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SYSTEMATICS AND MORPHOLOGY OF CHRYSOCHAETE BRITTANNICA (GODWARD) ROSENBERG AND PHAEOPLACA THALLOSA CHODAT (CHRYSOPHYCEAE)

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SUMMARY

A review is given of the taxonomic history of *Chrysochaete brittannica* and *Phaeoplaca thallosa*. Observations on field material and on unialgal cultures are presented to support their separate identity which has been a subject of doubt. Details of the ultrastructure of vegetative cells of both species are given. The taxonomic position of *Phaeoplaca thallosa* is discussed and its description emended.

1. INTRODUCTION

The genus *Chrysochaete* (subclass Heterochrysophycidae, order Chromulinales, fam. Chrysochaetaceae, according to BOURRELLY 1957, 1968) was created by ROSENBERG (1941) to accomodate a palmellloid Chrysophycean alga with gelatinous bristles described by GODWARD (1933) as *Naegeliella brittannica*, and one described by SCHERFFEL (1927) as *Naegeliella natans*. The separation of the genera *Naegeliella* Correns 1892 (type species *Naegeliella flagellifera* Correns 1892) and *Chrysochaete* seems justified by differences in zoid morphology and the absence of a "protoplasmic thread" in the gelatinous bristles of *Naegeliella* (ROSENBERG 1941).

Chrysochaete brittannica (Godward) Rosenberg has thus far been recorded from England (GODWARD 1933; ROSENBERG 1941), Austria (ROSENBERG 1941), France (BOURRELLY 1957) and The Netherlands (DOP & VROMAN 1976).

Phaeoplaca thallosa (subclass Acontochrysophycidae, order Phaeoplacales, fam. Phaeoplacaceae, according to BOURRELLY 1957, 1968), was described by CHODAT (1925) as a Chrysophycean alga resembling the green alga *Coleochaete scutata* in form, with a thick membrane, no visible pyrenoid, multiplying by segmentation or also by "spores", 4–8 in number, which may issue as zoöspores but the flagellae of which are not known. The description does not provide further information as to the form of the chloroplast. The plates show one irregularly circular and three roughly rectangular thalli; neither "spores" nor spore formation are illustrated.

GEITLER (1926) described *Placochrysis membranigera* one year later, and it was immediately recognised by CHODAT (1926) as being synonymous to his

Phaeoplaca thallosa; this was conceded by Geitler. Another species to be placed in the genus *Phaeoplaca*, according to BOURRELLY (1957), is *Chrysothallus baicalensis* Meyer 1930. All subsequent illustrated reports of *Phaeoplaca thallosa* Chodat (SKUJA 1939; MARGALEF 1948; SMITH 1950; BOURRELLY 1957) and of *Phaeoplaca baicalenis* (Meyer) Bourrelly (MATVIENKO 1951) agree on overall thallus shape: mostly regularly quadrate to rectangular, unilayered, formed by cell division in one plane, in two perpendicular directions; cells provided with thick, distinct walls.

P. thallosa has been recorded from Switzerland (CHODAT 1925), Austria (GEITLER 1926), Latvia (SKUJA 1939), Spain (MARGALEF 1947), U.S.A. (SMITH 1950; WHITFORD & SCHUMACHER 1963), France (BOURRELLY 1957), Poland (STARMACH 1966), and The Netherlands (DOP & VROMAN 1976). *P. baicalensis* has been recorded from the U.S.S.R. only (MEYER 1930; MATVIENKO 1951).

Due to a misunderstanding of MEYER's (1930) description of settled zoids, BOURRELLY (1957, 1968) placed the genus *Phaeoplaca* in the subclass Acontochrysophycidae, order Phaeoplacales, fam. Phaeoplacaceae (see DOP & VROMAN 1976).

GEITLER (1968) reports on a Chrysophyte from Lunz (Austria) which at first sight he would have named *Phaeoplaca thallosa* (it reminds him strongly of his *Placochrysis membranigera*). However, the presence of mucilaginous bristles with protoplasmic threads leads him to the conclusion that it actually is *Chrysochaete brittannica.* Chloroplast form, relation of pyrenoid and chloroplast and position of nucleus are meticulously described. On account of these observations, Geitler suggests that *Phaeoplaca* is synonymous with *Chrysochaete*; he could not be definite about it because his alga did not produce zoids.

TSCHERMAK-WOESS (1970) reports on a find of *Chrysochaete brittannica* from Vienna. In habit and cytology this alga was slightly different from Geitler's Lunz alga: it resembled the figures given by GODWARD (1933), ROSENBERG (1941), GEITLER (1926) and BOURRELLY (1957, 1968) for *Chrysochaete brittannica.* Details of chloroplast, pyrenoid and structure of zoöspores are given. Despite of several differences, the conclusion is drawn by Tschermak-Woess that hers and Geitler's alga both are *Chrysochaete brittannica.* In a later paper (TSCHERMAK-WOESS 1971) more finds of *Chrysochaete brittannica*, from the same location, are mentioned. Mucilaginous bristles were virtually absent in spring but present in autumn. This again is seen as a support for the opinion that *Chrysochaete* Rosenberg, *Phaeoplaca* Chodat, *Placochrysis* Geitler and *Chrysotallus* Meyer are all synonymous; the mucilaginous bristles of the last three would have been too difficult to observe or were not present at all at the time of observation.

In the course of a study on benthic freshwater Chrysophyceae, recent finds (DOP & VROMAN 1976) of several clones of two algae, strongly resembling the original descriptions of *Phaeoplaca thallosa* Chodat and *Chrysochaete brittannica* (Godward) Rosenberg enabled us to investigate this matter further.

2. MATERIALS AND METHODS

Three clones of *Phaeoplaca thallosa* were isolated from glass microscope slides, submerged in the "Botshol" and "'t Hol", peat ponds in process of eutrophication, respectively near Amsterdam and Hilversum, The Netherlands. Three clones of *Chrysochaete brittannica* were isolated from these ponds as well, and one from another peat pond near Hilversum, in the Stichts-Ankeveense polder.

The glass slides are placed in these ponds and are normally taken out monthly to study the periodicity of benthic Chrysophyceae. Standard unialgal cultures were maintained in Wood's Hole artificial freshwater medium (STEIN 1973) at 12°C and light cycle of 12 hrs light, 12 hrs darkness; light intensity was ± 1500 lux.

Field observations were done on thalli, settled on the slides submerged in the above-mentioned ponds; they were supplemented by observations on standard unialgal cultures. To determine the effect of nitrate content of medium on mucilaginous bristles, both species were also cultured in Wood's Hole medium with nitrate content varying from 0 to 1360 mg/litre.

For electron microscopy, best results were obtained by fixing the material for two hours in an ice-cooled, veronal-acetate buffered mixture of osmium tetroxide (final conc. 1%) and glutaraldehyde (final conc. 0.8%) at pH 7.4. After rinsing in aqua dest. and dehydration in a graded alcohol series, embedding followed in Epon 812. Ultrathin sections were cut on a Reichert ultramicrotome using glass knives and picked up on formvar-coated (1% in chloroform) copper grids. The sections were contrasted with an 1% aqueous solution of uranyl nitrate, followed by Reynolds' lead citrate and examined with a Zeiss EM9A or a Philips EM300 electron microscope.

3. OBSERVATIONS

3.1. Field occurrence

Both algae were found in waters classified as eu- to mesotrophic and bêtameso- to oligosaprobic.

Chrysochaete brittannica was found throughout the mentioned ponds, apparently being a rather common epiphyte, as already mentioned by GODWARD (1933) and ROSENBERG (1941).

Phaeoplaca thallosa was restricted, however, to rather isolated, small pools with an algal flora characterized by a number of other benthic Chrysophytes, e.g. *Epipyxis* spp., *Chrysosaccus* spp., *Chrysopyxis* spp., *Stephanoporus tubulosus* and the Chaetophoralean green algae *Chaetosphaeridium pringsheimii*, *Dicranochaete reniformis*, and the Xanthophycean algae *Mischococcus confervicolum*, *Ophiocytium* spp. and *Tribonema* spp. Most frequent accompanying algae for both species were: *Apiocystis brauniana*, *Bulbochaete* spp., *Chaetopeltis orbicularis*. *Chaetophora incrassata*, *Coleochaete irregularis* f. *minor*, C.

orbicularis, C. *scutata* f. *minor*, *Draparnaldia plumosa*, *Mougeotia* spp., *Oedogonium* spp., *Spirogyra* spp., *Stigeoclonium farctum* and *S. tenue*.

3.2. Habit of field material

Cells of *Chrysochaete brittannica* thalli are embedded in a mucilaginous matrix. Young, one-layered thalli sometimes show a confusing plasticity of habit (see *figs. 1–3*). Older thalli are mostly quite regular, hemisphaerical, multi-layered palmelloid masses of cells distributed throughout the mucilaginous matrix (see *figs. 4–6*). Mucilage bristles are seen quite often in field material; in most bristles, an axis issuing from each cell is often easily distinguishable. The bristles mostly stick together in one or several bundles, which branch farther away from the thallus. Cell shape is very irregular, varying from round or oval to elongate, measuring from 9.5 × 9.5 to 5.5 × 13 μm. Zoids were not observed in field material.

Phaeoplaca thallosa is always found as quite regular, rectangular cell plates (see *figs. 9, 10*) with thick walls. Maximum number of cells was thirty-two, once found on a four-week old slide. Mucilaginous bristles were not observed in field material. Cell shape is prismatic. Unlike in *Chrysochaete brittannica*, cell dimensions differ with thallus age, varying from 10–12 μm in cross section in few-celled, to 4 × 5.5 or 7.5 × 5.5 μm in older thalli. Cell height is 12–15 μm. Empty cells, due to the issuing of zoids, were often observed. The walls are quite distinct in these cells (*fig. 11*). If they collapse, which is often the case, the otherwise regular thallus structure is disturbed. Zoids were not observed in field material.

3.3. Habit of cultured material

Chrysochaete brittannica, when cultured in Wood's Hole medium, mostly shows the same hemisphaerical, palmelloid habit as in the field. Sometimes, however, no large thalli are developed, but swarmers are produced continuously and profusely, resulting in an irregular palmelloid mass of cells covering bottom, sides and meniscus of the culturing vessels. In Reichart's artificial freshwater medium (Reichart 1967), containing 2.5 times as much nitrate and phosphate, and 17 times as much carbonate, thallus form was more consistent.

Under standard culturing conditions in Wood's Hole medium, mucilaginous bristles are always present, with a clearly visible axis. Each cell is surrounded by an envelope of firm mucilage, distinct from the more fluid mucilage of the rest of the thallus. This is most clearly seen when zoids have issued (see *fig. 8*).

Cross sections of very large older thalli (up to 500 μm in diameter) show a tendency for the cells to become distributed peripherically.

Phaeoplaca thallosa largely retains its regular rectangular, unilayered habit in culture. Occasionally, roughly circular thalli are seen, probably due to release of zoids and consequent collapse of empty cells. The cell wall of *Phaeoplaca thallosa* is apparently rather elastic; daughter cells secrete new walls within the old mother-cell wall, stretching the latter as they grow. When cells

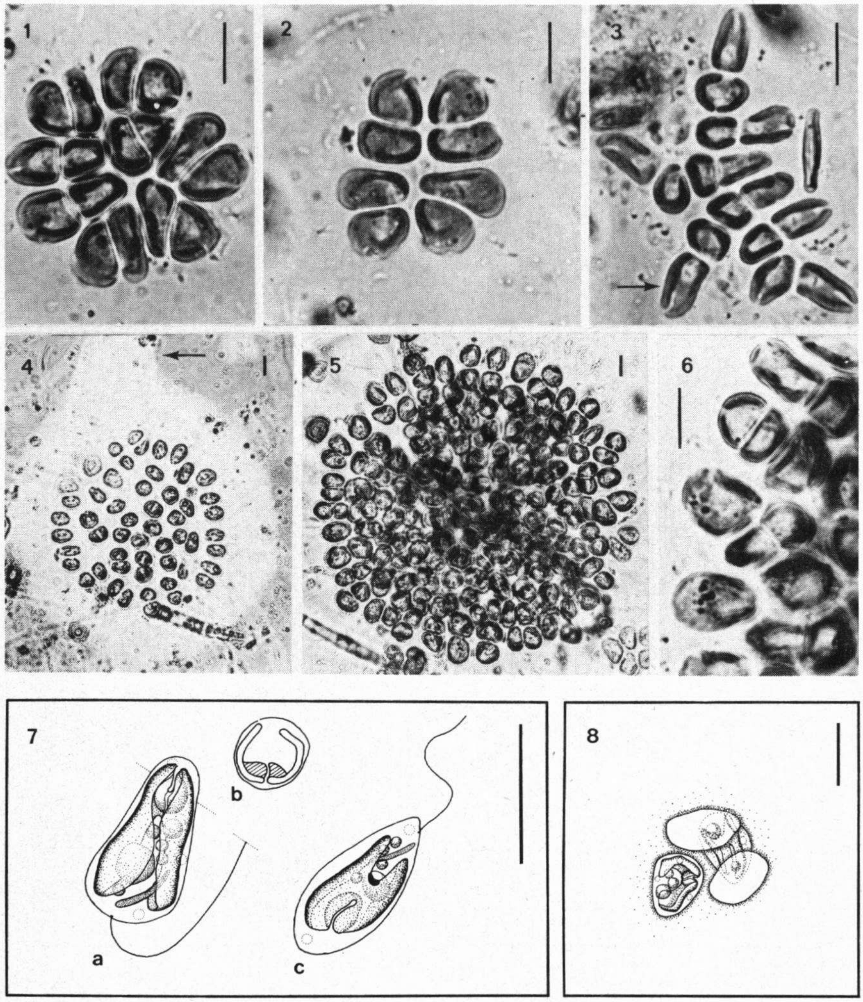


Plate 1. *Chrysochaete brittannica.* Light microscopy. Scale bar represents 10 μm.

Figs 1–3. Photographs of field material, showing variability of thallus shape.

In *fig. 3* the arrow indicates a cell in which two chloroplast lobes and connecting bridge are clearly visible.

Fig. 4. Field material. Thallus mounted in dilute India ink to show surrounding mucilage and tufted pseudocilla (arrow).

Fig. 5. Field material. Older thallus showing multilayered centre.

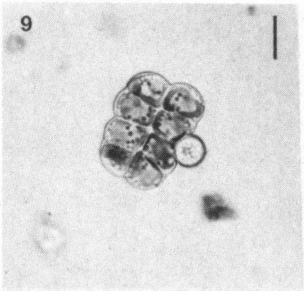
Fig. 6. Field material. Edge of older thallus showing irregular cell shape.

Fig. 7a. Drawing of vegetative cell showing bilobed chloroplast with pyrenoid on connecting bridge, contractile vacuoles, large leucosin vacuole and smaller lipid droplets, sausage-shaped golgi body, and pseudocilium axis.

Fig. 7b. Cross section of *fig. 7a* at dotted line, showing pyrenoid cleft by chloroplast incision.

Fig. 7c. Drop-shaped zoid showing same features as vegetative cell; stigma located in shallow chloroplast incision.

Fig. 8. Drawing of portion of thallus showing two empty cells; walls stand out among more fluid mucilage of rest of thallus.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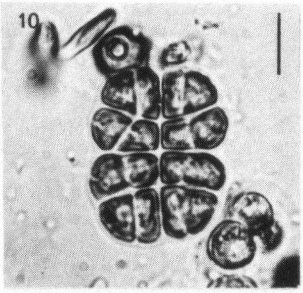
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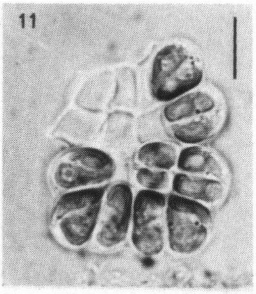
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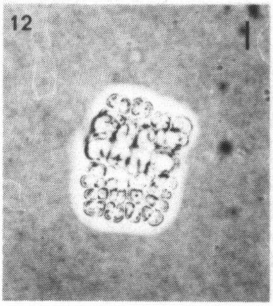
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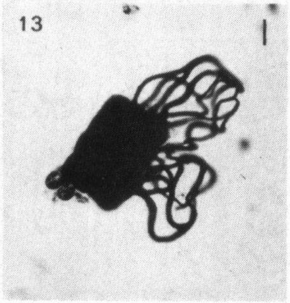
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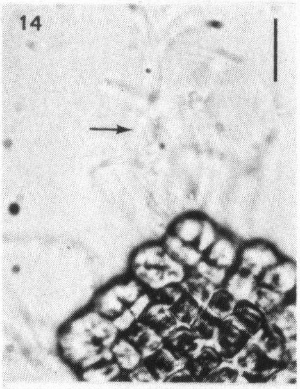
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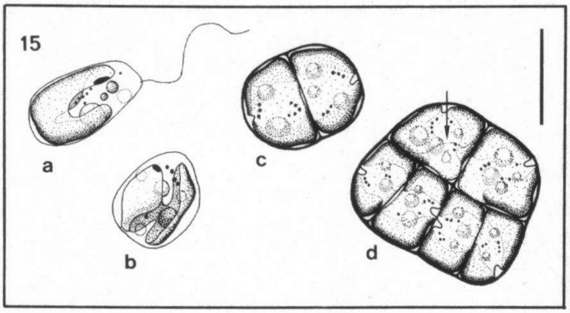
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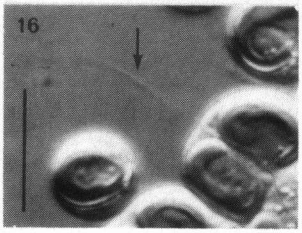
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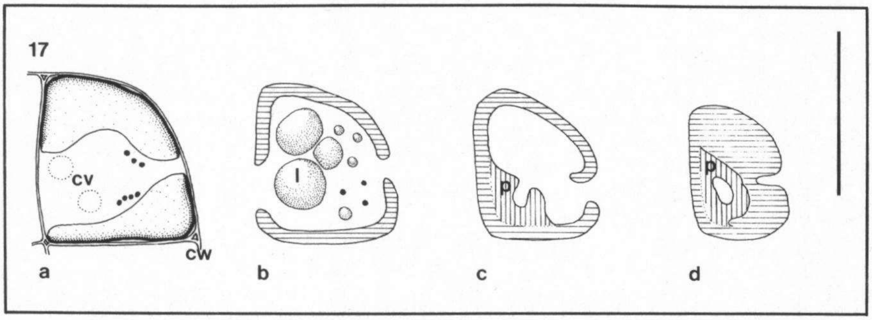
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are emptied or if the protoplast dies, the walls sometimes shrink a little. As a consequence, in the field or in cultures one may find empty thalli, the dimensions of which are significantly smaller than those of live ones. Also, uneven stretching of the parent cell walls may account for irregularities in thallus form. Large thalli (up to ± 140 cells have been observed), sometimes are bent in the middle, reminding one of MEYER's (1930) drawings of *Phaeoplaca (Chrysothallus) baicalensis*. They may also lose their rectangular shape due to the occasional emptying of cells when zoids escape.

Free-floating thalli consist of irregular clumps of cells, apparently having lost the regularity in cell division by absence of contact with a substratum. Cell division proceeds in a regular fashion; zoids that have settled, are rounded off, enlarge slightly from ± 6 μm to 9 μm and secrete a cell wall.

The first division results in an oblong, two-celled thallus; all further divisions take place synchronously in planes, perpendicular and parallel to the first one (see *fig. 15*). The stigma disappears before the first division. When mounted in dilute India ink, the cell wall is seen to be bordered by a fluid mucilaginous layer of varying width (*fig. 12*). Mucilaginous bristles were only seldom observed under standard culturing conditions. They were rarely visible under bright field illumination (*fig. 14*) and could be demonstrated best by colouring

Plate 2. *Phaeoplaca thallosa*. Light microscopy. Scale bar represents 10 μm.

Figs. 9, 10. Photographs of field material of young thalli, showing regular, rectangular eight- and sixteen- celled stadium.

Fig. 11. Field material. Thallus from which zoids have issued, showing thickness of cell walls and distortion of thallus shape through collapsing of walls.

Fig. 12. Cultured thallus mounted in dilute India ink to show fluid mucilage surrounding thallus.

Fig. 13. Methylene blue stained cultured thallus showing pseudocilia. Strong curvature of pseudocilia is due to shrinkage caused by the stain.

Fig. 14. Large, cultured thallus showing pseudocilia under bright field illumination.

Fig. 15a. Zoid showing bilobed chloroplast with deep, narrow and a shallow, wide incision, anterior contractile vacuoles, large leucosin vacuole and several oil droplets; stigma is located along shallow chloroplast incision.

Fig. 15b. Zoid having just settled and retracted its flagellum.

Fig. 15c. Young thallus after first division, seen from above. Leucosin vacuoles, oil droplets and narrow chloroplast incision are to be seen, as well as chloroplast lobes extending across cell bottom. Basally located contractile vacuoles and pyrenoid are not drawn in.

Fig. 15d. Older thallus showing same features as 15c; arrow indicates cell in which position of hollow pyrenoid is shown.

Fig. 16. Interference contrast photograph of thallus edge showing very delicate seta, probably the pseudocilium axis, since regular pseudocilia were not formed in this culture.

Fig. 17a-d. Series of interference contrast views from underside of thallus in which the focal plane shifts from bottom of cell upwards.

In a., chloroplast lobes extending across cell bottom are seen, as well as contractile vacuoles (cv), small oil droplets, and thick cell wall (cw).

In b., two chloroplast lobes, leucosin vacuoles (1) and oil droplets are seen.

In c., only the narrow chloroplast incision remains; the pyrenoid (p) is seen in a corner of the cell, with a hollow being excavated into it from the cell lumen side.

In d., the hollow pyrenoid is seen lying against the top of the bell-shaped chloroplast; the narrow chloroplast incision is seen to extend rather high upwards.

with methylene blue solution, which is readily absorbed by bristles and cell walls, obscuring cell contents (*fig. 13*). Bristles were detached very easily in mounting and colouring. A "protoplasmic axis" was sporadically seen. Zoids that had just settled, and cells of regular thalli, both lacking mucilaginous bristles, were sometimes observed to possess a very delicate seta (*fig. 16*), barely discernible using phase- or interference contrast illumination with × 100 objectives. It is assumed that this is the naked "protoplasmic axis", around which mucilage is secreted, to form the bristles.

3.4. Cell contents

Cells of *Chrysochaete brittannica* possess a golden-brown, distinctly two-lobed chloroplast; the two lobes are connected by a bridge. This bridge is not symmetrical in form, as is the case with two-lobed chloroplasts of other Chrysophyceae. At one side, there is a gradual curvature between the lobes, while at the other side the space between the lobes tapers to a narrow slit. The chloroplast may lie appressed to the cell wall, or be located more centrally; the bridge is observed to lie near the top or laterally in the cell (see *fig. 7*). A pyrenoid is to be seen appressed to the interior of the bridge. The narrow chloroplast slit also cuts in the pyrenoid, giving it a two-lobed appearance as well. Each lobe is appressed to a chloroplast lobe (see *fig. 7*). Up to three contractile vacuoles are present near the outer cell membrane, not confined to any particular position within the cell. The nucleus cannot be observed in live cells; in preparations of thalli, fixed for electron microscopy and embedded in Epon on glass slides, it is seen to be closely appressed to the pyrenoid.

In vegetative cells as well as in zoids, a narrow band is seen, between the chloroplast lobes, some distance beneath the pyrenoid (*fig. 7*). It is assumed to be the Golgi body, appressed to the nucleus. (See also electron microscopical observations.)

Several large refringent leucosin vacuoles (contents staining pink with brilliant cresyl blue), and some smaller ones with lipid contents, are present, their number depending on the nutritional state of the cells.

Vegetative cells of *Phaeoplaca thallosa* possess a chestnut-brown, two-lobed chloroplast. It is appressed to the outer membrane, and the bridge joining the two halves is positioned near the cell top. As in *Chrysochaete brittannica*, one chloroplast incision is shallow and wide, while the other is a deep, narrow slit. Recently divided cells lie with this slit turned away from each other. The chloroplast lobes sometimes partly extend across the cell bottom (*fig. 15, 17*). A pyrenoid is situated at the inside of the chloroplast bridge. Unlike in *C. brittannica*, it is not divided into two lobes.

In *P. thallosa*, the pyrenoid is hollow. When viewing a cell from the side, the pyrenoid can be seen as an inverted U-shaped body appressed against the top of the bell-shaped chloroplast, with its cavity turned towards the cell lumen. When observing a cell from above, the pyrenoid can be seen as an irregularly circular body with the cavity in its centre (*fig. 15d*). The cavity in the pyrenoid – it might be termed a short canal – is not oriented parallel to the vertical axis of the cell; it is slightly tilted so that the open end is near the top of the narrow chloroplast incision. In *fig. 17* the tilted pusition of the pyrenoid canal is illustrated in a series of views from the underside of a cell.

The nucleus is appressed to the pyrenoid; it could only be seen in thalli, fixed and embedded for electron microscopical observation. Just under the cell membrane, numerous small vesicles (diam. 0.5 μm) were visible using interference contrast illumination; they stain dark blue with brilliant cresyl blue. One to three large leucosin vacuoles are present, and several smaller ones, with lipid contents, depending on the age of the cultures. Observation of cytological details, especially the pyrenoid, is often very difficult because of these vacuoles.

3.5. Zoids

In both algae, the contents of vegetative cells may be converted into single zoids. Those of *Chrysochaete brittannica* are metabolic, mostly ovoid to almost fusiform, with a truncate anterior end. The flagellum is inserted subapically at the anterior end; 3–5 contractile vacuoles are distributed peripherally throughout the cell. The chloroplast is like the one in vegetative cells, except for a large orange-red stigma located in the gradually curved incision, or farther along the border of a chloroplast lobe, near the flagellum insertion point. See *fig. 7.*

Zoids of *Phaeoplaca thallosa* are also metabolic, varying from globular to drop-shaped. They never assume the almost fusiform shape of the *Chrysochaete* zoids, however. The flagellum is inserted apically; two contractile vacuoles are positioned near its base. The chloroplast is bell-shaped as in the vegetative cell, with its open end oriented towards the flagellar insertion point. A bright orange-red stigma is to be seen at the edge of one of the chloroplast lobes, near the flagellum. See *fig. 15.*

3.6. Influence of culture medium on bristle formation

An example of an alga with comparable pseudocilia is found in the Chlorophyceae: the Tetrasporalean alga *Chaetopeltis orbicularis* Berthold. It is known to often lack these structures in the field (BOURRELLY, 1972, and personal observations). In laboratory experiments, nitrate content of the culturing medium influences pseudocilium formation, suppressing their formation at high concentrations (WUJEK & CHELUNE 1975). To investigate this phenomenon in *Chrysochaete brittannica* and *Phaeoplaca thallosa*, thalli were cultured in media with nitrate content varying from 0 to 1360 mg/litre. A clone of *Chaetopeltis orbicularis* (a common epiphyte in the waters studied) was used as a control.

Results are summarized in *table 1.* All three species behave alike. At lower concentrations, pseudocilia of *C. brittannica* remain apart: at higher concentrations they become tufted. Pseudocilia of *P. thallosa* never were as well-defined, long and straight as those of *C. brittannica*: they are thicker and wavy.

Table 1. Formation of mucilaginous bristles under varying nitrate content of media.

	Conc. $NaNO_3$ (mg/litre)											
	0	0.5	2	5	10	25	40	85	170	340	680	1360
Chrysochaete brittannica	+++	+++	+++	+++	+++	++	++	+	o	o	o	o
Phaeoplaca thallosa	+++	+++	+++	++	++	++	+	o	o	o	o	o
Chaetopeltis orbicularis	+++	+++	+++	+++	++	++	+	o	o	o	o	o

Estimate of bristle formation as follows: +++ – numerous, well defined.
++ – less numerous, sometimes tufted.
+ – very few
o – none, or very small and stunted.

Optimal vegetative growth for all three species occurred at conc. from 40 to 689 mg $NaNO_3$/litre.

3.7. Electron microscopy

3.7.1. *Chrysochaete brittannica*

A low-power view of a vegetative cell of *Chrysochaete brittannica* is presented in *fig. 18*, showing the relative position of the main cell organelles: a two-lobed chloroplast with a pyrenoid lobe appressed to each half, the nucleus in close relation to the pyrenoid, and a large, active Golgi body close to the nucleus.

The chloroplast consists of ten to fifteen parallel lamellae: two or three of these are girdle lamellae. Between the girdle lamellae and the ends of the other lamellae at the edge of the chloroplast a space is left open, showing up as a circular spot in most sections, and elongate in glancing sections (*fig. 19*). The lamellae consist of three closely appressed thylakoids. Occasionally, small rows of osmiophilic droplets can be seen between the lamellae. The chloroplast matrix is finely granular. The chloroplast is enclosed by its own membranes, and by a layer of ER, to which ribosomes sometimes can be seen attached (*fig. 20*). This ER also envelopes pyrenoid and nucleus. The pyrenoid apparently consists of the same finely granular material: its two lobes are illustrated in *fig. 18*: in *fig. 21*, a section just beneath the bridge connecting the chloroplast lobes, it can be seen as one body. The pyrenoid lies within the chloroplast membrane (*fig. 22*).

The rather large nucleus lies closely appressed to the pyrenoid: the chromatin material is partly condensed into dark, irregular patches. A dark nucleolus is often seen (*fig. 23*). The nucleus lies within the chloroplast-associated ER (*fig. 22*).

The Golgi body lies close to the nucleus. It consists of twelve to fifteen cisternae which are very closely packed in the centre. It seems to be built of two stacks, one closely appressed to the nucleus and running parallel to the nuclear membrane, the other, distal part more curved and always active (*fig. 24*). From the outer edges of the cisternae, sacculi are given off, while from the centre small uniform vesicles (about 60 nm diam.) issue. Between the nuclear membrane and the Golgi body, vesicles of the same size are often seen (*fig. 25*).

Mitochondria are distributed peripherally, and are often found between chloroplast and cell membrane. They are elongate, irregularly shaped, sometimes branched (*fig. 24*), with tubular cristae.

ER is only occasionally found apart from the covering of chloroplast and nucleus: very rarely, short strands of rough ER are seen. Ribosomes are often seen to be distributed freely throughout the cytoplasm.

The vegetative cells apparently possess an almost complete flagellar apparatus. One very short flagellum is seen to fit into a small depression of the cell membrane (*fig. 26*). The other flagellum probably is the "cytoplasmic axis" seen in the gelatinous bristles of the vegetative cells: we assume it is somehow converted into the long flagellum of the zoids and vica versa. The exact relationship of these two structures is not apparent from our investigations, however. A cross-banded flagellar root is seen to run from the basal body of the long flagellum into a narrow, elongate depression of the nuclear

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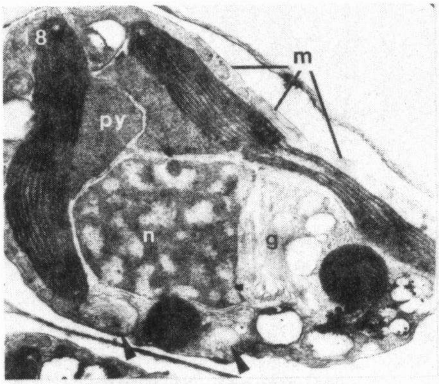

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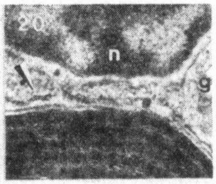

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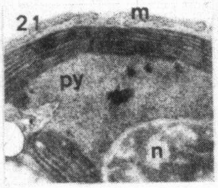

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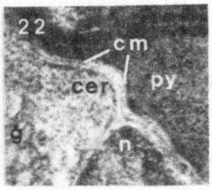

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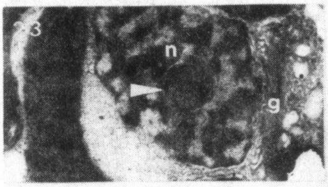

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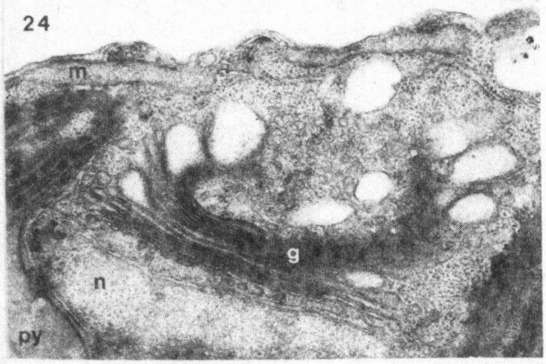

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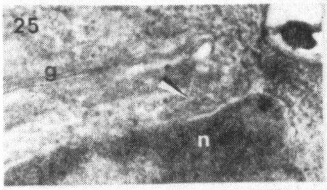

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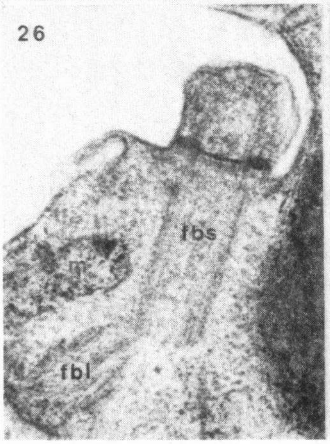

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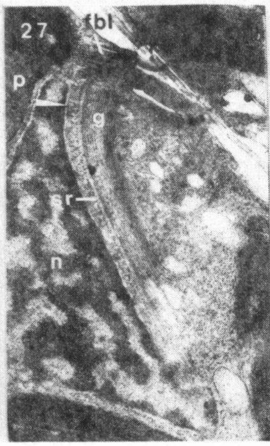

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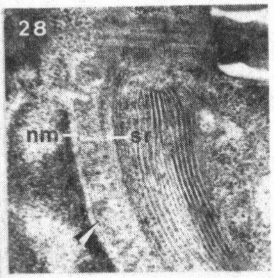

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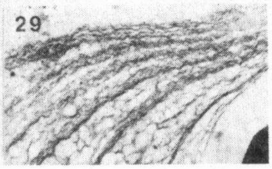

membrane (*fig. 27, 28*). Periodicity of the striations is about 100 nm. Between nucleus and root, the outer ER membrane is seen to be very wavy, giving off small vesicles of 60 nm diameter. The closely compressed part of the Golgi body runs parallel to the striated root, and also fits into the nuclear depression. It follows the root until close to the basal body, where the cisternae are bunched together slightly (*fig. 28*). Microtubular roots have not been observed nor has the presence of a periplastidial network unequivocally been established. In several sections vesicles with regularly oriented fibrillae of uniform diameter (15 nm) are seen (*fig. 18*). The mucilage surrounding the cells is seen to be fibrous, with a slight, apparent layering (*fig. 29*).

Plate 3. *Chrysochaete brittannica.* Ultrastructure.
cm = chloroplast membrahe.
cer = chloroplast-associated E.R.
fb = flagellar basal body.
fbs = basal body of short flagellum.
fbl = basal body of long flagellum.
g = golgi body.
m = mitochondrion.
n = nucleus.
nm = nuclear membrane
py = pyrenoid.
sr = striated flagellar root.

Fig. 18. Low-power view of vegetative cell showing two chloroplast lobes with parallel lamellae, two of which are girdle lamellae, bifid pyrenoid, golgi body appressed to nucleus, leucosin and oil vacuoles, peripherally distributed mitochondria, and two vesicles with fibrillar content (arrowheads). × 7.700.

Fig. 19. Periphery of cell showing glancing section of space between two girdle lamellae and other lamellae (cf. *fig. 18*), and superficial flattened vesicles, probably belonging to the contractile vacuolar apparatus (arrowhead). × 7.700.

Fig. 20. Ribosomes seen attached to chloroplast-associated E.R. (arrowhead). × 23.100.

Fig. 21. Section just beneath chloroplast bridge, showing pyrenoid still as one body, with starting incision. × 7.700.

Fig. 22. Pyrenoid seen to be included in chloroplast membrane; chloroplast-associated E.R. continuous with nuclear membrane. × 23.100.

Fig. 23. Nucleus with partly condensed chromatin and dark nucleolus (arrowhead). × 7,700.

Fig. 24. Compact golgi body giving off large sacculi from periphery and small vesicles from centre; also visible several peripherally distributed mitochondria with tubular cristae. × 23,100.

Fig. 24. Compact golgi body giving off large sacculi from periphery and small vesicles from centre; also visible several peripherally distributed mitochondria with tubular cristae. × 23,100.

Fig. 25. Detail of cell showing small vesicles between nucleus and golgi body (arrowhead). × 23,100.

Fig. 26. Periphery of vegetative cell showing longitudinally sectioned short flagellum immersed in small pocket of outer cell membrane and glancing section of long flagellum (= pseudocilium axis) basal body. × 23,100.

Fig. 27. Longitudinal section of nuclear depression containing striated root and part of golgi body; basal body of pseudocilium axis is also sectioned. Note wavy nuclear membrane (arrowhead). × 7,700.

Fig. 28. Detail of *fig. 27*, showing association of basal body, bunched golgi cisternae, striated root, lobe of nucleus and wavy nuclear membrane, giving off vesicles (arrowhead). × 19,200.

Fig. 29. Layered fibrilar structure of firm mucilage, surrounding cells. × 23,100.

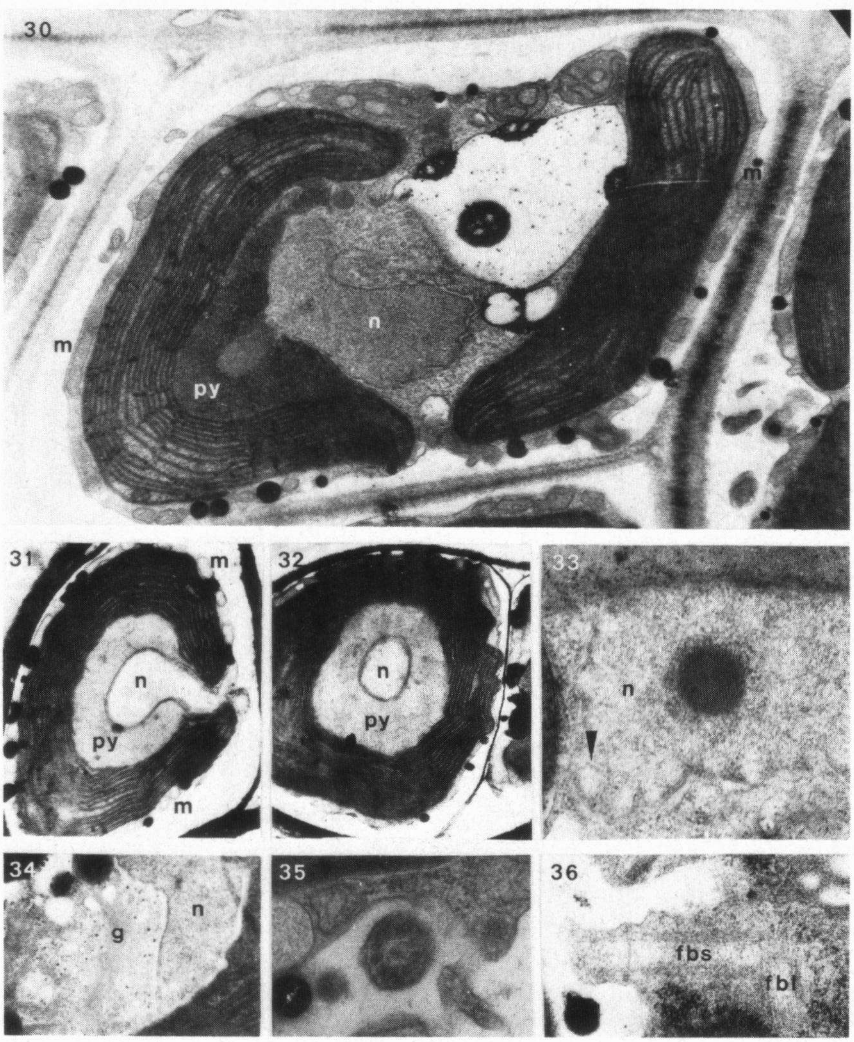

Plate 4. *Phaeoplaca thallosa.* Ultrastructure. For key, see plate 3.

Fig. 30. Low-power overall view of vegetative cell showing two chloroplast lobes with parallell lamellae and several girdle lamellae, hollow pyrenoid with closely appressed nucleus, nucleolus in pyrenoid hollow, large leucosin vacuole and peripherally distributed mitochondria and osmiophilic bodies. Note also thick cell walls. × 12,100.

Fig. 31. Cross section near top of cell from periphery of thallus; lobe of nucleus inside pyrenoid hollow. × 7,700.

Fig. 32. Cross section of cell in plane slightly higher than in fig. 31; chloroplast and pyrenoid seen as circular bodies with nucleus fitted into pyrenoid hollow. × 7,700.

Fig. 33. Light areas (arrowhead) seen at periphery of nucleus at cell lumen side. × 20,500.

Fig. 34. Golgi body inserted in depression of nucleus. × 12,100.

Fig. 35. Pseudocilium axis (long flagellum) sectioned just outside cell membrane. × 20,500.

Fig. 36. Cross section of short flagellum protruding only slightly from cell membrane, and glancing section of pseudocilium axis basal body (= long flagellum basal body). × 20,500.

3.7.2. *Phaeoplaca thallosa*

In *fig. 30*, an overall view of a vegetative cell of *Phaeoplaca thallosa* is given. The chloroplast lies close to the cell membrane: a pyrenoid is present, with the nucleus closely appressed to it. The Golgi body is positioned near the nucleus: one (or more) large and several small vacuoles fill the larger part of the cells.

The chloroplast consists of twelve to fifteen parallell lamellae; one or two of these are girdle lamellae. Lamellae are formed by three closely appressed thylakoids: the chloroplast matrix is finely granular. A pyrenoid apparently consisting of the same material lies within the chloroplast membrane. The canal in the pyrenoid, already described under light microscopical observations, can be seen as a circular spot in *fig. 32*, a section from the top of a cell. In *fig. 31*, a slightly lower section, it is seen to descend laterally into the cell. Chloroplast, pyrenoid and nucleus are enclosed by ER.

The nucleus is in close contact with the pyrenoid. In *figs. 31* and *32*, the nuclear membrane is seen to extend into the pyrenoid cavity, which is completely filled by a small lobe of the nucleus. The part of the nuclear membrane, turned towards the cell lumen, is rather wavy in several sections, with light patches in the otherwise uniformly grey, granular nuclear material (*fig. 33*): the chromatin otherwise seems to be evenly distributed. A nucleolus is often seen in the vicinity of the pyrenoid cavity.

An active Golgi body, consisting of twelve to fifteen cisternae, is seen in the close vicinity of the nucleus (*fig. 34*). Large vesicles are produced at the edges, and small ones near the central part.

Mitochondria are elongate, with tubular cristae, distributed along the cell membrane (*figs. 30, 31*).

Apart from the ER around chloroplast, pyrenoid and nucleus, no ER was found in the cytoplasm. Ribosomes are distributed freely in the cytoplasm.

In several sections, two flagellar basal bodies, lying at right angles to one another, can be seen (*fig. 36*). In *fig. 35* a flagellum just outside the cell membrane is seen in cross section. No flagellar root system as in *Chrysochaete brittannica* was found. Just beneath the cell membrane, small osmiophilic bodies are found (*figs. 30, 31*). They probably correspond with small, dark blue droplets seen in the light microscope when cresyl blue has been used to colour the large leucosin vacuoles. The cell wall is seen to be of a fibrous nature, rather compact, staining darkly as is the case with the light microscopial staining methods.

4. DISCUSSION

4.1. Comparison with older records

Our clones of *Chrysochaete brittannica* conform to the descriptions of GODWARD (1933), ROSENBERG (1941), BOURRELLY (1957, 1968), and TSCHERMAK-WOESS (1970) when thallus shape and form of vegetative cells and zoids are considered (see *table 2*). The chloroplast shape also corresponds to these de-

Table 2. Chrysochaete brittannica.

Reference	Thallus shape	Cell dimensions	Chloroplast	Other cell contents	Zoïds
Godward, 1933	discoid, in older colonies 2-layered	elongate; 4 × 9 – 10 × 15 μm.	one, V-shaped as seen from surface.	2–4, not confined to any special position.	not observed.
Rosenberg, 1941	idem.	spherical to long and narrow; 4 × 8 – 8 × 17 μm.	one, plate-shaped, sometimes lobed, bent into a V, parietal or central.	1 or 2, not strictly localised.	ovoid, slightly flattened with obliquely truncate anterior end, 10–15 μm long.
Bourrelly, 1957	discoid, 2-layered in centre of older colonies.	ovoid or elliptical; 6–8 × 10 μm.	one or two, parietal.	2, apical or median.	not observed.
Tschermak-Woess, 1970	exact shape not recorded; pseudoparenchymatous or loosely organised	6 × 7 – 8 × 10 μm.	one; mostly parietal, two-lobed plate. Isthmus oriented laterally, with bifid pyrenoid.	2–4, not stricly localised.	ovoid, 8 × 16 μm "conform Rosenberg".
Present study	discoid to semi-globose; multilayered in centre of older colonies; cells becoming distributed in peripheral layer of ± 1 mm large thalli.	variable in form from irregularly spherical to long and narrow; 9.5 × 9.5 – 5.5 × 13 μm.	one, mostly parietal, two-lobed plate. Isthmus oriented laterally, with bifid pyrenoid.	2–4, not strictly localised.	ovoid, to drop-shaped with flagella inserted subapically at the anterior, truncate end; 6 × 14 μm.

scriptions, except for the fact that the first three authors have not recorded the presence of the curiously cleft pyrenoid. This is only described in detail by Tschermak-Woess and confirmed by our observations. The absence of bristles she sometimes observed is also seen in our field material and as is shown by our experiments, probably depends on the chemical composition of the water.

It seems that the formation of mucilaginous bristles (since flagellum-derived structures are concerned, they should more properly be named pseudocilia, see WUJEK & CHELUNE 1975) as demonstrated in Tetrasporales (WUJEK & CHELUNE 1975) and of cellular hairs in Chaetophorales (TUPA 1974: YARISH 1976) and in our two Chrysophyceae are determined by environmental factors. In *Phaeoplaca* and *Chrysochaete*, the environment clearly influences mucilage formation. This is especially well apparent in *Phaeoplaca thallosa*, where at low nitrate content, besides pseudocilia, a copious layer of fluid mucilage is formed outside the cell walls: at higher concentration the mucilage disappears and so do the pseudocilia, but the "axis" of the pseudocilium often remains distinguishable in cultures. This has not been observed in *Chrysochaete brittannica.*

The descriptions of *Phaeoplaca thallosa* and *P. baicalensis*, as given by CHODAT (1925), MEYER (1930), SKUJA (1939), MARGALEF (1948), SMITH (1950), MATVIENKO (1951), BOURRELLY (1957, 1968) and STARMACH (1966), agree with ours of three Dutch clones (see *table 3*). As with *Chrysochaete*, the previous authors have overseen the pyrenoid. Mucilaginous bristles were not recorded either: we also have never observed them on field material. GEITLER's (1968) record of a Chrysophyte from Lunz should be named *Phaeoplaca thallosa*: he himself remarked that only on account of the presence of mucilaginous bristles he named the alga in question *Chrysochaete brittannica*, but otherwise he recognised it as his *Placochrysis membranigera* of 1926. His description of the pyrenoid is different from ours, however: the chloroplast is bell-shaped, with the open end oriented towards the cell base. It is cleft by two slits on opposite sides, thus consisting of two lobes, connected by an isthmus. On the inside of this bridge lies the pyrenoid, divided in two lobes in the same way. In each lobe a small, tubular hollow, open to the cell interior, can be discerned (GEITLER 1968, p. 137–138, plate 3). In most cells examined by us, the pyrenoid is not cleft in two halves, but consists of one body, with only one canal. This is illustrated in *fig. 17* (light microscopical observations) and also clear from our electron micrographs (*figs. 30, 31, 32*). However, in a few instances, especially in young thalli (up to eight cells) a cleft pyrenoid with two canals, as illustrated by Geitler, was seen. This may be interpreted as a pyrenoid being devided before cytokinesis. A comparable situation was occasionally found in *Chrysochaete*, where pyrenoids sometimes had two clefts.

4.2. Ultrastructure

Both algae show the usual features of the Chrysophyceae: a chloroplast with three-thylakoid lamellae of which one or more are girdle lamellae, chloroplast ER continuous with the nuclear envelope where these organelles are in close

Table 3. Phaeoplaca thallosa Chodat.

Reference	Thallus shape	Cell dimensions	Chloroplast	Other cell contents	Zoïds
Chodat, 1925	one-layered, ellipsoid, pleuro-coccoid or discoid in older colonies; 8–30 cells.	6–7 μm diam.	one, covering two-thirds of cell wall.	oil droplets.	not observed.
Geitler, 1926	one-layered, flat or curved, irregularly quadrate.	9–18 μm; the latter for cells about to divide.	one, parietal more or less irregularly lobed; two in cells before division.	leucosin, oil.	not observed.
Skuja, 1939	circular, one-layered longish, 17–28 μm × 15–20 μm, up to 11 μm thick.	quadrate to rectangular in cross section, marginal ones rounded off 5–6 μm × 5–11 μm, about 11 μm high.	two or three; parietal circular or lobed; yellow-brown, without pyrenoid.	nucleus one, more or less centrally.	not observed.
Margalef, 1948	one-layered, approx. quadrate, 2–16 cells.	5–10 μm diam.	two	not observed	not observed
Thompson in Smith, 1950	rectangular or discoid monostromatic plate.	6–9 μm diam.; angular because of mutual lateral compression.	one or two.	oil droplets, leucosin granules.	not observed.
Bourrelly, 1957	flat, rectangular or quadrate monostromatic plate of few cells, sometimes a little curved (max. 28 × 35 μm).	prismatic; diam. 6–7 (10) μm; 15 μm high.	one or two, irregularly lobed, parietal.	not observed.	not observed.

Starmach, 1966	flat, 2–8(16) cells.	polygonal, 6.5–9.0 × 8–13.5 μm and 9.3 μm high	two, after division sometimes one.	not observed.	not observed.
Geitler, 1968	parenchymatous plate; up to 64 cells, one-layered (seldom two). pseudocilia sometimes present, very hard to distinguish, united in bundles.	polygonal, higher than wide no dimensions given.	one, bell-shaped, with open end towards cell base, with two incisions; pyrenoid present in top, bifid, with a canal penetrating each half.	contractile vacuoles up to six; basal and elsewhere, mostly two or three.	not observed.
Present communication	monostromatic, parenchymatous, quite regularly rectangular or quadrate, flat or sometimes curved plate; pseudocilia sometimes present, difficult to distinguish, often united in bundles.	prismatic, rectangular in cross section. in young thalli (8 cells) 10–12 μm wide, in older thalli 4.0 × 5.5–7.5 × 5.5 and 12–15 μm high.	one, bell-shaped, with open end towards cell base, with two incisions; pyrenoid present in top, with small hollow excavated into it.	two basal contractile vacuoles; 2–3 large leucosin vacuoles and several oil droplets.	globular to drop-shaped with truncate anterior end; one flagellum inserted subapically; 7 × 12 – 6 × 6 μm.
Phaeoplaca baicalensis (Meyer) Bourr.					
Meyer, 1930	parenchymatous, one-layered, regularly quadrate or rectangular, larger thalli forming curved plates, 40–150 μm wide.	prismatic, ± 10 μm wide and ± 20 μm high.	one, before division two, parietal, horse-shoe shaped plate (as seen in optical section from the side) with open end downwards.	two basal contractile vacuoles; leucosin granules.	not observed.
Matvienko, 1951	one-layered plate, sometimes curved; quadrate or rectangular.	quadrate, 7–21 μm.	one, lamellate.	two basal contractile vacuoles; leucosin granules.	not observed.

contact, and mitochondria with tubular cristae ("microvilli"). In *Chrysochaete*, chloroplast form, position and bifid structure of pyrenoid are comparable to those in *Sphaleromantis marina* Pienaar (1976) (Heterochrysophycidae, Chromulinales, Chromulinaceae). The pyrenoid of *Phaeoplaca* is not directly comparable to those found in ultrastructural studies of other Chrysophyceae. In our species, the very close relationship of pyrenoid and nucleus is striking, especially in *Phaeoplaca thallosa*, where the latter organelle completely fills the pyrenoid hollow. In *Chrysamoeba* (HIBBERD 1971) and *Ochromonas* (SLANKIS & GIBBS 1972), only chloroplast envelope and periplastidial network penetrate the pyrenoid channels, although HIBBERD (1971) indicates that chloroplast ER and nuclear membrane possibly also penetrate into the *Chrysamoeba* pyrenoid channels. The flagellar apparatus which is apparently present but not functional in vegetative cells of both species, shows another example of Chrysophyceae from the order Chromulinales (according to BOURRELLY 1968) that actually possess a second flagellum, be it much reduced. In both species, the long flagellum apparently forms the axis of the pseudocilia, which are thus comparable to similar structures in the Tetrasporales (Chlorophyceae), where *Tetraspora*, *Paulschulzia* and *Chaetopeltis* are shown to possess pseudocilia with a flagella-like fine structure, except for irregularities like absence of central fibrils and gradual disappearance of peripheral fibrils distally from the cell (WUJEK & CHAMBERS 1965: LEMBI & HERNDON 1966: WUJEK 1968: LEMBI & WALNE 1971: WUJEK & CHELUNE 1975). Sections of thalli of *Chrysochaete* and *Phaeoplaca*, in which pseudocilia have been sectioned outside the cell membrane (*fig. 35*), show that besides the peripheral fibrils, the central pair of fibrils is also present.

The presence of a striated flagellar root in vegetative cells of *Chrysochaete brittannica* is remarkable, since the pseudocilia do not have any locomotory function. The appearance of the root – immersed, together with a part of the Golgi cisternae, in a cavity in the nuclear envelope – is conform the outline of Chrysophycean ultrastructure as given by HIBBERD (1976). From several sections, the impression is gathered that actually two branches of the striated root together with part of the Golgi body are immersed in such a long, narrow cavity in the nuclear envelope.

The fan-shaped Golgi body, with cisternae flat and bunched together, proximal to the basal bodies, and spread out and dilated at the other end, rather conforms to HIBBERD's (1976) description for Prymnesiophycean (Haptophycean) than for Chrysophycean types.

Beneath the striated root, the nuclear envelope is strongly folded and appears to give off small vesicles. BELCHER & SWALE (1971) reported the same type of small spherical vesicles to be present in the cytoplasm between nuclear envelope and Golgi body. The small dark bodies observed at the cell periphery of *Phaeoplaca thallosa* in electron micrographs may be termed "corps mucifères" (BOURRELLY 1957). They are not functional in any way like projectiles (discobolocysts) as is the case in several planktonic Chrysophyceae (for discussion see HIBBERD 1970).

4.3. Taxonomy

For *Phaeoplaca thallosa*, the findings now published have consequences as to its systematic position. Since its zoids are of the Chromulina type, it belongs in the subclass Heterochrysophycidae, order Chromulinales (systematics according to BOURRELLY 1968). On account of its parenchymatous habit, it should be placed in the suborder Thallochrysidineae containing the families Thallochrysidaceae (parenchymatous or pseudoparenchymatous thalli) and Chrysocloniaceae (simple or branched filamentous thalli). The latter was created by GAYRAL & HAAS (1969), after removing *Chrysomeris ramosa* Carter from this place to the order Ochromonadales. The family Thallochrysidaceae contains the monotypical genus *Phaeodermatium* and the genus *Thallochrysis* with *T. pascheri* and *T. litoralis*. *Phaeodermatium rivulare* is an encrusting alga, found in freshwater streams. It forms large, multilayered patches that coalesce to cover pebbles and stones completely. In young thalli, the growth habit is observed to consist of closely appressed, branching filaments (PASCHER 1925). *Thallochrysis pascheri* is an alga from brackish habitats, forming free-floating pseudoparenchymatous clumps, in which the filamentous habit is recognisable (PASCHER 1925). *T. litoralis* is a doubtful species, that may be the benthic phase of a Prymnesiophycean alga.

The monotypic family Chrysocloniaceae comprises *Chrysoclonium ramosum*, a *Phaeothamnion*-like, free-floating freshwater alga.

When comparing *Phaeoplaca thallosa* with the above-mentioned algae, it becomes clear that the strictly one-layered, parenchymatous growth habit and the possession of pseudocilia set *P. thallosa* apart from the families Thallochrysidaceae and Chrysocloniaceae. It is therefore proposed to maintain the monotypic family Phaeoplacaceae, and to move it from the subclass Acontochrysophycidae to the Heterochrysophycidae, order Chromulinales, suborder Thallochrysidineae, next to the Thallochrysidaceae.

The diagnosis of the suborder Thallochrysidineae is accordingly enlarged to encompass forms with pseudocilia. The diagnosis of the family Phaeoplacaceae Bourrelly 1957 should be augmented in the same way: Chrysophytes forming regular flat, rectangular or square thalli consisting of one layer of cells, each provided with a pseudocilium. Zoids are of the Chromulina type.

As a consequence of the rearrangement of the Phaeoplacaceae, the order Phaeoplacales of the subclass Acontochrysophycidae is reduced in scope. The family Sphaeridiotrichaceae, from which *Sphaeridiothrix* Pascher & Vlk was already removed (see DOP & VROMAN 1976), is now its only constituent, with the genera *Chrysonema* Anand and *Stichochrysis* Pringsheim remaining. The genus *Nematochrysopsis* Chadefaud was removed from it by GAYRAL & LEPAILLEUR (1971), to the Ochromonadales, Phaeothamniineae in its own monotypic family Nematochrysopsidaceae, and subsequently placed by GAYRAL (1972) in the newly proposed order Sarcinochrysidales. It is not surprising to see a gradual reduction in the subclass Acontochrysophycidae: it was predicted by BOURRELLY (1957, 1968) that a number of species, only provisionally placed here in absence of knowledge of zoids, would in due course take their place among the other subclasses.

Chodat's generic description of *Phaeoplaca* should be altered to include data about pseudocilia and type of zoids: Small pleurococcoid thalli, formed by regular division of cells, bounded by firm cell walls. Thallus cells rectangular or round, provided with one golden-brown to chestnut-brown chloroplast, oil and leucosin vacuoles, and contractile vacuoles. Each cell is provided with one mucilaginous pseudocilium. Multiplication is accomplished by zoids of the *Chromulina* type.

The specific description of *Phaeoplaca thallosa* poses somewhat of a problem. It points to the likeness of *P. thallosa* thalli to those of *Coleochaete scutata*, while three of the four illustrated thalli are clearly rectangular. The fourth thallus is a large one (about thirty cells), in which several empty cells are pictured. As indicated before, the elastic nature of the cell walls may account for their collapsing and the subsequent rounding off of the thallus concerned. Especially in older ones like that illustrated by Chodat, this becomes apparent. Taking all this into account, there does not seem to be any reason to doubt that all records of *Phaeoplaca thallosa* actually concern Chodat's alga. This view is strongly supported by the fact that Chodat himself immediately recognised GEITLER's (1926) clearly rectangular *Placochrysis membranigera* as his *Phaeoplaca thallosa.*

Therefore, the description of *Phaeoplaca thallosa* can now be changed to include details about chloroplast form, pyrenoid, and pseudocilia: Chodat's vague allusion to "spores" can be supplanted by a description of the zoids: Thallus flat, monostromatic, rectangular or quadrate, through regular cell division in two perpendicular directions. Shape of large thalli (up to 140 cells have been observed) is irregularly ellipsoid or discoid, sometimes curved. The cell wall is thick and firm, easily visible: cell shape is prismatic, rectangular or sometimes ellipsoid in cross section. Cell dimensions are: 10–12 μm in cross section in young thalli (up to eight cells) and 4 × 5.5 μm to 7.5 × 5.5 μm in larger thalli: cell height is 12–15 μm. Cells are provided with two basal contractile vacuoles, two or three leucosin vacuoles and several small lipid droplets. They have one parietal, bilobed chloroplast with one wide, shallow and one narrow incision. The bridge, joining the two chloroplast lobes is positioned at the cell top. A hollow pyrenoid lies appressed to the inside of this bridge. Each cell is provided with a pseudocilium with a protoplasmic axis 100 μm long and 2–3 μm thick: the latter is not always developed, however, and if present, difficult to observe without the aid of a colouring reagent. Zoids issue singly from thallus cells: they are oval with a truncate anterior end, or globose, 7 × 12 to 6 × 6 μm large. They have a single chloroplast identical to that of vegetative cells, with a red stigma located on a chloroplast lobe, near to the single, subapically inserted flagellum, and several leucosin and lipid droplets, and two or three contractile vacuoles.

When comparing the data for *P. baicalensis* (Meyer) Bourr. and *P. thallosa* Chodat (*table 3*), it becomes clear that there might not be sufficient reasons to maintain *P. baicalensis* as a separate taxon. The fact that the pyrenoid was not observed by most authors is not surprising, since it is very difficult to distinguish, except in one- or two-celled thalli that have not yet formed large leucosin vacuoles obscuring cellular details. In our opinion, conflicting records of number of chloroplasts are not significant either, since chloroplast fission preceding cell division and the difficulty to observe the exact chloroplast shape, with its sometimes irregularly shaped lobes, can account for these.

Since we have not yet been able to investigate type material – if available – of *P. baicalensis*, however, the definite decision about its taxonomic status must be postponed.

STARMACH (1968) discerns three species in the genus *Phaeoplaca*: *P. thallosa*, *P. baicalensis* and also *P. membranigera* (Geitler) Starmach. For reasons outlined above, this example does not deserve following.

As far as *Chrysochaete brittannica* is concerned, only the pyrenoid has to be included in Rosenberg's description. This is most readily accomplished by striking the words "sine pyrenoide" from her generic description of *Chrysochaete*:

Familiae epiphyticae, discoidae, in plantis aquaticis vel laminis vitri. Familiae cellulis 2 ad 310 constans, strato gelatinoso tecta: cellulae vel nonnullae, integumentis gelatinosis praeditae: setae longae mucosae, in familiis juvenalibus e tubo singulo constantes, in familiis senioribus, elaboratae valde ramosae, saepe furcatae, e tubis mucosis plurimis constantes; filum protoplasmaticum in quoque tubo unum, e cytoplasmate cellularum quarumque ortis, in vivo conspicuum. Chromatophora unum vel duo, flavo-fusca, saepe curvata in forma V, cellulae guttis oleae et leucosine praeditae, 1 ad 5 vacuolis contractibilibus. Reproductio zoosporis uniflagellatis, similibus cellulis somaticis mobilibus, flagellum longitudine duarum cellularum vel longius. Divisiones ante formationem zoosporarum non observatae. Zoosporae liberatae per imbibitionem muci, primo modo amoebae deinde per flagellum moventes; quietae novas familias formantes.

Chloroplast form and presence of pyrenoid can now be included in the specific description of *C. brittannica*:

C. brittannica (Godward) Rosenberg

Familiae 2–320 cellulis constans; strato gelatinoso 3–4 μ lato, non laminato tecta; cellulae stratum singulum sed in parte centrale familiarum vetustarum strata duo superposita formantes: setae 1–10 in familia: fila protoplasmatica nonnumquam basin versus furcata ad cellulas duas juncta: cellulae globosae vel elongatae, 1–4 vacuolis contractibilibus praeditae: chromotophora singula, biloba: pyrenoidum atque bilobum, ad lobarum chromatophorae junctionem positum: stigmate ante formationem zoosporae patente: zoospora paulo complanata, apice obtuse truncata, stigmate aurantiaco-rubro, ad chromatophorum affixo; vacuolis contractibilibus duobis versus apicem praedita. Dimensiones: familia 204 μ diametro maximo: setae 150–400 μ longae, 3 μ latae: cellulae 4–9 μ × 8–17 μ; zoosporae 10–14 μ longae, flagellum maximum 25 μ.

The separate identity of the genus *Naegeliella* remains debatable: nothing can be added to the discussion as given by ROSENBERG (1941) and GEITLER

(1968) until the type species is found again. For a key to *Chrysochaete* and *Naegeliella*, see ROSENBERG (1941).

The records for *C. brittannica* and *P. thallosa* now include finds from the following countries:

Chrysochaete brittannica (Godw.) Rosenberg
England, GODWARD 1933 (as *Naegeliella brittannica*): ROSENBERG 1941.
Austria, ROSENBERG 1941: TSCHERMAK-WOESS 1970, 1971.
France, BOURRELLY 1957.
The Netherlands, DOP & VROMAN 1976.

Phaeoplaca thallosa Chodat
Switzerland, CHODAT 1925.
Austria, GEITLER 1926 (as *Placochrysis membranigera*); GEITLER 1968 (as *Chrysochaete brittanica*).
Latvia, SKUJA 1939.
Spain, MARGALEF 1947.
U.S.A., SMITH 1950: WHITFORD & SCHUMACHER 1963.
France, BOURRELLY 1957.
Poland, STARMACH 1966.
The Netherlands, DOP & VROMAN 1976.

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