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Cell structure of an unusual chrysophyte *Phaeaster pascheri* with particular emphasis on the flagellar apparatus architecture

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Phaeaster pascheri SCHERFFEL was examined with the fluorescent and electron microscopes. Chloroplast lacks both girdle lamella and genophore, and chloroplast DNA is of scattered or strand-like. The short flagellum is bulbous and situated in the flagellar pocket to which the eyespot is closely associated. The eyespot is disposed at the tip of a particular process arising from the base of star-shaped chloroplast. Configuration of basal bodies, flagella and microtubular flagellar roots is unusual. Both the long and short flagella extend towards the swimming direction, anterior direction, forming an acute angle of ca. 45°. This is interpreted as that rotation of basal bodies and associated roots may have occurred in the evolution of the chrysophytes. Two microtubular roots associated with the long flagellum extend anteriorly just beneath the bottom of the flagellar groove. One of these, three stranded root showing clockwise path, is responsible for organization of microtubules, and cytoskeletal microtubules are seen arising from this root and extend up along the flagellar groove. Two microtubular roots associated with the short flagellum extend also anteriorly along the mouth of the flagellar pocket. Observation of serial sections showed that mitochondrion is single and ring-shaped.

Key Index Words: absolute configuration—chloroplast DNA—Chrysocapsaceae—Chrysophyceae—flagellar apparatus—Phaeaster pascheri.

HIBBERD (1976) described the class Chrysophyceae by illustrating motile cell organization. The components of chrysophyte cells were reviewed later by PIENAAR (1980) and KRISTIANSEN (1986), in which the same cell organization as Hibberd's was emphasized as a basic form of chrysophyte cells. HIBBERD (1986) in a discussion on some algal groups such as prymnesiophytes, silicoflagellates, pedinellids and choanoflagellates as well as some aberrant chrysophyte-allied genera such as *Olisthodiscus* and *Bicosoeca* suggested that removal of these algae leaves a well-defined natural group. ANDERSEN (1987) who recently established the Synurophyceae for silica scale-bearing chrysophytes such as *Synura* and *Mallomonas* described the Chrysophyceae *sensu stricto* using various features including morphology, chemical composition and life cycle. The Chrysophyceae now seems to be a clear-cut taxon; it is a very diverse algal group however, and contains algae of various life forms such as flagellate, palmelloid, coccoid, amoeboid, plasmodial, sarcinoid, filamentous and parenchymatous. To understand natural affinities between taxa in such a diverse group, detailed studies on motile cell organization would be very useful. The taxonomic relevance of the flagellar apparatus ultrastructure has been emphasized for green algae (for bibliography see e.g. MATTOX and STEWART 1984). In the chromophytes, brown algae and some allied algae have been studied from this point of view (e.g. MOESTRUP 1982, O'KELLEY and FLOYD 1985). In contrast, few studies have focused on the flagellar apparatus of the chrysophytes, and *Poterioochromonas* (SCHNEPF *et al.* 1977) and *Hibberdia magna* (ANDERSEN, 1989) are the only species for which structure of the flagellar apparatus has been revealed in

enough detail. Information is too limited to understand natural affinities and taxonomic relationships between various taxa in the chrysophytes, and many more taxa should be investigated.

Phaeaster pascheri SCHERFFEL is a unique alga in the class by its very compressed cell body and its star-shaped chloroplast (BELCHER 1969). This is a palmelloidal colony-forming chrysophyte and is generally accommodated in the Chrysocapsaceae, an assemblage of palmelloidal or gloeocystoidal chrysophytes which produce *Chromulina*-type motile cells (BOURRELLY 1957, 1968, STARMACH, 1985). Since its original description, the general features of colonial and motile forms of this alga have been studied by BELCHER (1969) and BELCHER and SWALE (1971). However, cell organization, including the flagellar apparatus, has not been described in enough detail to allow comparison with other chrysophyte algae. In this paper we will describe features of motile cells of *P. pascheri* which have not been mentioned before. Then, based on comparison of available data for other chrysophytes, we will discuss the taxonomic relevance of several features, especially of the flagellar apparatus in the Chrysophyceae.

Material and Methods

Culture: Motile and palmelloidal cells of *Phaeaster pascheri* were obtained from mud sample collected from Shishizuka pond in Tsuchiura, Ibaraki Prefecture, Japan on 14 April 1987. They were isolated by micropipettes and cultured in AF-6 medium (KATO 1981) modified by the addition of 5 mg/*l* $NaSiO_3 \cdot 9H_2O$ and 5 m*l* soil extract to 1 *l* of medium. The cultures were maintained at 15°C and a 12 : 12 LD cycle at 3,000 lux provided by white fluorescent tubes.

Fluorescent microscopy: Autofluorescence of chlorophyll was observed to define morphology of the chloroplast. For observation of chloroplast DNA, 0.5 m*l* of cell suspension was mixed with solution containing 1.25% glutaraldehyde and 4′,6-diamidino-2-phenylindole (DAPI) (12 μg/m*l*) prepared in NS buffer (KUROIWA *et al.* 1981). Cells were then crushed on the cover slide and viewed with a fluorescence microscope (Olympus BHS-RFK) under UV excitation.

Electron microscopy: Material for sectioning was fixed in a mixture of 1% glutaraldehyde, 0.5% osmium tetroxide in 0.1 M cacodylate buffer containing 0.1 M saccharose (pH 6.8) at 4°C for 2 hours. The fixative was prepared just before the fixation was undertaken. After dehydration in a graded ethanol series, followed by a transfer to propylene oxide, the cells were embedded in resin (SPURR 1969). Thin sections cut with a diamond knife were double stained with 2% aqueous uranyl acetate and Reynolds' lead citrate (REYNOLDS 1963) and viewed with a JEOL 100CXII transmission electron microscope.

Results

General features: Illustrations of the motile cell of *Phaeaster pascheri* are given in Fig. 1, by which the general cell organization obtained from our observations can be understood. Light micrographs (Figs. 2, 3) are also helpful. In side view, the cell is heart-shaped, and one flagellum emerges from the convex side of the cell (Figs. 1a, 2), where there is a flagellar groove (Fig. 1b). The cell is elliptical in plane view (Figs. 1b, 3). The organization of the cell is not typical for the chrysophytes, and requires designation of cell orientation for description. The position of the cell where a visible flagellum arises is similar to that of brown algae and a raphidophyte *Olisthodiscus luteus* and is thus designated as the ventral side, and the opposite as the dorsal side, as it is usually called in these algae (O'KELLY and FLOYD 1984, HARA *et al.* 1985). The direction to which the flagellum extends and the cell swims is designated as anterior and the opposite as posterior. Lateral sides are called right and left sides. These orientations are indicated in Figs. 1a and b.

Fig. 4 is a section cut in a plane parallel to

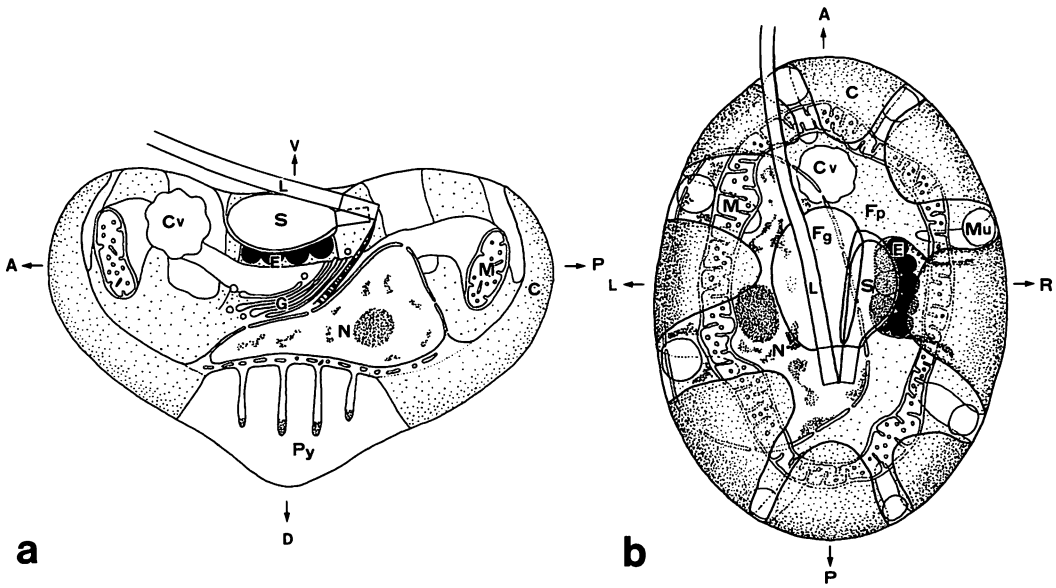


Fig. 1. Diagrammatic representation of the cell in which the general cell organization is shown. a. Half cell viewed from left side of the cell. Both the long and short flagella extend anteriorly. b. Cell viewed from ventral side. Note that the chloroplast is lobed ventrally and a special process is in contract with the flagellar pocket where the short flagellum is ensheathed. Note also the single ring-shaped mitochondrion. Illustrations not to scale. **Abbreviations used in figures:** 1, 2, 3, 4: microtubular roots R1, R2, R3 and R4; A: anterior basal body; A with arrow: anterior direction of the cell; C: chloroplast; Cv: contractile vacuole; Cb: connecting band; cMT: cytoskeletal microtubules; D: dorsal direction of the cell; E: eyespot; Fg: flagellar groove; Fp: flagellar pocket; G: Golgi body; L: long flagellum; L with arrow: left direction of the cell; M: mitochondrion; Mu: mucocyst; N: nucleus; P: posterior basal body; P with arrow: posterior direction of the cell; Py: pyrenoid; R with arrow: right direction of the cell; Rh: rhizoplast; S: short flagellum.

the anterior-posterior axis and perpendicular to the dorsi-ventral axis. Fig. 6 is a similar section but cut through the dorsi-ventral axis. Fig. 7 is cut in a plane parallel to the left-right axis and the dorsi-ventral axis. These sections give a three-dimensional image of the cell organization including organelle configurations illustrated in Fig. 1. The ring-shaped mitochondrial profile in Fig. 1b was based on serial sections of whole cells which are not shown here.

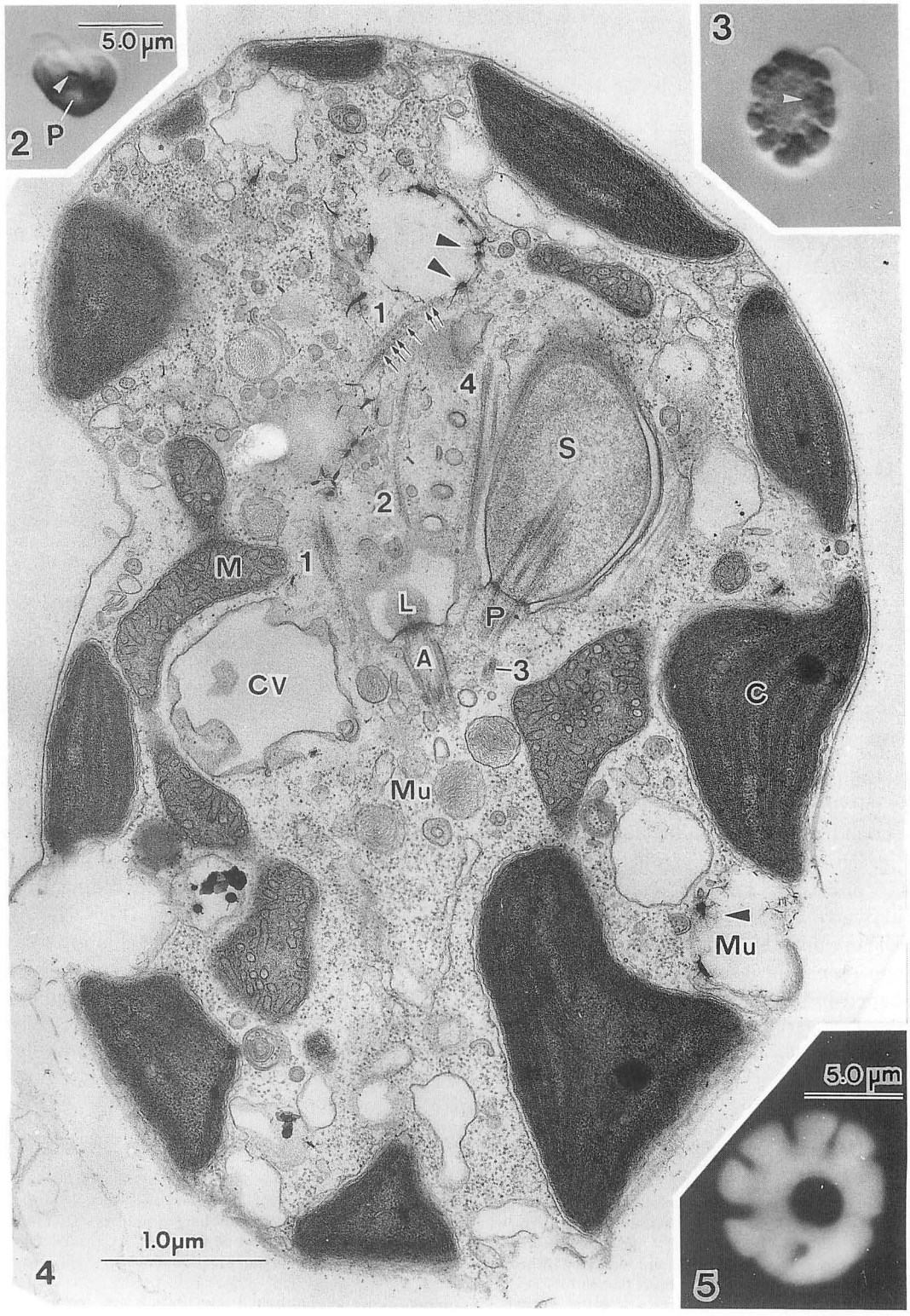
There is a shallow groove with a flat bottom (Fig. 7), the flagellar groove, at the ventral side of the cell from where a long flagellum emerges anteriorly (Figs. 4, 6, 17–22). Many coated pits and vesicles are scattered near the plasmalemma of this region (Figs. 18–20, 28). At the right side of the flagellar groove is a pocket, called the flagellar pocket, in which another hidden flagellum, the short flagellum, is accommodated (Figs. 4, 7, 14–24). The mouth of the flagellar pocket is a narrow slit,

(p. 14)

Figs. 2 and 3. Light micrographs of the cell viewed from left (2) and ventral (3) sides (same magnifications). Arrowheads indicate eyespots.

Fig. 4. Longitudinal section of the cell cut parallel to the anterior-posterior axis and perpendicular to the dorsi-ventral axis. Peripherally located chloroplast lobes, mitochondrial profiles, contractile vacuole and mucocysts with or without content are seen. Arrowheads indicate fibrous material in discharged mucocysts. The long and short flagella, their basal bodies and associated four microtubular roots are seen. Cytoskeletal microtubules arising from R1 are indicated by arrows. Note that no indication of the transitional helix is visible in the transition region of the short flagellum.

Fig. 5. Fluorescence microscopy of the cell. Autofluorescence of chlorophyll directly indicates the morphology of the chloroplast. It is star-shaped and the pyrenoid region is seen as a black space at the center.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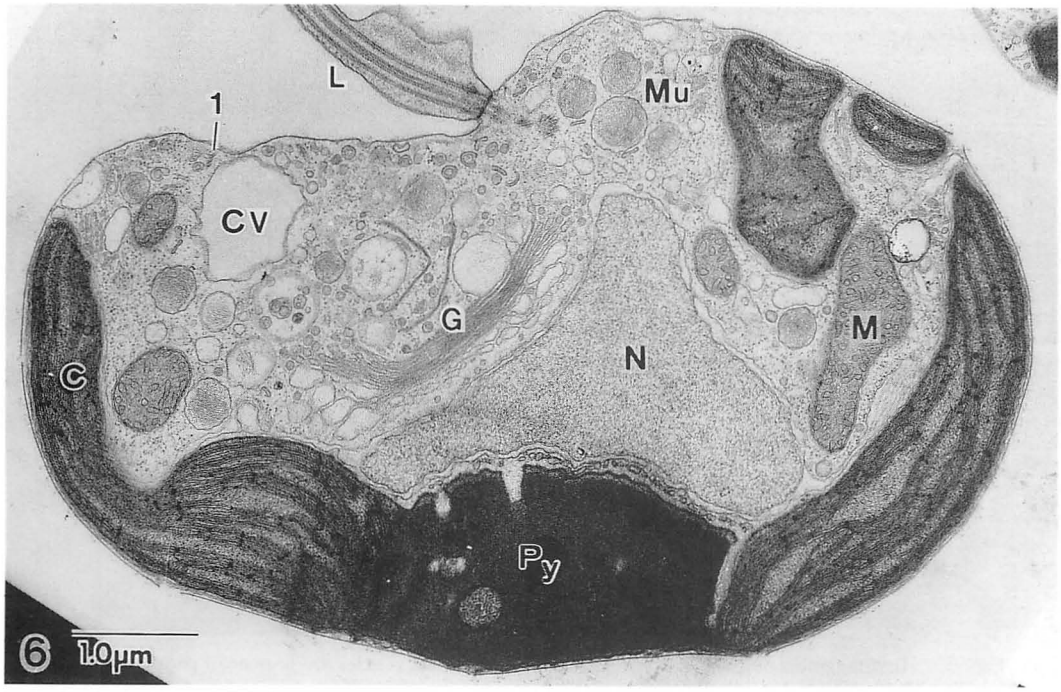
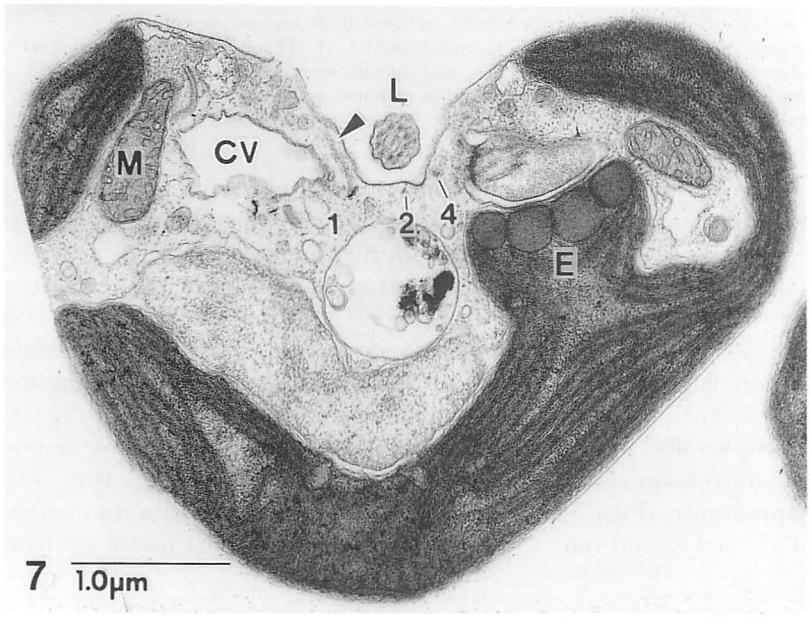




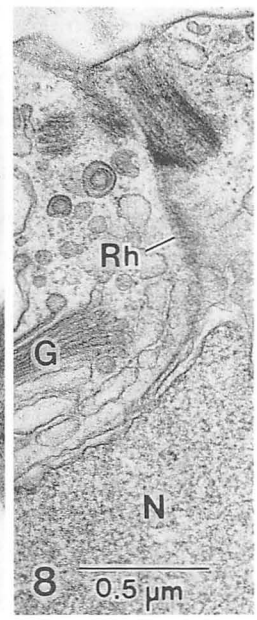


Fig. 6. A cell cut parallel to the anterior-posterior axis and dorsi-ventral àxis of the cell. The long flagellum is obliquely arising from the cell. Transitional helix gyres are visible. The chloroplast is cup-shaped, and at the base is a pyrenoid with tubular grooves penetrated from the ventral side. The nucleus is in contact with the pyrenoid region and its outer membrane is continuous with the chloroplast endoplasmic reticulum. Golgi body is situated at the anterior side of the nucleus. Contractile vacuole, R1, mucocysts and mitochondrial profiles are also visible.

Fig. 7. A cell cut parallel to the dorsi-ventral axis and left-right axis of the cell. Flagellar groove with flat bottom, and transverse sections of three microtubular roots are visible. Cytoskeletal microtubules (arrowhead) arise from R1. The short flagellum is ensheathed in the flagellar pocket to which a process of the chloroplast with conspicuous eyespot is attached.

Fig. 8. A striated root, rhizoplast, connects the basal body complex and the nucleus.

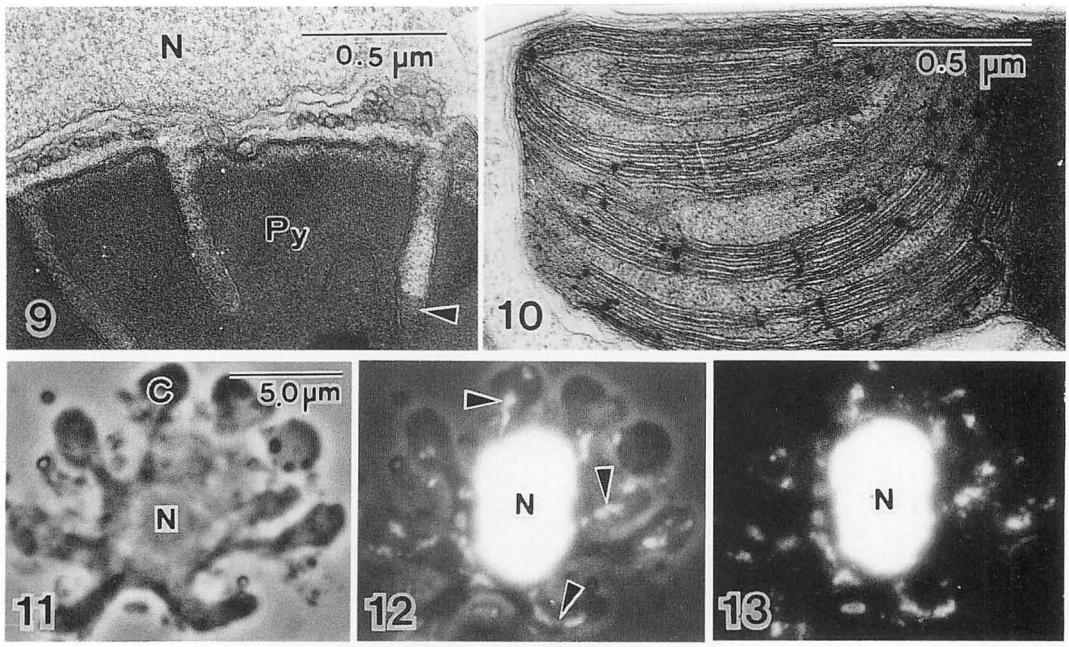


Fig. 9. High-magnification of the pyrenoid region. Numerous vesicles are present in periplastidal space. Note electron dense material in tubular groove of the pyrenoid (arrowhead).

Fig. 10. Part of chloroplast. Note that both girdle lamella and genophore are not present.

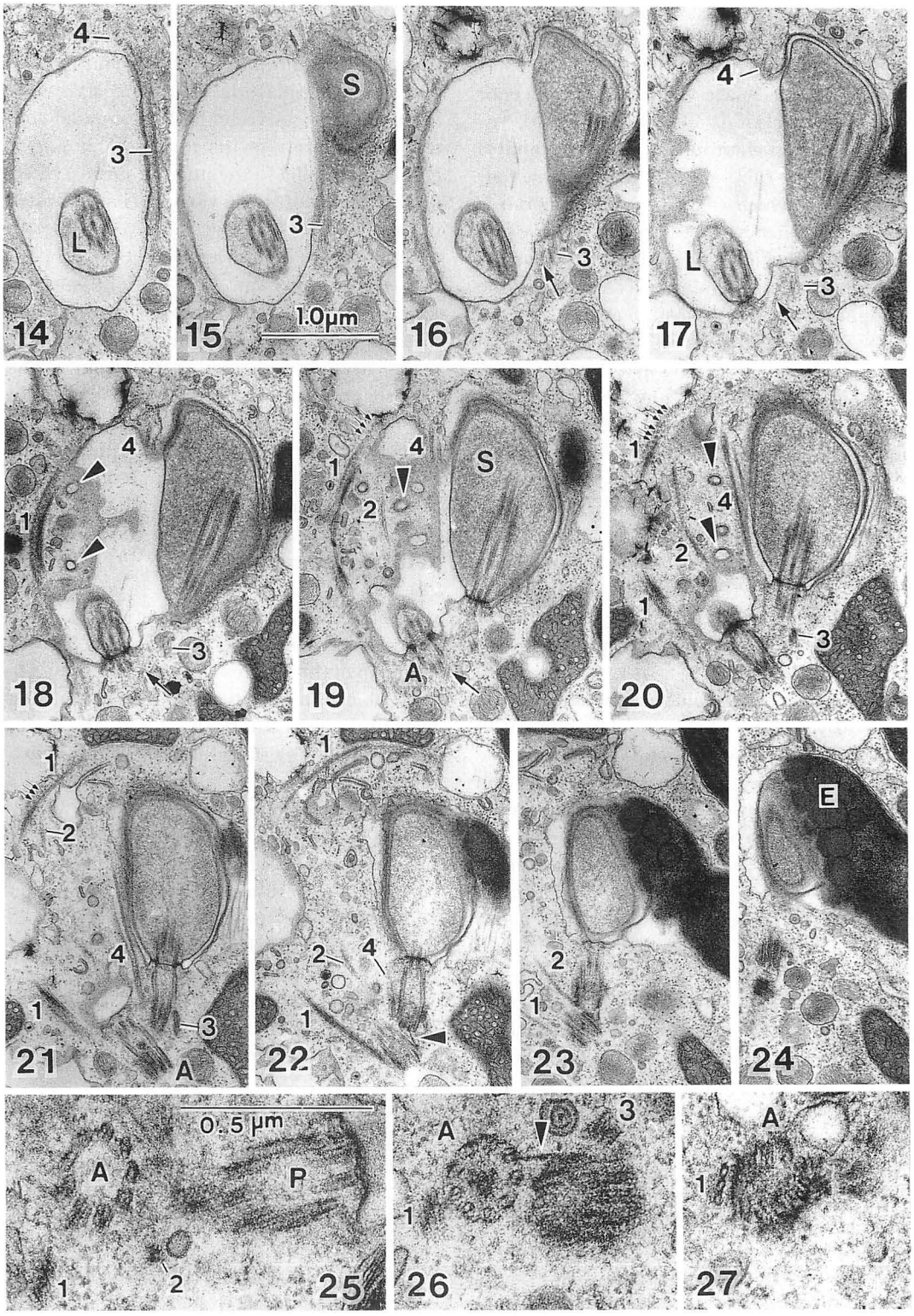
Figs. 11–13. Micrographs of a crushed cell (same magnifications). 11. Phase contrast. Star-shaped chloroplast and the centrally located nucleus are seen. 12. Phase contrast with superimposed fluorescence of DNA stained with DAPI. Chloroplast nucleoids are scattered or strand-like aligned in the lobes (arrowheads) and not ring-shaped. 13. Fluorescence only.

ca. 200–300 nm wide (Figs. 30, 31). The short flagellum is bulbous and ca. 1 μm in diam. so that it never emerges outside the flagellar pocket; this, together with a conspicuous eyespot situated close to the flagellum (Figs. 7, 22–24, 30, 31), makes it difficult to observe the short flagellum with the light microscope (Figs. 2, 3).

The chloroplast is peripherally located (Figs. 6, 7). Fluorescence microscopy clearly shows its star-shaped appearance (Fig. 5). Lobes are variable, 6 to 13, and extend ventrally along the periphery of the cell (Figs. 3, 4). Beside these peripheral lobes, a process arises from right inner side extends ventrally and reaches to the dorsal side of the flagellar pocket (Fig. 7). At the tip of this particular process is an eyespot comprising of a single layer of pigmented globules juxtaposing the contour of the flagellar pocket (Figs. 7, 22–24, 30, 31). Chloroplast lamellae are mainly made up of three thylakoids (Fig. 10). The dorsal side of the chloroplast is a transparent region that can be observed under the light

Figs. 14–24. Consecutive serial sections of the flagellar apparatus cut from the ventral towards dorsal side of the cell. Orientation of the flagella, basal bodies and microtubular roots can be traced. Note that these basal bodies are interlinked by a proximally located connecting band (Fig. 22 arrowhead). Association of the short flagellum with eyespot is also seen. Large arrows in 16–19 indicate one of R3 microtubules extending and in contact with the anterior basal body. Cytoskeletal microtubules arising from R1 are indicated by small arrows in 19–21. There are coated pits or vesicles scattered around the flagellar groove (arrowheads in 18–20). Magnifications the same as Fig. 15.

Figs. 25–27. Three of a series of serial sections of the anterior and posterior basal bodies. Micrographs are printed as to be viewed from the posterior side of the cell. Path of R1 and the connecting band (arrowhead) are shown. R1 is made up of three stranded microtubules at its proximal end (Fig. 27). Profiles of R2 (Fig. 25) and R3 (Fig. 27) are also visible. Magnifications the same as Fig. 25.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microscope (Fig. 2). This is a pyrenoid (Fig. 6) as has previously been demonstrated by BELCHER and SWALE (1971), and is seen as a black circular space when autofluorescence of the chloroplast is observed (Fig. 5), indicating lack of chlorophyll. The pyrenoid is penetrated by tubular grooves from the ventral side, in which electron dense material is deposited, but never penetrated or traversed by thylakoids (Figs. 6, 9). The girdle lamella and ring-like chloroplast DNA region, the genophore, both typical features of the chrysophytes (GIBBS *et al.* 1974, COLEMAN 1985), have never been observed in *P. pascheri* (Figs. 4, 10). Lack of the genophore was confirmed using DAPI-stained material. Figures 11–13 are micrographs of a crushed cell, in phase contrast, phase contrast plus superimposed fluorescence of DAPI and fluorescence only. These figures indicate that the chloroplast DNA does not form a ring-shaped profile but is scattered in the lobes. The fluorescence of DAPI in the chloroplast is often seen as slender strands parallel to the lobes (Fig. 12).

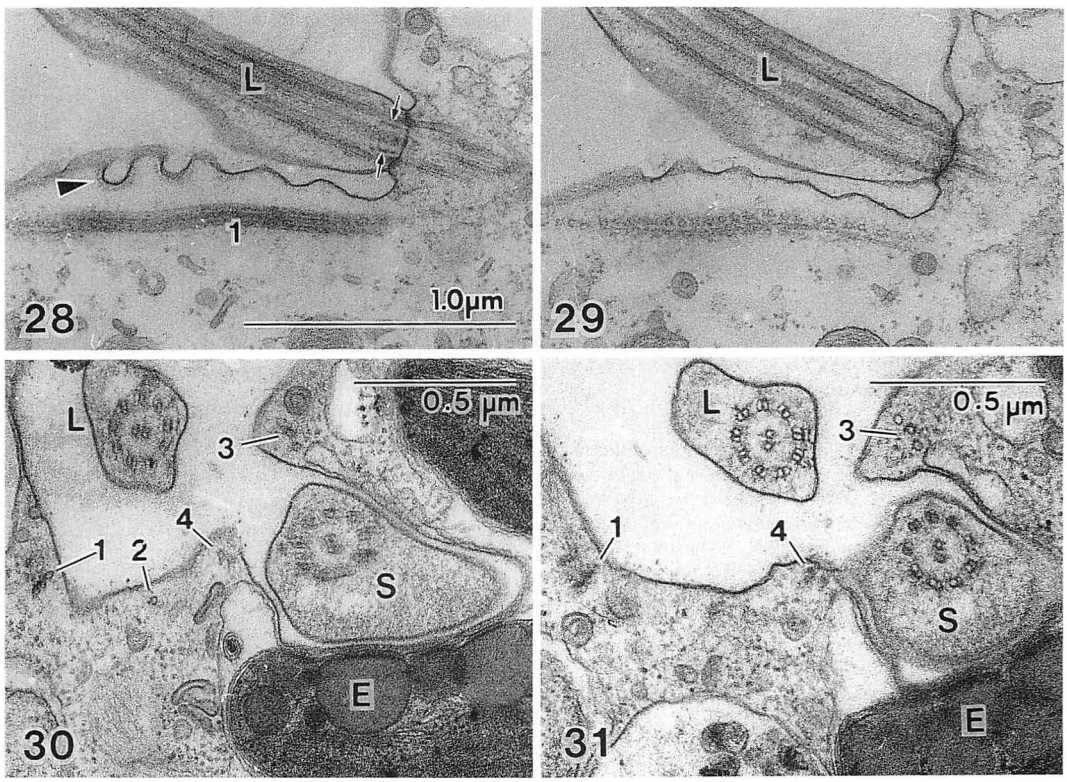
The space between chloroplast lobes are occupied by vesicles (Fig. 4). The content of these almost empty vesicles may have dissolved away during preparation for electron microscopy. However, some vesicles contain residue of a fibrous material (Fig. 4) that seems to be of the same nature as that in small vesicles scattered around the Golgi body (Figs, 4, 6). These vesicles are thus called here as mucocysts. This suggests their common origin from Golgi boby. These contents may be released outside the cell and contribute to form mucilaginous material in which cells are embedded in the palmelloidal stage. BELCHER and SWALE (1967) reported that a dominant stage of *P. pascheri* in culture and also in nature is palmelloidal stage, and it is also true in our strain of *P. pascheri*. The fibrous vesicles described in *P. pascheri* by BELCHER and SWALE (1971) may be of the same nature.

The nucleus is situated ventrally to the pyrenoid and its outer membrane is continuous with the outer membrane of the chloroplast endoplasmic reticulum (ER) (Figs. 6, 9). There are many ER profiles between the nucleus and pyrenoid, and we suggest that a periplastidal ER forms a network in this region. A Golgi body is situated ventral and anterior to the nucleus aligning its cisternae parallel to the nuclear surface (Figs. 6, 8). The contractile vacuole is also located in this region (Figs. 4, 6, 7), often at the left anterior side of the nucleus, however, its position is not constant. In sections such as Figs. 4, 6 and 7, several mitochondrial profiles are seen. However, serial sections (not demonstrated) confirmed that it is single and ring-shaped, and is situated on the inner side of the chloroplast, as illustrated in Fig. 1b.

Flagella and basal body complex: The long and short flagella are situated in definite positions against each other. The long flagellum arises in the flagellar groove oblique to the ventral surface of the cell (Figs. 6, 28, 29) and extends anteriorly. It is coated by rows of mastigonemes (not illustrated). In its transition region, the transitional helix is made up of three gyres (Figs. 6, 28, 29). The short flagellum is situated right to the long flagellum, also anteriorly, lying about 45° against the long flagellum in ventral view (Figs. 4, 14–24). It is bulbous and contains a normal nine-plus-two axoneme (Figs. 30, 31) as well as electron dense material surrounding the axoneme (Figs. 16–24). This dense material is presumably flavin-like material and responsible for autofluorescence of the short flagellum, a feature widely distributed in chlorophyll *a*- and *c*-containing algae (KAWAI 1988, COLEMAN 1988, KAWAI and INOUYE 1989). No transitional helix has been observed in its transitional region (see Figs. 19–22).

Although orientation is different, the long and short flagella are obviously homologous to the anterior and posterior flagella of typical chrysophytes such as *Ochromonas* so that, in the following descriptions, basal bodies associated with the long and short flagella of *P. pascheri* are called anterior basal body and posterior basal body, respectively.

Two basal bodies are arranged to make an



Figs. 28–29. Two of a series of serial sections cut through the long flagellum and proximal part of R1 (same magnifications). Transitional helix gyre (arrows) and three aligned microtubules of R1 (Fig. 28) and associated cytoskeletal microtubules (Fig. 29) are shown. Coated pit (arrowhead) is also visible.

Figs. 30–31. Two similar sections cut parallel to the dorsi-ventral and left-right axis of the cell. Four microtubular roots are seen along the surface of the flagellar groove and the flagellar pocket. The number of microtubules comprising roots is three for R1, single for R2 (Fig. 30), and two for R4 and three for R3 (Fig. 31). The eyespot closely associated with the short flagellum is also clear in these micrographs.

angle of about 45° in ventral view (Fig. 23). The proximal end of the posterior basal body faces the right lateral side of the anterior basal body (Figs. 21–23). Proximally the basal bodies are interlinked by a slender non-striated connecting band (Figs. 22, 26) and no other connecting structure has been observed. The connecting band links the ventral part of the posterior basal body and ventral-right part of the anterior basal body (Fig. 26).

A fibrous cross-banded root, the rhizoplast, arises from the proximal end of the basal bodies and descends down to and along the anterior side of the nucleus (Fig. 8). It is slender and easily overlooked.

Each basal body has two associated microtubular roots, termed R1 and R2 for those associated with the anterior basal body and R3 and R4 for those associated with the posterior basal body. R1 is a three-stranded microtubular root (Figs. 7, 27, 30). It arises from the left side of the anterior basal body (Figs. 22–23, 27), and extends anteriorly first going down dorsally and then parallel to the cell contour of the left bottom margin of the flagellar groove (Figs. 18–23, 28, 29). This root has a clockwise path when viewed from the ventral side (Figs. 4, 18–23). Cytoplasmic microtubules arise from R1 (Figs. 4, 19–21, 29), extend up along the flagellar groove and terminate in a short distance of about 0.5 μm (Fig. 7). This indicates that R1 carries a microtubule organizing center (MTOC). The microtubular root, R2, arises from the right-dorsal side of the anterior basal body (Figs. 23, 25). It is a

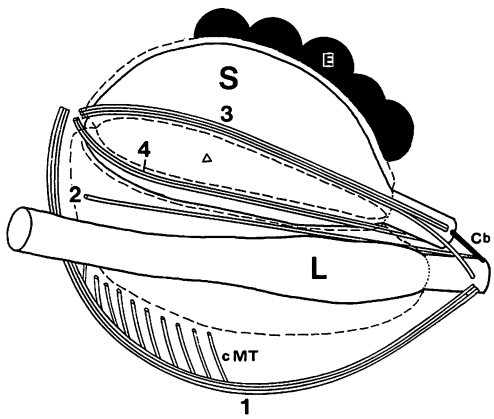


Fig. 32. Diagramm of the flagellar apparatus of *Phaeaster pascheri* viewed from left anterior side of the cell. Two flagella and basal bodies are arranged making an acute angle and four microtubular roots extend in an anterior direction. Note that R1 is responsible for microtubule organization and there is only a proximally located connecting band and no distally located connecting fiber. Associated eyespot is shown. Flagellar groove and flagellar pocket are drawn by broken lines. Mouth of the flagellar pocket is indicated by triangle. Illustration not to scale.

single microtubule (Fig. 30) and extends anteriorly beneath the basal body and then just beneath the bottom of the flagellar groove (Figs. 19–23). It terminates inside the region surrounded by R1's path (Fig. 19).

R3 comprises of three microtubules (Fig. 31). It arises from the right-ventral side of the posterior basal body (Figs. 21–22), but proximally one of the component microtubules extends and makes contact with the anterior basal body at its ventral side (Figs. 16–19). Distally, R3 extends anteriorly along the ventral side of the mouth of the flagellar pocket (Figs. 14, 15, 30, 31). R4 is a two-stranded root (Figs. 14, 20). It arises from the left side of the proximal end of the posterior basal body (Fig. 22) and extends anteriorly along the dorsal side of the mouth of the flagellar pocket (Figs. 20, 21, 30, 31). It extends up towards the ventral surface along the anterior end of the mouth and terminates there (Figs. 14–18). It almost attaches to R3 (Fig. 14) so that R3 and R4 together make a long flattened loop along the contour of the flageller pocket. The flagellar apparatus is illustrated in Fig. 32.

Discussion

The cell of *Phaeaster pascheri* is characterized by the following features: 1) dorsi-ventrally compressed cell body, 2) highly differentiated chloroplast morphology, 3) lack of girdle lamella, 4) scattered or strand-like chloroplast DNA and lack of the ring-like genophore, 5) short flagellum embedded in the flagellar pocket, 6) anteriorly oriented anterior basal body which makes an angle of about 45° against the posterior basal body in the ventral view, and 7) anteriorly extended microtubular roots of the short flagellum. All these characteristics are distinct from typical chrysophyte cell organization.

The lack of the girdle lamella and ring-shaped genophore has been found in some other chrysophytes such as *Rhizochromulina marina* HIBBERD et CHRETIENNOT-DINET (HIBBERD and CHRETIENNOT-DINET 1979), *Chrysamoeba radians* KLEBS (HIBBERD 1971), *Saccochrysis pyriformis* KORSH. (ANDERSEN 1986) as well as two silica-scaled genera, *Chrysosphaerella* and *Spiniferomonas* (*Chromophysomonas*) (PREISIG and HIBBERD 1983). In these algae, peculiar characteristics not typical for the chrysophytes were found such as rhizopodia (*Rhizochromulina, Chrysamoeba*), two flagella arranged at a rather acute angle (*Chrysamoeba* see Fig. 17 in HIBBERD 1971) and scales covering the cell surface (*Chrysosphaerella*).

The flagellar pocket is not common in the chrysophytes, but a groove which ensheathes the short flagellum has been found in some species such as *Chromulina psammobia* (ROUILLER and FAURE-FREMIET 1958), *Chromulina placentula* (BELCHER and SWALE 1976) and *Microglena butcheri* (COUTE and PREISIG 1981). These algae also possess unusual features, e.g. a highly differentiated striated fibrous root, a pseudocaryophore (*C. psammobia*, see Fig. 9 in ROUILLER and FAURE-FREMIET 1958, *M. butcheri,* COUTE and PREISIG 1981) and a dorsi-ventrally compressed cell (*C. placentula*).

The lack of the girdle lamella and genophore and presence of the flagellar pocket observed in *P. pascheri* are advanced features in the evolution of the chrysophytes, because they are associated with other unusual features mentioned above.

Orientation of the short flagellum, basal bodies and roots in *P. pascheri* is most unusual, when we compare it with previously published data for other chrysophyte genera. ANDERSEN (1987, 1989) summarized the flagellar apparatus of the Chrysophyceae, and incorporating some other features which were not mentioned by ANDERSEN, we characterize it as follows and illustrated in Fig. 33 together with that of *P. pascheri* for convenience. 1) The long flagellum arises from the cell at an angle of about 90° against the cell surface so that it is seen more or less in transverse section in the view shown in Fig. 33a. 2) The short flagellum is disposed parallel to the cell surface making an angle of about 90° against the long flagellum. 3) The connecting devices to interlink basal bodies are two proximally located bands. A distal fiber, which is common in many other groups of algae, has never been reported. 4) One of microtubular roots, R1, associated with the long flagellum extends anteriorly and bends clockwise. Cytoskeletal microtubules arise from this root, indicating the presence of an associated MTOC. 5) R2, another root associated with the long flagellum, extends straight for a rather short distance compared to R1. 6) R3 and R4 arise from the short flagellum, and extend away from the anterior basal body and bend respectively counterclockwise and clockwise, joining each other and forming a loop. The eyespot underlies roots. The flagellar apparatus possessing these features is termed here as *Ochromonas*-type, because they are mainly based on studies on *Ochromonas* (BOUCK and BROWN 1973, ZHANG unpublished data) and *Ochromonas*-allied genus, *Poterioochromonas* (SCHNEPF *et al.* 1977).

When we compare Figs. 33a and b, there are clear homologous relationships of basal bodies and microtubular roots, though orientation of basal bodies and roots is different. Homologous structures between these flagellar apparatuses are labelled by the same letters or numbers. It is conceivable that *Phaeaster*-type flagellar apparatus is assigned distal to *Ochromonas*-type flagellar apparatus in chrysophyte phylogenetic tree, because *Phaeaster* has advanced features such as lack of genophore and girdle lamella and possession of the flagellar pocket. The following events may have occurred in the *Ochromonas*-type flagellar apparatus, giving rise to the *Phaeaster*-

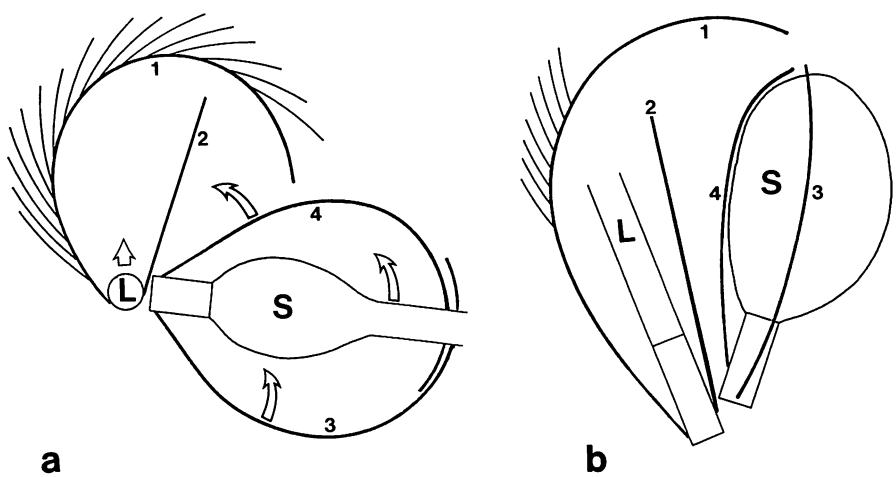


Fig. 33. Schematic illustrations of the flagellar apparatuses of *Ochromonas*-type (a) and *Phaester pascheri* (b). *Ochromonas*-type flagellar apparatus may have given rise to *Phaeaster*-type flagellar apparatus by rotation of the long and short flagella with associated microtubular roots (arrows). Illustration not to scale.

type flagellar apparatus. 1) The anterior basal body rotated anteriorly with its proximal end as a fulcrum, resulting in its distal end being oriented anteriorly. 2) The short flagellum with associated microtubular roots rotated counterclockwise in the plane illustrated in Fig. 33, resulting in all of them directing towards the anterior end of the cell.

Cell organization and the flagellar apparatus of *P. pascheri* are highly specialized, and we suggest that this alga has evolved into a very specialized direction. The characteristics described here may serve to understand its taxonomic and phylogenetic position; however, our knowledge of chrysophyte algae as a whole is too limited and at this time it is difficult to determine its precise position in the class. Thus it will remain until more information on many other genera becomes available.

Finally, some differences between observations of *P. pascheri* made by BELCHER and SWALE (1971) and ours should be commented on. These are scales covering the cell surface, the long flagellum widened into a bilateral wing at the base, and rhizopodia around the flagellar groove. All of these were reported by BELCHER and SWALE (1971) but never been observed in our strain. Of these, scales of *P. pascheri* could be artifactual because no clear indication of scales was given. Only in their Fig. 15 (BELCHER and SWALE 1971, p. 167), are scales shown in section. These scales seem to be situated just above the chloroplast membrane and no plasmalemma is observed in this figure. We therefore suggest that these scales are part of the plasmalemma broken down into small pieces (compare well preserved plasmalemma in their Fig. 12 and "scales" in their Fig. 15). The bilateral wing of the long flagellum and rhizopodia were clearly shown by these phycologists and are undoubtedly their natural features. In our strain, the basal part of the long flagellum is swollen and wide (Fig. 31) but never clearly forms a wing. These structures may or may not be variable in culture conditions, the cell cycle or in stages of the life cycle such as motile and palmelloidal stages. We have not detected these features in our strain in either motile or palmelloidal stages (not illustrated) and in specimens fixed at different times. Most of the other features are identical between our strain of *P. pascheri* and that of BELCHER and SWALE (1971). These features could thus be strain differences, but at present should remain as an unsolved taxonomic problem.

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井上　勲・張　暁明・榎本瑞子・千原光雄：黄金色藻類 *Phaeaster pascheri* の細胞構造，特に鞭毛装置について

Phaeaster pascheri の細胞構造を蛍光顕微鏡および透過型電子顕微鏡を用いて調べた。葉緑体は星状で，ガードルラメラを欠くこと，核様体がリング状ではなく分散あるいは糸状である点で特殊なものである。短鞭毛は棍棒状で，鞭毛ポケットと呼ぶ細胞の窪みに収納されている。葉緑体から眼点を持つ裂片が伸張してこの鞭毛ポケットに密着している。鞭毛小体、鞭毛および4本の微小管性の鞭毛根の配列は特異なもので，すべて細胞の遊泳方向に伸びる。鞭毛小体は約45度の角度で配列する。このような配列は黄金色藻の鞭毛装置の進化において鞭毛小体と鞭毛根の回転が起こったと考えることで解釈できる。長鞭毛から前方に伸び時計回りに旋回する鞭毛根は骨格微小管の形成にあずかっている。ミトコンドリアは1個でリング状である。(305 茨城県つくば市天王台1–1–1 筑波大学生物科学系)