

The ultrastructure of gametes of *Spongomorpha duriuscula* (Acrosiphoniales, Chlorophyta), with special reference to the flagellar apparatus

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The fine structure of the biflagellate gametes of the multinucleate, septate siphonous green alga, *Spongomorpha duriuscula* (RUPRECHT) COLLINS, was investigated with particular reference to the flagellar apparatus. The gametes have features believed to be most reliable for the taxonomic definition of the Ulvophyceae sensu STEWART and MATTOX, namely the 11/5 o'clock position (counterclockwise) of basal bodies and their associated microtubular rootlets, and the presence of terminal caps. In addition, they have other characters which are presumably shared with some members of the Ulvophyceae; 180° rotational symmetry, basal body overlap, the absence of scales and rhizoplasts, the presence of a one-piece, non-striated capping plate, electron dense material inside basal bodies, striated X-membered rootlet associated bands, the tiny, second proximal connecting fibre, proximal sheaths and a mating structure.

Additional features which have not been reported so far in other green algae are the presence of the third, indistinct proximal fibre and a gap between two anterior triplets of basal body when viewed in cross section.

Key Index Words: Acrosiphoniales; flagellar apparatus; green alga; Spongomorpha duriuscula; ultrastructure; Ulvophyceae.

Studies on cell division and the flagellar apparatus of the green algae by electron microscopy have provided the ultrastructural criteria useful for the modern taxonomy of green algae (e.g. STEWART and MATTOX 1975-1978, STEWART *et al.* 1973, SLUIMAN *et al.* 1983, O'KELLY and FLOYD 1983). However, these features have been investigated less in the septate siphonous green algae (species of the Cladophorales and Acrosiphoniales).

The ultrastructure of mitosis and cytokinesis has been studied in *Cladophora glomerata* (L.) KÜTZING (MCDONALD and PICKETT-HEAPS 1976), *C. flexuosa* (GRIFFITHS) HARVEY (SCOTT and BULLOCK 1976), *Acrosiphonia*

spinescens (KÜTZ.) KJELLM. (HUDSON and WAALAND 1974), and that of the flagellar apparatus in *Urospora penicilliformis* (ROTH) ARESCHOUG (KRISTIANSEN 1974, SLUIMAN *et al.* 1982), *Cladophora* sp. (FLOYD 1981) and *Chaetomorpha spiralis* OKAMURA (HIRAYAMA and HORI 1984).

The order Acrosiphoniales is a group of filamentous, branched or unbranched, uninucleate or multinucleate green algae. The order is small and composed of three genera, *Acrosiphonia* J. AGARDH, *Spongomorpha* KÜTZING and *Urospora* ARESCHOUG. On the basis of the quadriflagellate zoospore ultrastructure of *U. penicilliformis*, it has been suggested that *Urospora* should be assigned

to the Ulvophyceae (SLUIMAN *et al.* 1982), in spite of its unusual microanatomy. Based on the ultrastructural study of the mitosis-cytokinesis in *U. neglecta* and *U. wormskoldii*, LOKHORST and STAR (1983) suggested that *Urospora* can be placed in the Chlorophyceae, since they regarded that *Urospora* has a reduced type of phycoplast, and pose a question about the maintenance of the Ulvophyceae as a separate class.

Study on life history of *Spongomorpha duriuscula* (RUPRECHT) COLLINS by laboratory culture (MIYAJI unpublished observation) has revealed that the filamentous gametophytes of this alga are identical in the morphology of thallus, but dioecious. They produce biflagellate isogametes. In the present study the ultrastructure of the gamete of one sex was examined.

Materials and Methods

The isolate of *Spongomorpha duriuscula* (RUPRECHT) COLLINS used in this study was originally established from zoospores released from green unicellular endophytes (*Chlorochytrium inclusum* KJELLM.) of the red alga, *Rhodophysema* sp. collected on 27 June, 1975, at the coast of Rausu, Hokkaido, Japan, by Dr. Michio MASUDA. Since then unialgal culture has been maintained at 10°C in Provasoli's Enriched Sea Water (PES) medium. Illumination at about 5000 lux is provided by cool-white fluorescent lights on a 16:8 (L:D) photoperiod. The release of gametes is induced by immersing the cultured thallus into fresh medium or lighting the thallus. Fresh gametes have positive phototaxis, and they gather towards the light source. After collecting by centrifugation at ca. 3,000 rpm, they were fixed in 5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.1) containing 0.25 M sucrose for 2-3 h at the room temperature. Then they were rinsed in the same buffer. During this procedure the concentration of sucrose was gradually reduced. The gametes were post-fixed in 2% OsO₄ for 3 h at the room temperature.

Specimens were dehydrated in a graded

ethanol series and embedded in Epon. The materials were sectioned by LKB 8800 ultratome using a diamond knife and double stained with uranyl acetate and lead citrate and examined in Hitachi HU-12A electron microscope.

Results

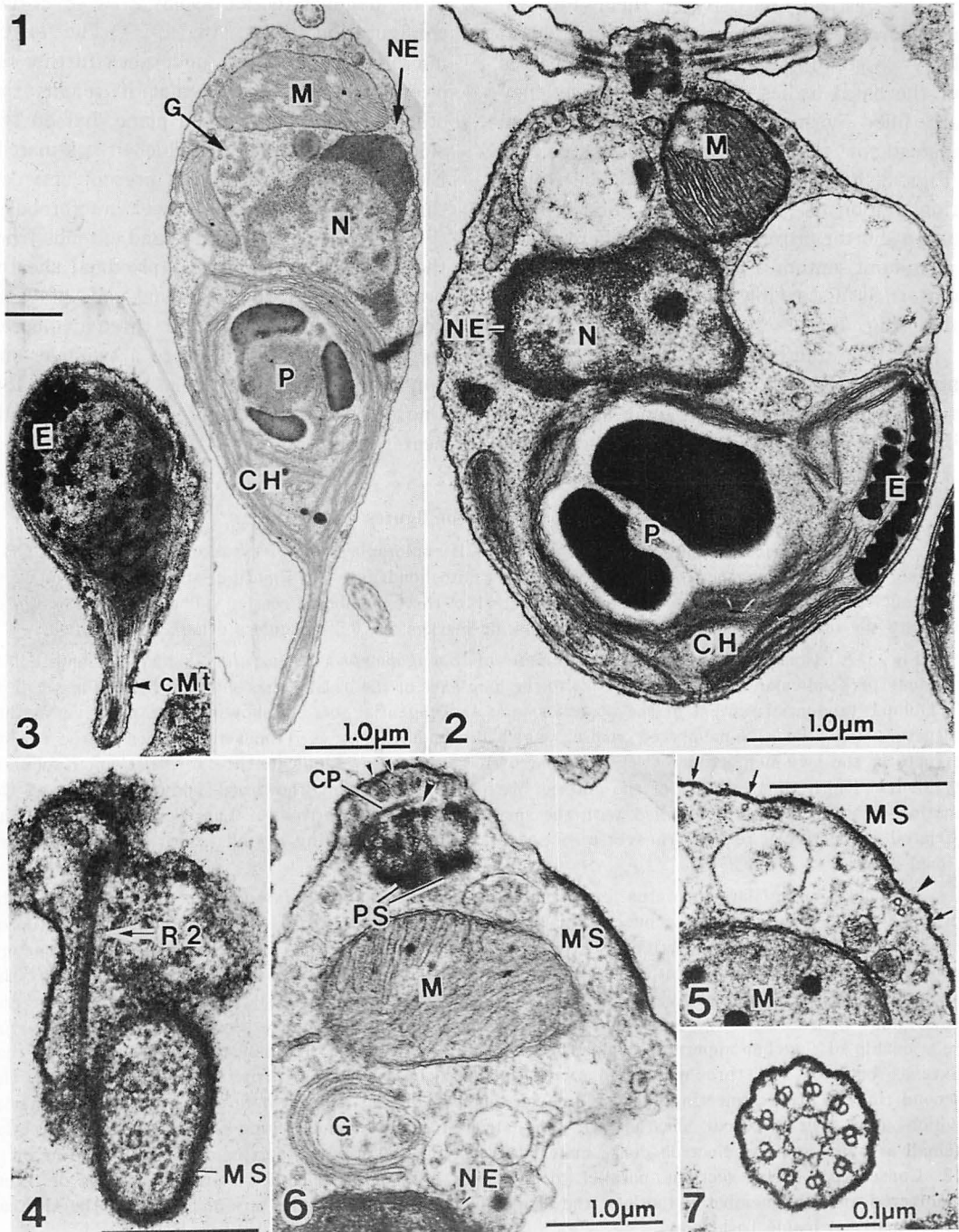
General cell structure: The gametes are oblong or elliptical in shape, approximately 5-7 μm in length, 2-3 μm in width and bear a conspicuous tail (Figs. 1, 3). A papilla present at the cell anterior contains small vesicles filled with electron dense material (Fig. 6). The nucleus is located at the centre of the cell and the lumen of the nuclear envelope is filled with electron dense material (Figs. 1, 2). A single giant mitochondrion with many, well developed cristae lies between the nucleus and the basal bodies (Figs. 1, 2, 6). A golgi body is often found in the area between the nucleus and the mitochondrion (Fig. 6). The endoplasmic reticulum extends from the outer membrane of nuclear envelope, but is poorly developed (not shown). A single cup-shaped chloroplast, situated in the posterior portion of the gamete and extending into the posterior tail (Fig. 1), includes a large central pyrenoid ensheathed by polypyramidal starch plates (Fig. 1). The dense matrix of the pyrenoid is never traversed by thylakoid. The chloroplast also contains an eyespot composed of two layers of closely packed osmiophilic globules (Figs. 2, 21). The eyespot is situated on the lateral surface of the cell in the longitudinal plane passing between the two basal bodies (Fig. 2). The posterior tail of the cell body is filled with cytoskeletal microtubules (Fig. 3) which originate in the vicinity of the flagellar apparatus and extend posteriorly beneath the cell periphery.

Posterior to the basal bodies there is a uniquely differentiated portion of the plasmalemma which is underlaid by a thick layer of electron dense material, 30-50 nm in thickness (Figs. 4-6). This structure protrudes slightly to the rest of the plas-

malemma. Longitudinal and transverse sections indicate that this structure is oval in shape (Fig. 4), measuring 0.8–1.3 μm in length and 0.4–0.7 μm in breadth. This may correspond to the mating structure known in the gametes of *Ulva lactuca* L. (MELKONIAN

1980b). No scales are present on either cell or flagellar surface.

Flagellar apparatus: Two flagella emerge from a papilla, and longitudinal and transverse sections show that their basal bodies lie in the same plane perpendicular to the



longitudinal axis of the cell (Fig. 2). When viewed from the cell anterior, the basal bodies are displaced relative to each other and are oriented at the 11 and 5 o'clock positions (by terminology of ROBERTS *et al.* 1982, MELKONIAN and BERNS 1983) relative to the vertical line between them (Fig. 13) and parallel to the long axis of each basal body (Figs. 13, 14). The proximal halves of the basal bodies are unusual since they are filled with the electron dense material instead of the usual cartwheel structure (Figs. 8, 10b, c, e, 12b, 13b, c). The transition region is composed of a longer distal and a shorter proximal part and there is the prominent septum (Figs. 12b, 13b). A stellate pattern is discernible in the transverse section (Fig. 7).

The four microtubular rootlets are cruciately arranged (Fig. 13). The three-membered rootlets originate from the inner sides of the overlapping basal bodies and are displaced

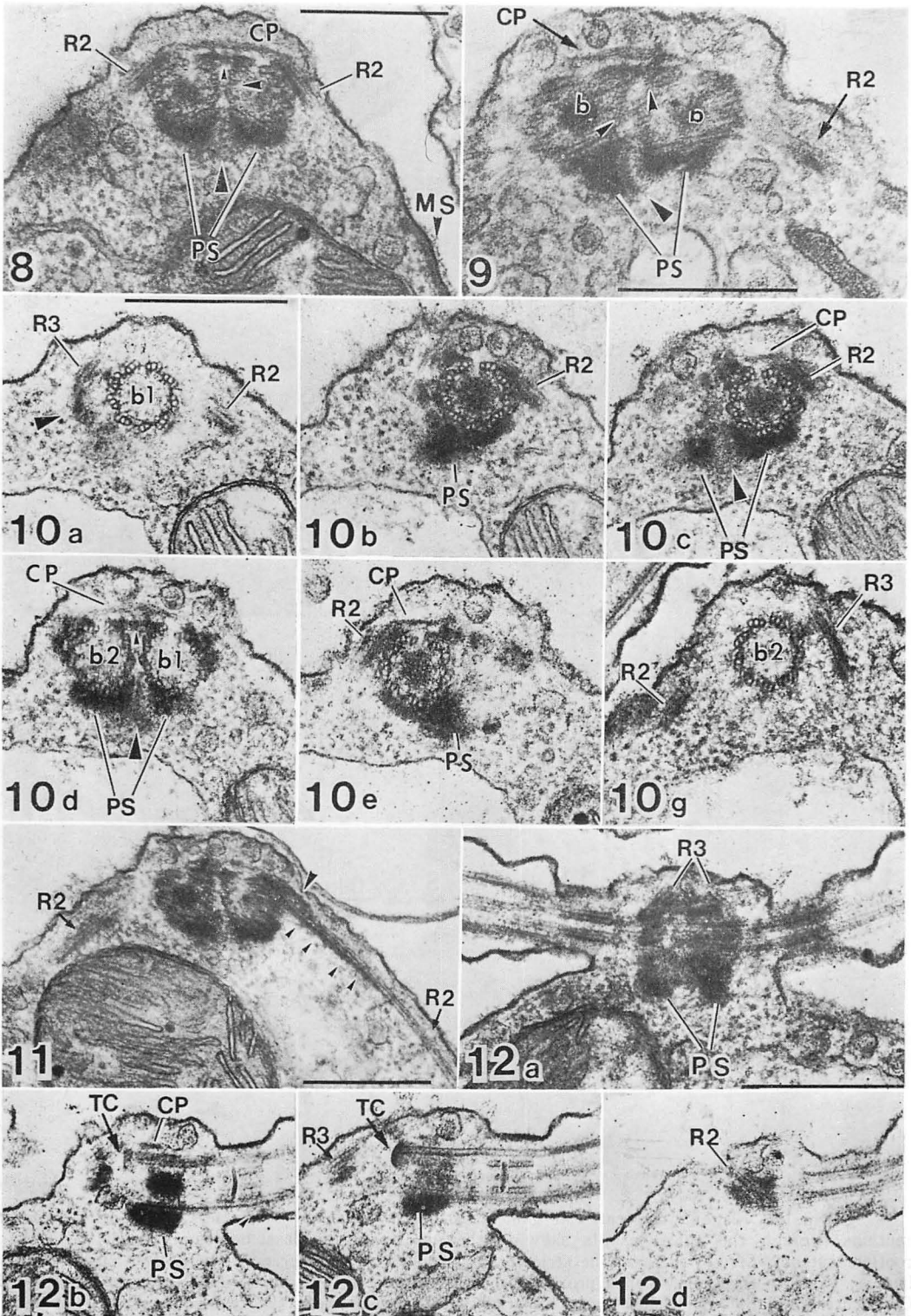
in the 11/5 o'clock configuration (Fig. 14). In the immediate vicinity of the origination, rootlet microtubules lie linearly (Fig. 17), but one microtubule very soon becomes reorientated so that it lies under the other two, thus for some distance transverse sections of the flagellar rootlet display a two-over-one configuration (Figs. 18, 19). The lower microtubule, however, undergoes further reorientation (Fig. 20) so that it rejoins the other two in the original plane, but on the side opposite to that on which it originated. Electron dense material is present between the two upper and the lower microtubules (Figs. 18, 19). A striated band extends from the electron dense material (proximal sheath) present around the proximal ends of basal bodies and attaches to the three-membered rootlets at the point where a two-over-one configuration of microtubules begins (Fig. 18). One of the three-membered rootlets descends near the eyespot (Fig. 21).

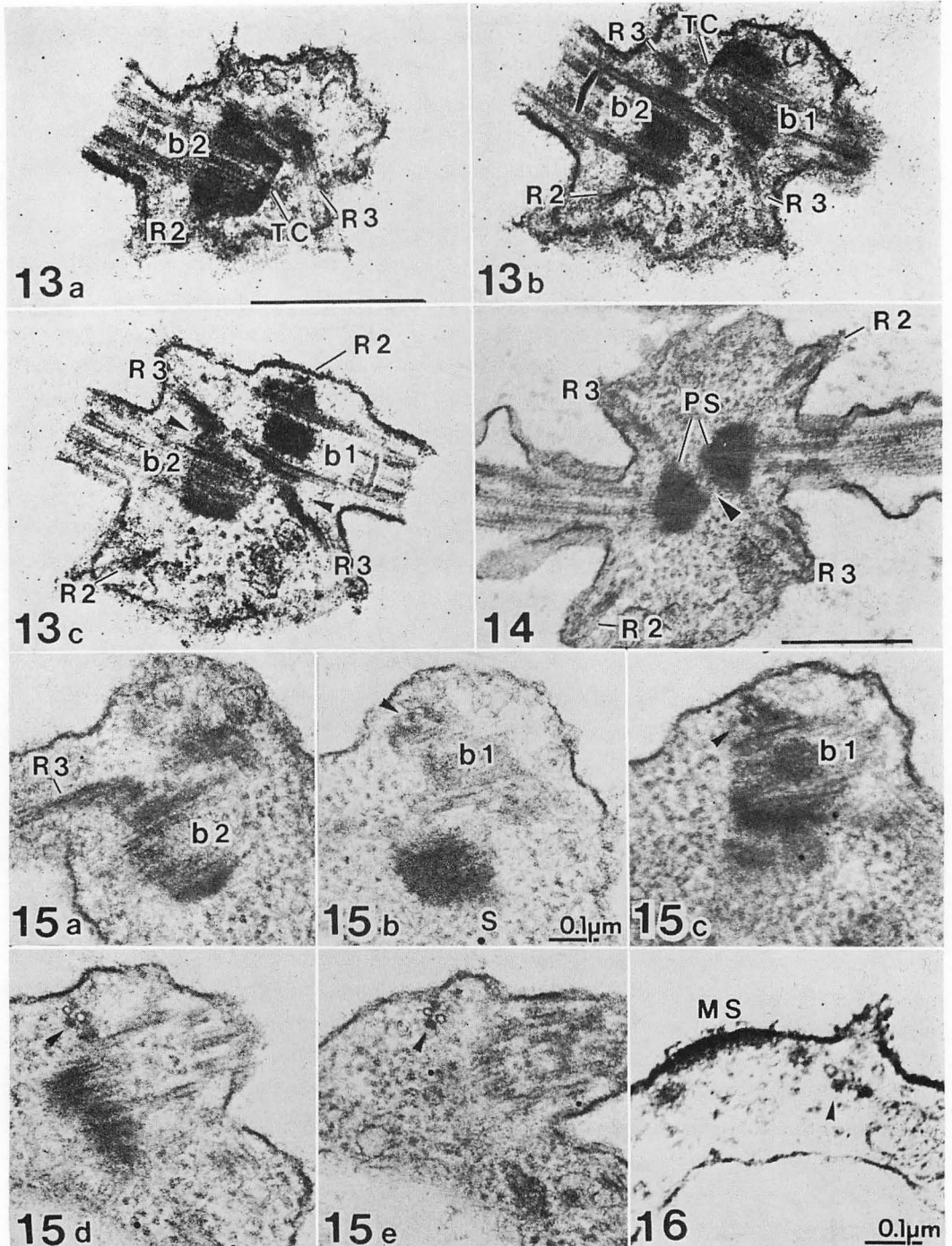
Explanation of figures

Abbreviations used in figures: b=basal body; CH=chloroplast; cMt=cytoskeletal microtubule; CP=capping plate; E=eye spot; G=golgi body; M=mitochondrion; MS=mating structure; N=nuclues; NE=nuclear envelope; R2=two-membered rootlet; R3=three-membered rootlet. The alphabets in figures indicate the order of section in a series. All scale marks are 0.5 μm unless otherwise indicated.

Fig. 1-7. General features of the gamete of *Spongomorpha duriuscula*. 1 and 2. Longitudinal sections perpendicular (1) and parallel (2) to the long axes of the basal bodies showing the cell organelles; 3. Oblique tangential section of the posterior tail; 4. Tangential section showing the putative mating structure and the two-membered rootlet which descends nearby; 5. Transverse section of the mating structure, the two-membered rootlet (large arrow). Small arrows indicate the cytoskeletal microtubules; 6. Median longitudinal section of the anterior part of a cell showing the basal body complex and the mating structure. Papilla is filled with the small vesicles (small arrows). Large arrow indicates tiny striated connective fibre; 7. Transverse section of a flagellum showing a stellate pattern in the transitional region.

Fig. 8-12. Flagellar apparatus in gametes of *Spongomorpha duriuscula*. 8. Section showing the proximal ends of basal bodies connected by a non-striated capping plate, a tiny striated fibre (upper small arrow) and a fine connective fibre (middle arrow). Lower arrow indicates the striated structure connecting two proximal sheaths; 9. Oblique section showing two proximal sheaths connected by the striated structure (lower arrow). Upper arrow indicates the second tiny striated connecting fibre and middle one indicates the third tiny fibre; 10. Consecutive serial transverse sections showing the spatial relationship of flagellar apparatus components. Large arrow in Fig. 10a indicates the striated band that extends between the three-membered rootlet and basal body. Upper arrow in Fig. 10d indicates the second tiny striated connecting fibre and lower arrows in Fig. 10c, d indicate the striated material which joins two proximal sheaths; 11. The striated material underlying the two-membered rootlet (small arrows) and the electron dense material overlaying the proximal portion of rootlet (large arrow); 12. Consecutive serial sections parallel to the long axes of basal bodies showing insertion of three-membered and two-membered rootlets, the shape of proximal sheath, the terminal cap and the electron dense material inside basal body.

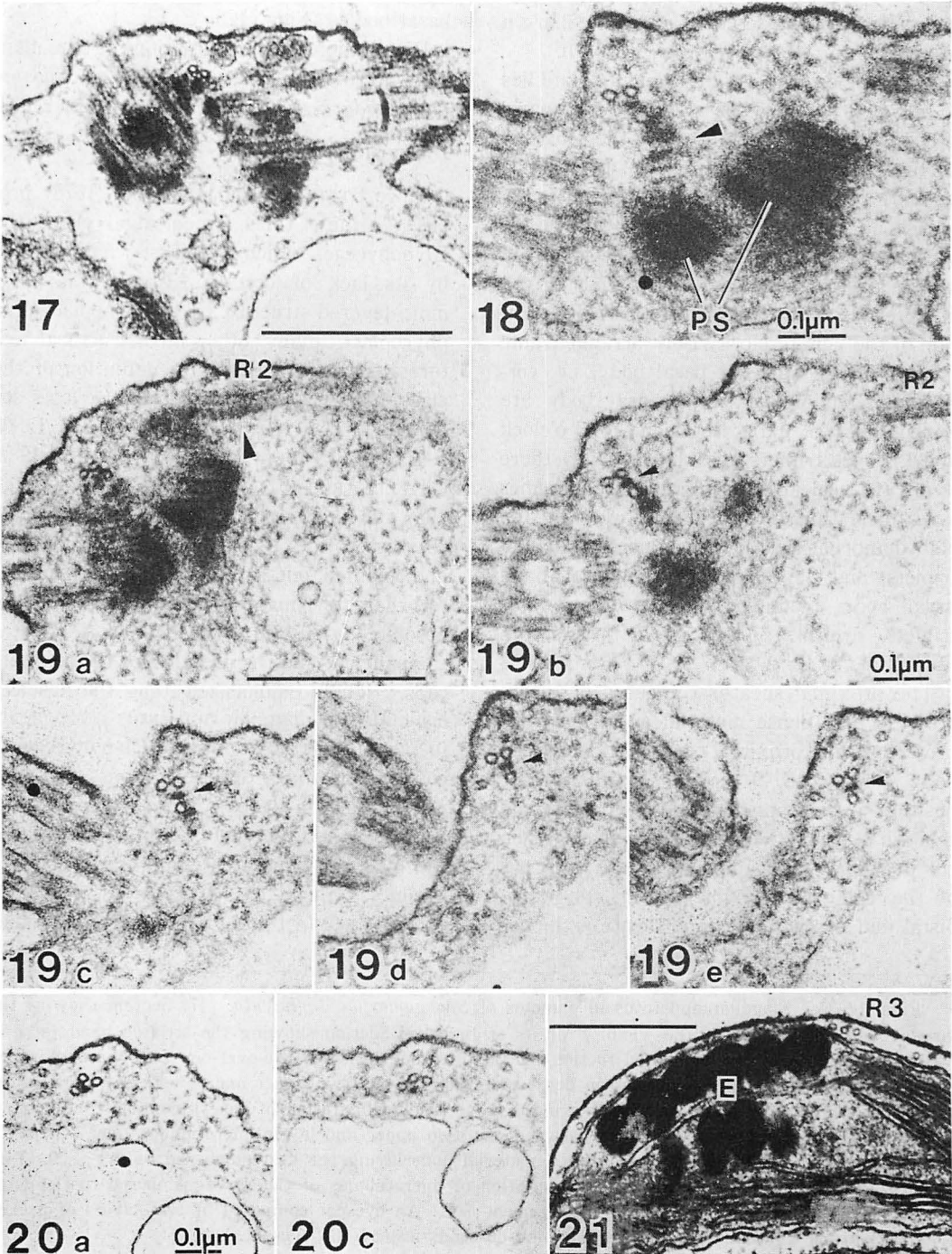




Figs. 13-16. Flagellar apparatus in gametes of *Spongomorpha duriuscula*. 13. Serial transverse sections through the apical papilla showing the overlapping of basal bodies and cruciately arranged rootlet system. Arrows indicate the striated band connecting the three-membered rootlets to the basal bodies; 14. Two triangular-shaped proximal sheaths connected by the striated material (arrow); 15. Consecutive serial sections showing the spatial relationship between the two-membered rootlet and the basal body. Arrows indicate the striated material underneath the two-membered rootlet; 16. Transverse section showing the two-membered rootlet, which descends near the mating structure. The underlying striated material of the two-membered rootlet still remains (arrow).

The two-membered rootlets emanate from the outer sides of the basal bodies (Figs. 14, 15). Two rootlets form a straight line. Striated material underlies two-membered rootlet (Figs. 11, 19a), and ends near the

anterior edge of the putative mating structure (Fig. 16). In addition the proximal part of these rootlets is covered for some distance by an electron dense material (Fig. 11). It starts at a point slightly posterior to the



point of attachment to the basal body (Fig. 15c) and soon bifurcates, part being associated with each microtubule (Fig. 15d). One of them runs for only a short distance over its microtubule, whereas the other extends further posteriorly (Fig. 15e). One of two-membered rootlets descends along the margin of the mating structure (Figs. 4, 5, 16).

A one-piece, non-striated capping plate lies to link two basal bodies at their distal parts (Figs. 8, 9, 10d). In these cells the proximal portions of basal bodies are also joined by a second, more tiny striated fibre. It is attached at one end to the triplet in the 11 o'clock position of the clockwise arranged nine triplets of one basal body, and at the other end to the triplet in the 1 o'clock position of the counterclockwise arranged nine triplets of the adjacent basal body, i.e. corresponding triplets in each basal body are joined (Figs. 8, 10d). Between the 11 o'clock and 1 o'clock triplets in each basal body there is always a clear gap (Fig. 10d). Sometimes it is found that the 9 o'clock triplet of the right-hand basal body (clockwise rotation of triplets) and the 3 o'clock triplet of left-hand basal body (counterclockwise rotation of triplets) are also joined by a further thin fibre (Fig. 8, 9).

The proximal sheaths composed of unstriated electron dense material are closely appressed to the proximal portion of each basal body (Figs. 6, 8, 9, 10b-e, 12a-c). Their position in relation to the basal bodies and relative to each other, and their shape when cut in a plane perpendicular to the long axis of the cell, are shown in Fig. 14. The distal end of each proximal sheath is thicker

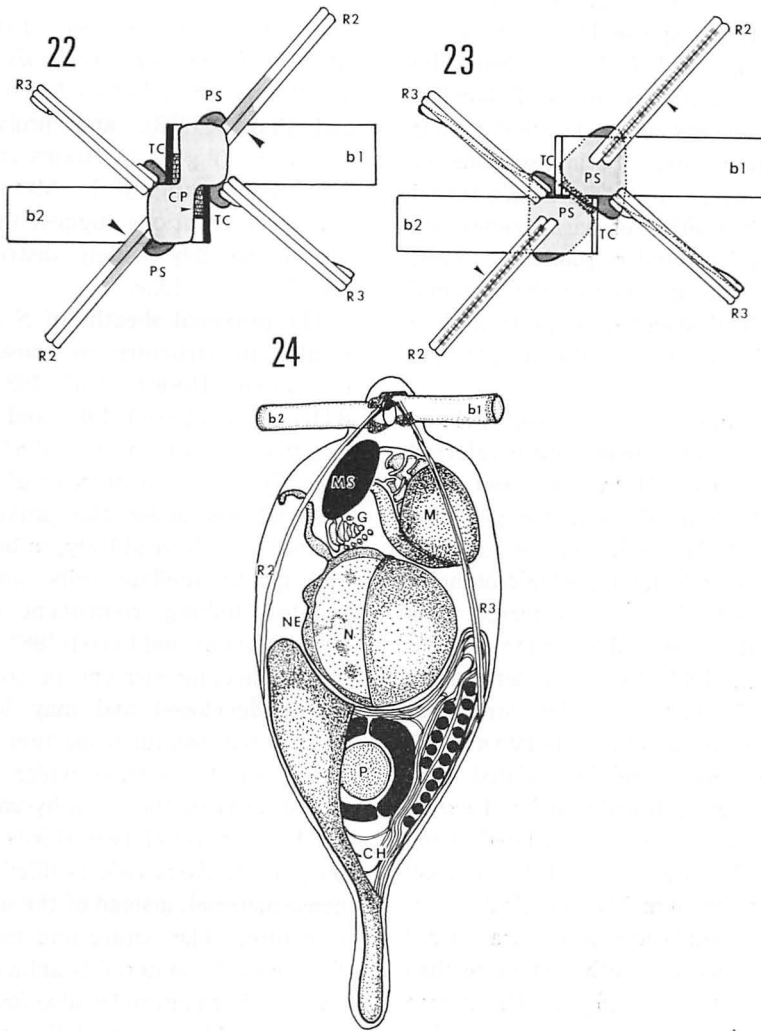
on the inner than on the outer side and curves towards the other basal body (Figs. 10b-e). The two triangular sheaths are connected by the striated material (Figs. 8, 9, 10c, d, 14). Terminal caps are attached to the anterior side of the proximal ends of basal bodies (Figs. 12b, c, 13a, b).

Diagrammatic reconstructions of the flagellar apparatus and the gamete of *Spongomorpha duriuscula* are given in Figs. 22-24.

Discussion

Since STEWART and MATTOX (1978) proposed a new third green algal class, the Ulvophyceae, which was first characterized by its lack of certain features, that is, a multi-layered structure, a phragmoplast or a phycoplast, many other ultrastructural features presumably useful for definition of the class have been suggested (for reviews see HOOPS *et al.* 1982, MELKONIAN 1979 1980b 1981 1982, MELKONIAN and BERNIS 1983, O'KELLY and FLOYD 1983, SLUIMAN *et al.* 1980 1982). O'KELLY and FLOYD (1983) have reassessed the usefulness of those features and pointed out that more reliable features for characterizing the Ulvophyceae are the absolute orientation of flagellar apparatus components, and the presence of the terminal caps. They emphasized that the absolute orientation of flagellar apparatus components in algae referable to the Ulvophyceae is counterclockwise, different from clockwise orientation in the Chlorophyceae *sensu* STEWART and MATTOX. Their concept of the flagellar apparatus configuration closely resembles those of ROBERTS *et al.* (1982) and MELKONIAN and BERNIS (1983), in which

Figs. 17-21. Flagellar apparatus in gametes of *Spongomorpha duriuscula*. 17. Section showing the three-membered rootlet in the vicinity of its origin; 18. Section showing the striated band (arrow) which connects the three-membered rootlet and the proximal sheath. Two-over-one configuration of the three-membered rootlet, and an electron dense material between two upper and lower microtubules are seen; 19. Consecutive serial sections showing two-over-one configuration of the three-membered rootlet. The electron dense material is present between the two upper and lower microtubules (small arrows). Large arrow in Fig. 19a indicates a striated material underlying the two-membered rootlet; 20. Two sections from a series showing the reorientation of microtubules of the three-membered rootlet from two-over-one configuration to a linear arrangement; 21. An eyespot composed of two layers of packed globules and the three-membered rootlet which descends nearby the eyespot.



Figs. 22-24. Diagrammatic representations of the flagellar apparatus and the gamete of *S. duriuscula*; 22. The flagellar apparatus viewed from the anterior of the cell. Small arrow indicates the second tiny striated connecting fibre. Large arrows indicate the electron dense material over the two-membered rootlet; 23. The flagellar apparatus viewed from the anterior of the cell, but this drawing illustrating transparently the posterior part of the flagellar apparatus. Arrows indicate the striated material underneath the two-membered rootlet. For simplicity, the striated bands connecting the three-membered rootlets to the proximal sheaths have been omitted in both figures; 24. Diagrammatic representation of the positional relationships among the flagellar apparatus, mating structure, eyespot and other cell organelles in the gametes.

the configuration of the basal bodies in the Ulvophyceae is described as being "the 11/5 o'clock" arrangement. The main difference between two definitions is that the former takes into consideration the arrangement of the basal bodies and associated microtubular rootlets in quadriflagellate as well as biflagel-

late cells, while the latter is concerned only with the biflagellate cells. HIRAYAMA and HORI (1984), however, found the different absolute orientations between two pairs of basal bodies in the quadriflagellate zoospore of *Chaetomorpha spiralis* OKAMURA, that is, 11/5 o'clock in the upper pair of basal bodies

and 1/7 o'clock in the lower pair of basal bodies. Thus, they suggested that the designation 11/5 o'clock and 1/7 o'clock should be applied to the respective pairs of flagellar apparatus components when describing their absolute configuration. Serial sections of biflagellate gametes of *S. duriuscula* reveal the 11/5 o'clock position of basal bodies and X-membered microtubular rootlets. This, together with the presence of the terminal caps and proximal sheaths, suggests a close affinity of *S. duriuscula* with the ulvophycean algae.

It has been suggested that the tiny striated fibrous band is found in many algae referred to the Ulvophyceae (HIRAYAMA and HORI 1984). The band extends from the proximal posterior end of the basal body and specifically attaches to the X-membered microtubular rootlet. This band is usually referred to as the system II fibre (MELKONIAN 1980a, ROBERTS *et al.* 1981 1982) as defined by MELKONIAN (1980a); but the structures named as the lateral fibre (SLUIMAN *et al.* 1982), spindle-shaped straight striated fibre (HERTH *et al.* 1981), broadly striated extension (HOOPS *et al.* 1982), striated band (O'KELLY and FLOYD 1983) or "SB2" (STUESSY *et al.* 1983) are presumably identical to it. These striated bands are also characterized by their shortness in length (not more than 1 μm long, mostly 0.2–0.6 μm) (HIRAYAMA and HORI 1984). In contrast the typical system II fibre, the rhizoplast, approaches the cell surface or the nucleus (MELKONIAN 1980a) and is much longer (1.1–5.2 μm in length) (for a review see HIRAYAMA and HORI 1984). The striated band found in *S. duriuscula* agrees with the criteria summarized above.

The flagellar apparatus of *S. duriuscula* has other characteristics worth to mention, although their diagnostic and phylogenetic implications are not yet clear. The tiny basal body connecting band present in this alga is striated and links single triplets of the adjacent basal bodies at their proximal ends. Since such a connecting band was first observed in the male gamete of *Bryopsis maxima* (HORI 1977), it has been reported to

occur in *Derbesia tenuissima* (ROBERTS *et al.* 1981), *Pseudobryopsis* sp. (ROBERTS *et al.* 1982), *Friedmannia israelensis* (MELKONIAN and BERNS 1983), *Entocladia viridis* (O'KELLY and FLOYD 1983), and probably *Ulvaria oxysperma* (fig. 14 in HOOPS *et al.* 1982) and *Ulva lactuca* (fig. 10 in MELKONIAN 1979). These observations suggest that this structure is possibly widely distributed in the ulvophycean algae.

The proximal sheaths of *S. duriuscula* are similar in structure to those of *Ulvaria oxysperma* (HOOPS *et al.* 1982), *E. viridis* (O'KELLY and FLOYD 1983) and *Enteromorpha intestinalis* (STUESSY *et al.* 1983) and *Urospora penciliformis* (SLUIMAN *et al.* 1982). This material lies under the proximal posterior surface of each basal body, in both biflagellate and quadriflagellate cells, and there is a striated linking component (HOOPS *et al.* 1982, O'KELLY and FLOYD 1983). The sheaths and connecting element in some algae are poorly developed and may be easily overlooked, but careful inspection will probably reveal in due course wider occurrence of the sheaths in the Ulvophyceae.

About proximal two thirds of the basal body in *S. duriuscula* is filled with electron dense material, instead of the usual cartwheel structure. The nature and functional significance of the material is unknown at present, but a similar material is also found in *Ulvopsis grevillei* (MOESTRUP 1978) and *E. viridis* (O'KELLY and FLOYD 1983).

Acknowledgement

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Note added in proof,

Since this paper was prepared, an article containing relevant information on the flagellar ap-

paratus of the gametes of *Acrosiphonia arcta* and *Urospora gregaria* has appeared (FLOYD and O'KELLY, Amer. J. Bot., 71: 111-120, 1984).

宮地和幸*・堀 輝三**：緑藻類モツレグサの配偶子の微細構造，特にその鞭毛装置について

有隔多核緑藻モツレグサ (*Spongomorpha duriuscula*) の双鞭毛性配偶子の細胞構造，特に鞭毛基部装置を調べた。この配偶子はアオサ綱 (sensu STEWART and MATTOX 1978) の定義に現在最も有効と考えられている次のような形質を有していた：(1) 2 個の鞭毛基部とそれに付属する 2 組の微小管性鞭毛根系の 1 組の反時計方向にずれた 11/5 時配列，(2) ターミナル・キャップ構造の存在。さらに，この配偶子はアオサ綱に所属すると考えられている藻のいくつかと共通する形質も有している。それらは 180° 回転対称性，鞭毛基部の部分的なかさなり，鱗片およびリゾプラストの欠損，無紋性鞭毛基部結合構造，鞭毛基部内電子密度物質，X 本微小管性鞭毛と鞭毛基部とを結ぶ有紋繊維帯，第二鞭毛基部結合繊維，鞭毛基部鞘構造および配偶子接合構造の存在，等である。

また，本研究では他の緑藻類では従来知られていなかった特徴もいくつか明らかになった。(*274 千葉県船橋市三山 2-2-1, 東邦大学理学部生物学教室 **305 茨城県新治郡桜村天王台 1-1-1 茨波大学生物科学系)