle and attach to available substrata. Released zoospores are active, crossing a 400 \times field of view within several seconds and tend to swim in one direction. Mixing spores from several thalli has no apparent effect on behaviour and no indication of cell fusion was found. Rare quadriflagellate spores were also present.

Spores germinate into a uniseriate filament (Figs. 40-41) which in turn becomes saccate (Fig. 41). The above features were also observed in plants from Vancouver harbour.

Discussion: *Monostroma oxyspermum* refers to an asexual species that recycles blades with biflagellate zoospores. The spores germinate into a uniseriate, filamentous stage which becomes tube-like, then saccate and finally opens into a monostromatic blade (BLIDING 1935, as *M. wittrockii* BORNET; IWAMOTO 1960, as *M. tubiforma* IWAMOTO; KIDA 1964, as *M. wittrockii*; KORNMANN 1964; GAYRAL 1965; BLIDING 1968, as *Ulvaria*; TATEWAKI 1969).

Monostroma oxyspermum is a polymorphic species of brackish waters which led to it being described as several different species. Culture studies from areas as widespread as Japan (KIDA 1964) and Scandinavia (BLIDING 1968) and British Columbia have given similar



results, showing the conspecificity of several taxa. Material from Prince Rupert differed from other descriptions in becoming saccate almost immediately with the *Enteromorpha*-like stage being transitory.

The account of spore release given here differs markedly from that given in most accounts, where *Monostroma oxyspermum* is considered to have a dissolution-type of release (GAYRAL 1965, TATEWAKI 1969, VINOGRADOVA 1969).

Distribution: *Monostroma oxyspermum* is widely distributed in the northern hemisphere from the tropics to the arctic. The species is reported from the southern hemisphere, but the necessary culture studies to confirm this distribution have not been carried out. In Pacific North America it is present in brackish areas from California to Alaska.

Discussion

Monostroma sensu WITTRÖCK (1866) and the broader concept of ROSENVINGE (1893) has been recognized as a heterogeneous assemblage of species for about fifty years, based upon culture studies. Thus the segregation of *Ulvaria* with its type species *U. obscura* (GAYRAL 1965, BLIDING 1968), *Kornmannia* with its type species *K. leptoderma* (KJELLMAN) BLIDING (BLIDING 1968), and the tentative placement of *M. groenlandica* J. AGARDH in *Capsosiphon* (VINOGRADOVA 1969, see GARBARY *et al.* 1982 for discussion) have received general acceptance. However, there is no consensus among systematists as to the classification of the taxa remaining in *Monostroma*. For example, *M. oxyspermum* has been treated by various workers as belonging to three genera (*Monostroma*, *Ulvaria*,

Gayralia), three families (Monostromataceae, Ulvaceae, Gayraliaceae) and two orders (Ulvales, Ulotrichales). Such divergences of opinion are the result of the differential weight given to specific morphological, developmental and life history features.

Monostromataceae sensu KUNIEDA (1934) has a life history characterized by an alternation of codium and blade phases. Further divisions utilized the ontogeny of the codium zoospores as generic or family criteria (GAYRAL 1965, KORNMANN 1964, VINOGRADOVA 1969). More recently, ultrastructure of pyrenoids (HORI 1972) and flagellated cells (e.g. O'KELLY *et al.* 1984) has been used in the search for natural groupings. Mechanisms of spore release are usually claimed to support such classifications.

This paper examines details of spore release and, contrary to previous reports (e.g. GAYRAL 1965, TATEWAKI 1969), we find the process to be similar in the species studied. Thus all taxa show release of spores through a pore in the sporangial wall, spore movement through the thallus wall matrix, and liberation through regions where the cuticle is absent. In all cases this process is followed by disappearance of the thallus wall on the releasing side, and its retention on the opposite side. In *M. grevillei* emptied gametangia remain on the thallus wall, whereas in other species they are shed (or not resolved).

Anatomical details of releasing sporangia are difficult to resolve. In the rare instances when released sporangia have been found, the morphology is similar (i.e. *M. grevillei* and *M. undulatum*). The previously unreported flared necks on gametangia of *M. grevillei* (c.f. DUBE 1967, Fig. 9, for *Ulvaria*)

Figs. 31-41. *Monostroma oxyspermum*. 31. Field collected plants with saccate juvenile. Scale=150 μm ; 32. Secondary rhizoids from perennating prostrate plant. Scale=40 μm ; 33. Grouping of cells on dried thallus. Scale=40 μm ; 34. Transition area between normal vegetative and rhizoidal cells. Scale=80 μm ; 35. Detail of cells in rhizoidal region. Scale=40 μm ; 36. Biflagellate swimmers. Scale=10 μm ; 37. Cleared margin of released thallus with *Microthamnion kuetzingianum* NAEG. (arrow) Scale=100 μm ; 38. Portion of actively releasing thallus with some sporangia on surface of remaining wall. Arrows indicate remains of sporangial impressions in wall. Scale=100 μm ; 39. As in previous figure. Note outer wall absent. Scale=100 μm ; 40. Three celled sporeling. Scale=10 μm ; 41. Cluster of cultured plants with various developmental stages. Scale=50 μm .

were only seen using material stained with aniline blue. Such structures are of potential phylogenetic importance and may reflect common ancestry with the Ulvaceae.

It is our opinion that the residual *Monostroma* group should be treated as a single genus in which three subgenera (*Monostroma*, *Protomonostroma*, *Gayralia*) may be recognized based on the ontogeny of the blade. The subgenus *Monostroma* has a disc-sac ontogeny as described for *M. grevillei*; the subgenus *Gayralia* has a filament-tube-sac ontogeny as described for *M. oxyspermum*; the subgenus *Protomonostroma* has a filament-blade ontogeny as described for *M. undulatum*. If additional, correlating features are found, these subgenera may warrant generic rank. We feel that too few species have been examined for flagellar ultrastructure (i.e. only *M. grevillei*, *M. bullosum* (ROTH) THURET and *M. oxyspermum*) (review in FLOYD and O'KELLY 1984) to base generic segregation on such features. The taxa examined only include representatives of two of the three subgenera.

If *Monostroma* is monophyletic, then ontogenetic patterns are not as conservative in evolutionary terms as is generally assumed. Laboratory culture of various green algae has demonstrated a range of developmental patterns that are controlled by environmental or apparently stochastic factors. Thus *Urospora* spp. may develop a prostrate habit at high temperatures (KORNMAN and SAHLING 1977, HANIC 1965). TANNER (1979) also reports that *Ulva californica* WILLE in COLLINS *et al.* develops a prostrate system first when grown at high temperatures, and an erect uniseriate filament first when grown under lower temperatures. In addition, TATEWAKI (1969) described the development of three different ontogenies in *Kornmannia zostericola* for plants grown under similar culture conditions. This variation suggests that developmental features may have functional significance, and not provide adequate foundation for segregating higher taxonomic levels (i.e. genera or families).

Given the present absence of data on hy-

bridization and comparative cytology, we contend that wide species concepts are appropriate. By using anatomical and culturing criteria, *Monostroma grevillei*, *M. undulatum* and *M. oxyspermum* are indistinguishable in Europe, Pacific North America and Pacific Asia. Furthermore, given BORASO's (1977) results for *M. undulatum* from Argentina, we predict that many South American and Antarctic species will be conspecific with boreal ones. Such taxa may include *Protomonostroma rosulatum* VINOGRADOVA (1983), *M. hariotii* GAIN (1912), *M. ecuadorenum* TAYLOR, and *M. dactyliferum* TAYLOR (1945).

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L. ゴールデン*・D. ガーベリイ**：ブリチッシュコロロンビア産 *Monostroma* (緑藻ヒトエグサ科) の胞子放出様式を特性とした分類研究

ブリチッシュコロロンビア北部のトリプル島及びマックニコール入江における海藻類の野外観察と培養実験から、*Monostroma grevillei*, *M. oxyspermum* と *M. undulatum* の3種類の生育が確認された。*M. undulatum* は東部太平洋域では、初めての記載である。*M. arcticum* sensu KORNMAN et SAHLING は *M. grevillei* と同種であると思われる。凡ての種類の培養による形態、胞子発芽及び初期発生は、ヨーロッパと日本産のこれらの種での観察と一致した。胞子放出は凡ての種で共通しているが、これは *Monostroma* が一つの自然グループであること示す根拠となり、*Ulvopsis*, *Protomonostroma* 及び *Gayralia* は *Monostroma* としてまとめられる。(*バッグ3670, トリプル島灯台, プリンスルーパット, ブリチッシュコロロンビア, カナダ V8J 3M3 **ブリチッシュコロロンビア大学植物学科, バンクーバー, B. C. カナダ V6T 3B1)。