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Chrysocystis fragilis gen. nov., sp. nov. (Chrysophyceae, Sarcinochrysidales), with Notes on Other Macroscopic Chrysophytes (Golden Algae) on Guam Reefs

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Abstract—Golden algae up to several centimeters long occur on the reefs of Guam and other western Pacific islands. In particular, a sometimes-abundant saccate chrysophyte occurs that does not fit any of the known genera. This alga forms fragile colonies with the cells dispersed in a common matrix, and forms motile cells by two successive divisions of the vegetative cells. The motile cell possesses two unequal, lateral flagella. These features suggest that this alga is a new member of the order Sarcinochrysidales in the class Chrysophyceae. Another macroscopic member of the Sarcinochrysidales, the filamentous *Chrysonephos lewisii* (Taylor) Taylor, also occurs on Guam, together with some stiff gelatinous colonies and the enigmatic alga *Phaeocystis taylori* Lewis et Bryan.

Introduction

The Chrysophyceae comprises golden-brown microscopic algae (containing chlorophylls *a* and *c*, and fucoxanthin as a major accessory pigment) and their colorless relatives. They are classified in the Division (Phylum) Chrysophyta, which is part of the new Kingdom Chromista (Cavalier-Smith 1986, 1989). The

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Chrysophyceae were relatively poorly studied until recently, perhaps because many are small or rare phytoplankton (Andersen 1987). Studies in the last twenty years or so have led to the separation of several new classes, most recently the Pelagophyceae (named after the nannoplankter *Pelagomonas,* not the giant kelp *Pelagophycus*) (Andersen et al. 1993). Thus the presence of macroscopic species or large colonies of chrysophytes is of interest for extending our knowledge of this class, and potentially for better understanding its relationships with other Chromista (such as the brown algae) (O'Kelly & Floyd 1985, O'Kelly 1989, Gayral & Billard 1977, 1986).

Among the red, green, and brown seaweeds on the reefs of Guam and other islands in the western Pacific Ocean are some golden-yellow algae, most of which proved to be in the Sarcinochrysidales—an order of Chrysophyceae which Andersen et al. (1993, p. 713) characterized as "enigmatic." One of these, which can be abundant and conspicuous, is in a new genus. We also report the presence of several other macroscopic chrysophytes.

Materials and Methods

Field observations were made by snorkeling or diving on the reef platforms and fore-reef slopes of Guam, Iriomote (Ryukyus), Palau, Pohnpei, and Majuro. The fragile colonies of *Chrysocystis* were collected by floating them into plastic bags or sucking them off the algal turf with large pipettes. Other species were coherent enough to pick by hand.

Cultures of *Chrysocystis* were established from single cells isolated from samples collected from Guam and Iriomote. Single cells were isolated by capillary pipette and transferred into ESM medium (cf. Watanabe & Kasai 1985). Cultures were maintained at 20°C and 25°C on a 12:12h light-dark cycle.

For light microscopy, an equal volume of cell suspension and 2% glutaraldehyde solution (prepared in cacodylate buffer [pH 7.2] containing 0.5M sucrose) were mixed and observed with a Nikon Optiphot ZF and XF-NT fitted with a Nomarski interference differential contrast objective.

For observation of chloroplast DNA, a drop of cell suspension was mixed with 2% glutaraldehyde solution and 1μg mL^{-1} 4',6-diamidino-2-phenylindole (DAPI) solution. Both solutions were prepared in TAN buffer consisting of 0.25M sucrose, 20mM Tris-HCl (pH 7.6), 0.5mM EDTA, 1.2mM spermidine, 7mM 2-mercaptoethanol and 0.4 mM PMSF (Nemoto et al. 1988). Cells were then viewed

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Figures 1–2 (color plate). *Chrysocystis fragilis* colonial morphology. Figure 1. Natural habitat at a depth of 5 m, Anae Island, Guam. Figure 2. The fragile, saccate colonies attached to dead coral ca. × 4.


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with an epifluorescence microscope (Olympus BHS-RFK) under ultra-violet excitation.

For observations of non-fixed zoospores, we used a VHS high-speed video of NTSC format (NAC MHS-200) mounted on a Nikon Optiphot bright field microscope at 200 frames per second.

Chrysocystis fragilis

HABITAT

Colonies are present year round on the reefs of Guam, from lower water to at least 20m deep. Water temperatures are 28–30°C. Colonies are extremely abundant in shallow water in April–June, when they form extensive epiphytic masses on algal turf over rocks and dead coral (Fig. 1). Scattered colonies of a filamentous chrysophyte, *Chrysonephos lewisii* (Taylor) Taylor (Taylor 1951, 1952), are often intermixed with *Chrysocystis fragilis.* Colonies have been rarely found on the windward side of the island except in flowing seawater tanks. On the leeward side, many sites have significant wave action during the wet season when tropical storms and typhoons are common, and at these sites we have only found colonies during the "spring bloom". These observations suggest that *C. fragilis* can exist in the microbenthos and is probably very widespread. Other factors besides wave action are expected to be involved in the abundant development of saccate colonies, but we have not attempted to define these.

Records (partial list)—Orote Pt., 6/10/89 (GU38A), 10/3/89 (GU38F, G); Glass Breakwater/Luminao Reef, 7/1/89, 9/5/89 (GU41C), and many subsequent occasions; Anae I., 4/10/89 (GU35A); Hilaan Reef, 11/11/89 (GU6H); Manoan Channel, Merizo, 9/15/89 (GU14K). Chance observations on other islands indicate that *C. fragilis* is also abundant on Tinian, Saipan and probably other northern Mariana Islands in April–June. In Japan, *C. fragilis* was observed on Iriomote Island (Ryukyu Islands), 3/91.

MORPHOLOGY

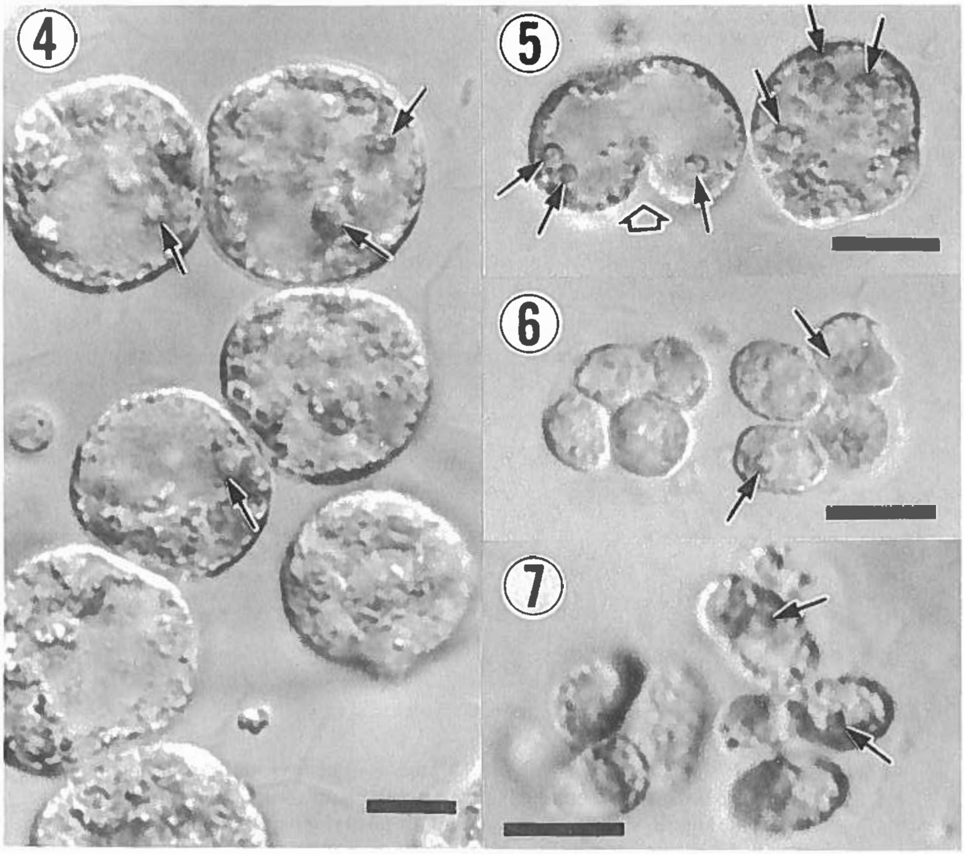
Colonies are cylindrical or irregular sacs in which cells distribute in a layer of very fragile, amorphous mucilage (Fig. 2). The interior of the colony contains very watery mucilage (Fig. 3). Colonies are too fragile to pick up by hand and are easily dislodged by water currents such as from a diver's fins. However, they grow in areas where there is some water exchange or slow currents. The colonies are usually 20–50mm long and about 5mm wide in size, but may be much wider or longer because we observed 0.3m long specimens in calm places. Probably the colony size is affected by the extent of water motion or other disturbance. In culture condition this alga never formed cylindrical narrow colonies. It formed irregular, gelatinous, heaped colonies on the bottom of the culture dish. There is no distinct holdfast or point of attachment; rather, the lower part of the colony engulfs the turf. Colonies often harbor other algae, especially diatoms, benthic dinoflagellates and cyanophytes. Older colonies are invaded by small crustaceans, other animals and protists.

Cells are irregularly spherical, 8–14μm in diameter, and disposed mainly at the periphery of the colony (Figs. 3, 4). There are neither boundary lines nor layered structures in the gelatinous material surrounding the cells. They contain four to eight light-brownish chloroplasts which are slightly constricted disk-shaped. Each of them possesses one pyrenoid (Figs. 4–7). Under the cell membrane there are noticeable refractive muciferous bodies which give the cell outline a faintly beaded appearance, especially in optical section (Figs. 4, 5).

Reproduction by motile cells has been infrequently observed; the abundance and fragility of colonies suggest that fragmentation may be an important means of dispersal. When freshly collected colonies were put in an air-conditioned room (22–24°C) overnight, motile cell formation sometimes occurred. Motile cell production involves two successive cell divisions of vegetative cells, resulting in formation of four biflagellate cells (Figs. 5–8). Although this is suggestive of meiosis, we could not count chromosome number and have no evidence of cell fusion. Cytokinesis takes place by furrowing of plasmalemma from one side of the cell (Figs. 5, 8). While chloroplast division occurs at vegetative cell division, at the cell divisions of the motile cell formation it does not occur and the chloroplasts are distributed among the daughter cells.

Each motile cell is oval or somewhat pyriform, measuring typically 4–5 μm long and 2–3 μm diam. (Figs. 9, 10). One light-brownish chloroplast is present at the posterior part of the cell. Two unequal flagella are inserted laterally near the edge of the chloroplast. The anterior locomotive flagellum, 9–13 μm long, displays rapid sinusoidal quivering. The posterior flagellum, 5–6 μm long, exhibits

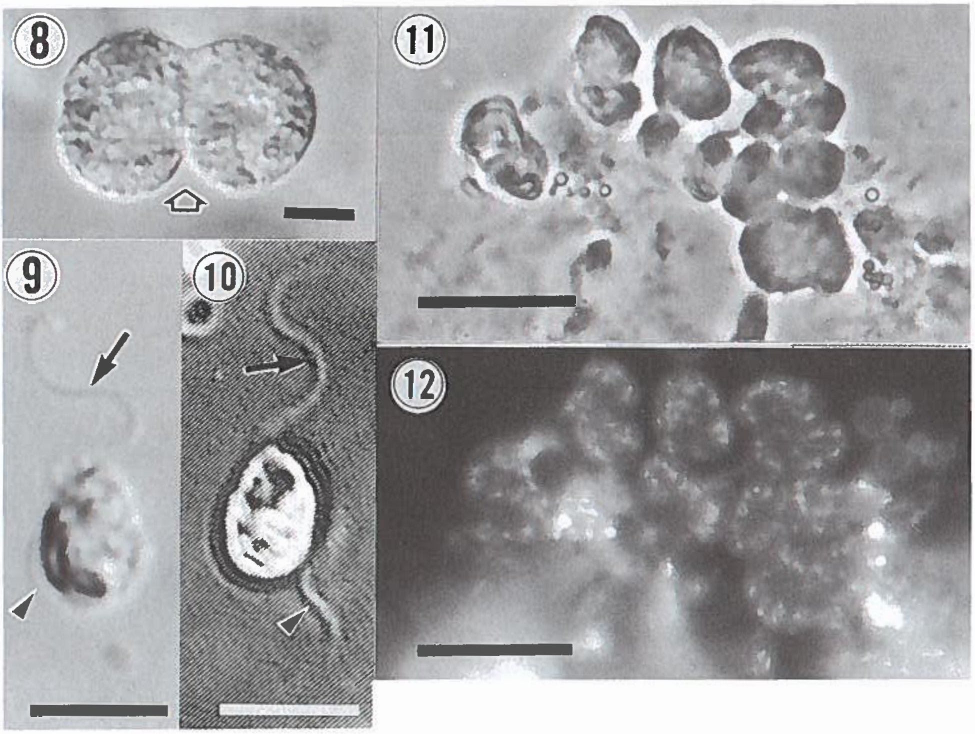
Figure 3. *Chrysocystis fragilis.* Section of the colony. Note cells disposed mainly at the periphery. 3: Scale bar = 10 mm.



Figures 4–7. *Chrysocystis fragilis* cellular morphology. Figure 4. Vegetative cells. Note the refractive muciferous bodies at the periphery of the cell and several pyrenoids (arrows). Figures 5–7. Motile cell formation. Arrows indicate pyrenoids. Figure 5. The vegetative cell (right) and the first successive cell division of a vegetative cell (left), showing the cleavage furrow from one side (open arrow). Figure 6. Two clusters of four non-flagellate cells after two successive cell divisions of each vegetative cell. Figure 7. Two clusters of four motile cells with flagella. Scale bars 4, 5, 7: = 10 μm; 6 = 5 μm.

active lashing or undulating. The cell swims with a rotary motion. Although the eyespot is absent, the basal portion of the posterior flagellum faces a part of the chloroplast. The cell has muciferous bodies and the electron dense cell covering as do vegetative cells (Figs. 13–14). Under the electron microscope the pyrenoids are seen to be stalked (Fig. 16). Scale-like structures have been noticed in a vacuole (Fig. 15).

Unlike typical chrysophytes, the chloroplast DNA is not ring-shaped. Many small DNA-containing areas are scattered throughout the chloroplast (Figs. 11, 12). Their distribution pattern is stable throughout the life history of this alga.



Figures 8–12. *Chrysocystis fragilis*. Figure 8. Cytokinesis of a vegetative cell showing the cleavage furrow from one side (open arrow). Figures 9 and 10. Motile cells, showing the anterior flagellum (arrow) and the posterior flagellum (arrow head): Figure 9. Fixed motile cell. Fig. 10. Swimming motile cell (high-speed video image). Figures 11 and 12. Crushed vegetative cell fixed and stained for DNA with DAPI in phase contrast (Figure 11) showing the chloroplasts and the same cell under ultraviolet excitation (Figure 12) showing a number of separate small fluorescences of chloroplast DNA in the chloroplasts. Scale bars = 5 μm.

DESCRIPTION

Chrysocystis Lobban, Honda et Chihara gen. nov.

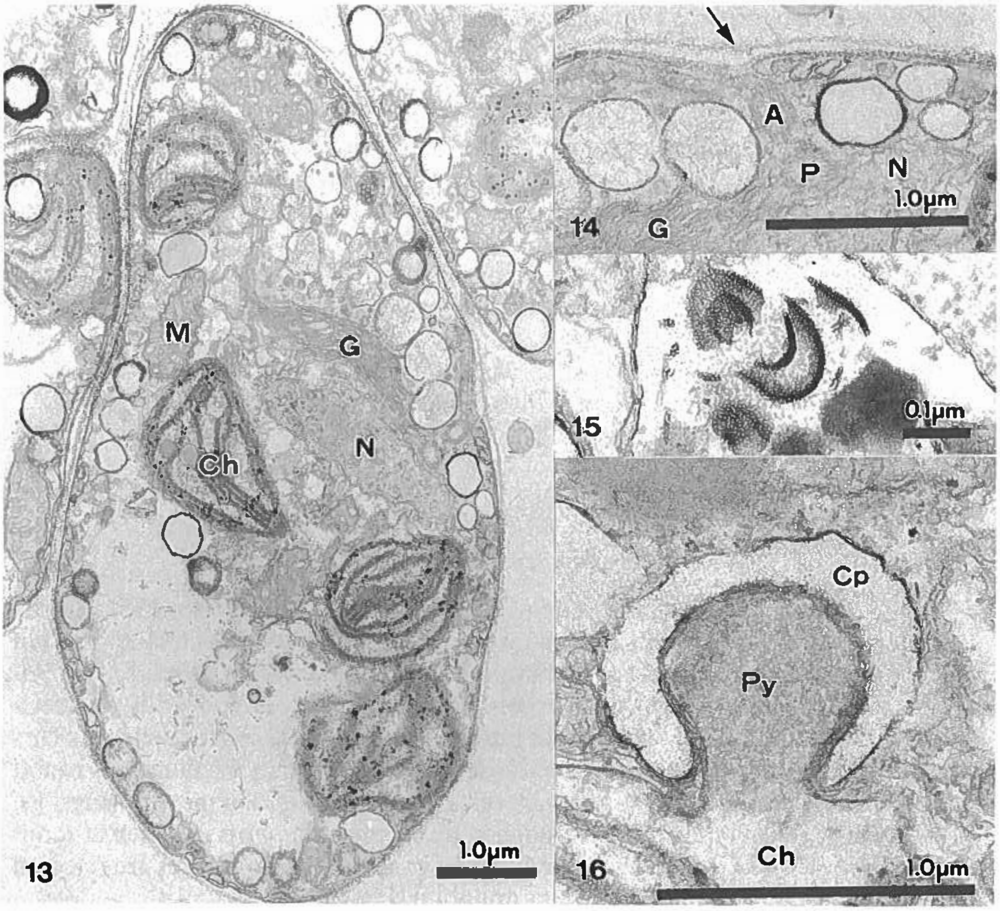
Planta colonialis, gelatinosa, solida, pallide aurea, cellulis periphericue locatis constans; cellulae chloroplastos aureos habentes.

Reproductio asexualis a fragmento coloniae vel forma zoosporarum effecta; reproductio sexualis ignota; zoosporae per duas successivas divisiones cellularum vegetativarum, factae pyriformes vel ovatae, unum aut aliquot chloroplastos et flagella bina inaequalia inserta lateraliter habentes, sine stigmate.

Typus generis: Chrysocystis fragilis sp. nov.

Plant colonial, gelatinous, solid, pale golden yellow, consisting of peripherally located cells; cells having golden yellow chloroplasts.

Asexual reproduction by means of fragmentation of colony or formation of zoospores; sexual reproduction unknown; zoospores formed by two successive



Figures 13–16. EM sections of *Chrysocystis fragilis* zoospores. Figure 13. Longitudinal section of zoospore. The Golgi body (G) is situated anterior to the nucleus (N), which is located at the middle part of the zoospore. The entire cell body is surrounded by an external cell covering. Figure 14. Detail of the external cell covering (arrow) near the insertion of anterior (A) and posterior (P) flagella. Figure 15. Scale-like structures showing three layers. Figure 16. Projecting pyrenoid (Py) with the capping vesicle (Cp). Other abbreviations: M, mitochondrion; Ch, chloroplast.

cell divisions of vegetative cells, pyriform or ovoid, with one or several chloroplasts and two laterally inserted unequal flagella; stigma absent.

Type of the genus: *Chrysocystis fragilis* sp. nov.

Etymology: *chrysos,* Greek: gold + *kystis,* Greek: bladder.

Chrysocystis fragilis Lobban, Honda et Chihara sp. nov.

Colonia cylindrica, gelatinosa, fragilis, 30–50 mm longa, ca. 5 mm diam.; cellulae sphaericae, 8–14 μm diam., pariete tenui obtectae, corporibus mucilaginis parvis parietalibus; 4–8 chloroplasti parietales, aurei, elliptici, acetabuliformes, *saepe ad centra constricti, cum una vel duabus pyrenoidibus protuberantibus; zoosporae pyriformes vel ovatae, 4–5 μm longae, 2–3 μm latae, chloroplasto unico, postice; flagellum anticum 9–13 μm longum, flagellum posticum 5–6 μm longum.*

Typus: TNS-AL39667. *Isotypus:* TNS-AL39669-39672.

Colony cylindrical, gelatinous, fragile, 30–50 mm long, about 5 mm in diameter; cells spherical, 8–14 μm in diameter, covered with a thin thecate wall, with small muciferous bodies peripherally located; four to eight peripheral chloroplasts, elliptical, saucer-shaped, often constricted at the center; possessing one or two projecting pyrenoids; zoospores pyriform or ovoid, 4–5 μm long, 2–3 μm wide, with single posterior chloroplast; anterior flagellum 9–13 μm long, posterior flagellum 5–6 μm long.

Type: TNS-AL39667 (glass slide with zoospores). Isotypes: TNS-AL39669-39672 and at UC. Luminao Reef (Glass Breakwater), Guam. 13 Feb. 1990.

Paper mounts of colonies: TNS-AL39674-896777; UC1612796; and at UMICH.

Etymology: *fragilis,* Latin: fragile.

Chrysonephos lewisii (Taylor) Taylor

Dichotomously branched filaments forming yellow tufts (Taylor 1951; Taylor 1960, p. 195 and pl. 28). Tufts as seen on Guam are generally short (10–20 mm) in the field, but plants found in seawater tank were very much longer (Figs. 17, 18). Although filaments resemble an ectocarpoid brown alga, they are not truly multicellular but comprise mucilaginous tubes into which individual cells are packed. This structure becomes evident during reproduction, when cells in the filaments round up and become motile swarmers that are released from the end of the tube (Figs. 19, 20). Zoospore release may often be induced by keeping filaments in a dish at room temperature (20–22 C—cool compared to field conditions). Zoospores are released after about 24 h and showed photoaccumulation (Fig. 21).

Records—GUAM (partial): Anae I., 6/10/89 (GU38B), 4/13/90; Orote Pt., 10/3/89 (GU38D); Glass Breakwater/Luminao Reef, 12/1/89; Hilaan Reef, 11/11/89 (GU6I). SAIPAN: Obyan Beach, 12/17/89 (S13B). PALAU: Ngesol Reef, Koror, 1/7/90 (PA-4); Ngercheu Islets (Rock Islands), 1/14/90 (PL-3). HAWAII: Punalu'u, Oahu, 8/89 (H8A). Voucher deposited in UMICH.

Other Sarcinochrysidales

Sturdy gelatinous colonies, resembling *C. fragilis* except for being firm and stiff have been occasionally found on Guam. We have tentatively identified these

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Figures 17–20 (color plate). *Chrysonephos lewisii.* Figure 17. Unusually long colonies in seawater tank, rising ca. 30 cm from bottom and forming floating mats. Figure 18. Normal colony in seawater tank, approx. 2× life size. Figure 19. Zoospore release. Scale = 50 μm. Figure 20. Detail of zoospore in mucilage tube. Scale = 10 μm.

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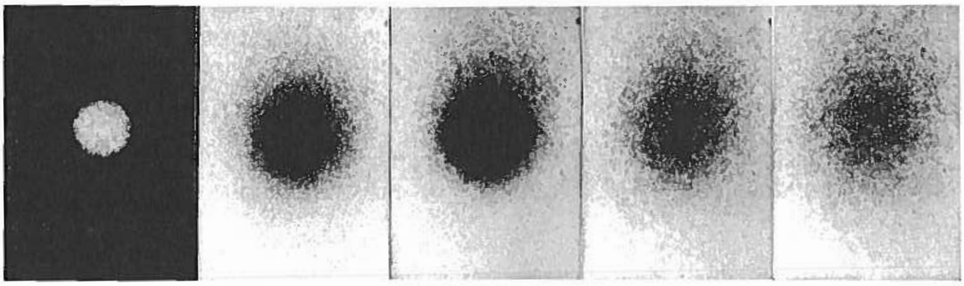
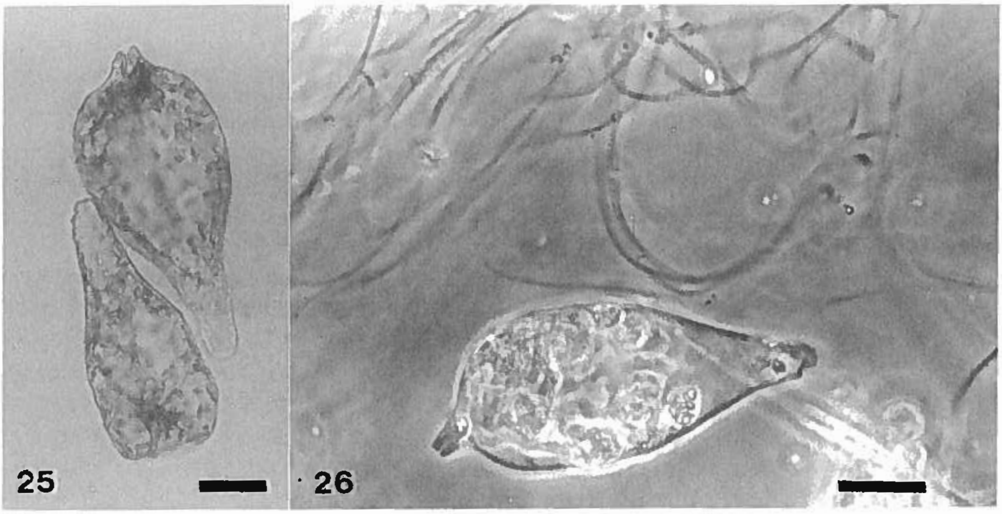


Figure 21. *Chrysonephos lewisii.* Time series at 4 s intervals showing dispersal of zoospores. Cells had concentrated into light spot caused by closing iris diaphragm on microscope. 4× objective.



Figures 25, 26. *Chrysophaeum taylori.* Microscopic views showing mucilage stalks and characteristic shape of cells. Scale = 10 μm.

as including *Sarcinochrysis* sp. and *Pulvinaria* sp. (Figs. 22, 23). *S. marina* has been reported from enrichment cultures from a Hawaiian reef (West 1969).

Chrysophaeum taylori Lewis et Bryan

Clumps of gelatinous streamers which have the texture of large blue-green algal colonies, but with yellow cells powdering the tips (Fig. 24). Cells are on the ends of delicate, intertwined stalks but the stalks cohere in the copious mucilage. The cells are very unusual, with a tubular invagination at the anterior end (Figs. 25, 26). While Lewis & Bryan (1941) described this as a "putative Cryptophyte", no work has been done on the cytology or pigmentation of this organism. See also Taylor (1960, p. 194). This species has sometimes been abundant on Rizal

Beach, Guam, and blooms at Townsville, Australia were extensive enough to be considered a public nuisance (I. R. Price, pers. communication).

Discussion

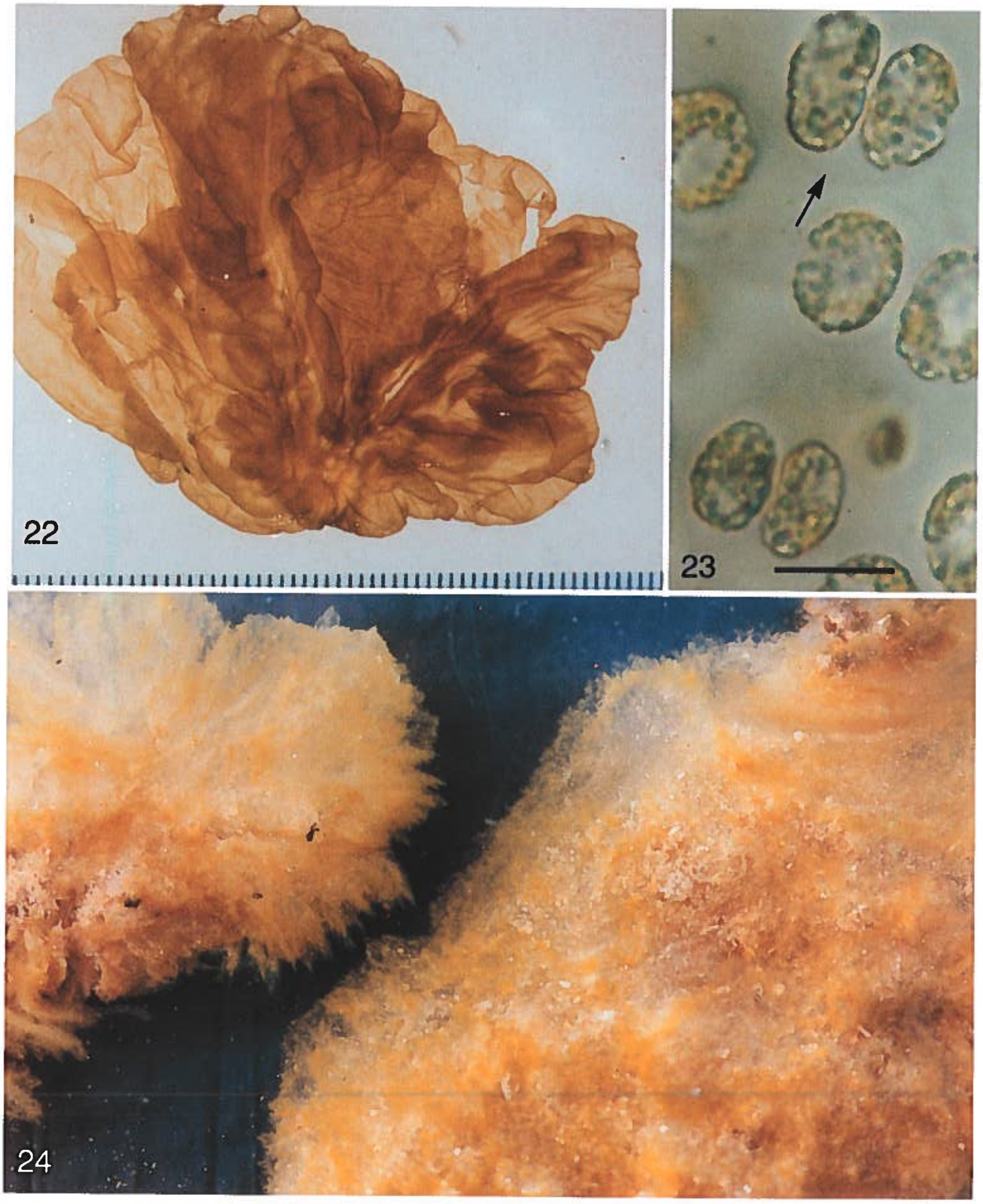
The structures of vegetative and motile cells of *Chrysocystis* are similar to those of *Pulvinaria* (Billard & Fresnel 1980) but *Chrysocystis* has a distinctive

Table 1. Comparison of *Chrysocystis* with related Sarcinochrysidaceae[a]

	Chrysocystis fragilis	*Pulvinaria*	*Sarcinochrysis*
Colony type	Delicate saccate colonies 30–50 mm long by 5 mm wide.	Pulvinate colonies a few mm in diameter	Unicellular & planktonic or small palmelloid colonies
Habitat	Sublittoral, epiphytic; stenohaline?	*P. feldmannii*: upper littoral, saltmarsh; epiphytic and epithithic; euryhaline *P. algicola*: epiphyte; sublittoral, stenohaline *P. giraudii*: epiphyte; littoral, stenohaline	Upper littoral, saltmarsh; sublittoral; epiphytic; euryhaline
Arrangement of cells	Irregularly dispersed in a common matrix	Irregular packets surrounded by thick matrix; layers of matrix around older cells	Cube; short filament; irregular packet
Muciferous bodies	Yes	Yes	Yes
Plastid: number	4–8	*P. feldmannii*: 2 (more in mature cells) *P. algicola*: 4	1–2
pyrenoid	Type III	Type III	Type III
genome	Scattered	Scattered	Scattered
Motile cell formation	Two successive divisions of vegetative cell	*P. feldmannii*: "emission" of single flagellated cells	"Emission" of single flagellated cells
Motile cells	4–5 × 2–3 μm; 1 plastid; no eyespot	2.5–3 × 6–7.5 μm; 1 plastid; no eyespot	No eyespot
Flagella	Ant: 9–13 μm; Post: 5–6 μm	Ant: 7–8 μm; Post: 5–6 μm (for genus)	Ant: 10–12 μm; Post: 6–7 μm

[a] Data on *Pulvinaria* and *Sarcinochrysis* from Geitler (1930), Gayral (1972); and see Billard & Fresnel (1980) and Billard (1984).

Figures 22–24 (color plate). Figures 22–23. Stiff gelatinous colony, possibly *Pulvinaria*. Fig. 22. Whole colony. Fig. 23. Detail of cells showing evidence of layered mucilage (arrows). Scale = 10 μm. Figure 24. *Chrysophaeum taylori* colonies, approx. × 3.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macroscopic morphology and formation of motile cells (Table 1). *Chrysocystis* should thus be placed in the Sarcinochrysidales, Sarcinochrysidaceae. The cell covering, projecting pyrenoid, scattered chloroplast DNA, and scale-like structures suggest that *Chrysocystis* belongs to the Sarcinochrysidales *sensu stricto* (O'Kelly 1989, Honda & Inouye 1995).

The mode of thallus formation suggests an extension of the series identified by Billard & Fresnel (1980, p. 291), "Dans cette famille [Sarcinochrysidaceae] une série évolutive serait esquissée qui, partant de formes planctoniques telles *Ankylonoton luteum,* en passant par un genre intermédiaire, le *Sarcinochrysis,* aboutirait à une organisation strictement benthique et palmelloïde chez *Pulvinaria.*" The tendency of *Chrysocystis* to form heaped colonies in culture rather than the typical field morphology emphasizes the basically palmelloid type of colony, and distinguishes *Chrysocystis* from more-organized genera in the Sarcinochrysidalean family Phaeosaccionaceae, such as *Phaeosaccion* and *Antarctosiphon.*

These little-known algae are common and very visible on the reef platforms of Guam, and (as suggested by the scattered records) probably much more widely on tropical Pacific reefs. Part of the reason for their being little-known is that they are not "typical" seaweeds (i.e., Chlorophyta, Phaeophyta and Rhodophyta) but belong to Protistan/Chromistan Divisions that have mostly microscopic members. Yet, their unusual taxonomic position makes them fascinating and important for further study.

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References

Andersen, R. A. 1987. Synurophyceae classis nov., a new class of algae. American Journal of Botany 74:337–353.

Andersen, R. A., G. W. Saunders, M. Paskind & J. P. Sexton. 1993. Ultrastructure and 18S rRNA gene sequence for *Pelagomonas calceolata* gen. et sp. nov. and the description of a new algal class, the Pelagophyceae classis nov. Journal of Phycology 29:701–715.

Billard, C. 1984. Recherches sur les Chrysophyceae marines de l'ordre des Sarcinochrysidales. Biologie, systématique, phylogénie. Thése de doctorat d'état. Université de Caen.

Billard, C. & J. Fresnel. 1980. Nouvelles observations sur le *Pulvinaria feldmannii* (Bourelly et Magne) comb. nov. (Chrysophycée, Sarcinochrysidale) formant une ceinture sur substrat meuble. Cryptogamie: Algologie 1:281–292.

Cavalier-Smith, T. 1986. The kingdom Chromista: origin and systematics. Progress in Phycological Research 4:309–347.

Cavalier-Smith, T. 1989. The kingdom Chromista. *In* J. C. Green, B. S. C. Leadbeater & W. L. Diver (eds) The Chromophyte Algae: Problems and Perspectives. Clarendon Press, Oxford. pp. 255–278.

Gayral, P. 1972. Sur les Chrysophycées à zoïdes phéophycéens notament *Sarcinochrysis marina* Geitler. Bulletin du Société Phycologique de France 17:40–45.

Gayral, P. & C. Billard. 1977. Synopsis du nouvel ordre des Sarcinochrysidales (Chrysophyceae). Taxon 26:241–45.

Gayral, P. & C. Billard. 1986. A survey of the marine Chrysophyceae with special reference to the Sarcinochrysidales. *In* J. Kristiansen & R. A. Andersen (eds) Chrysophytes: Aspects and Problems. Cambridge University Press, Cambridge, pp. 37–48.

Geitler, L. 1930. Ein grünes Filarplasmodium und andere neue Protisten. Archiv für Protistenkunde 69:615–636.

Honda, D. 1993. *Chrysocystis fragilis* Lobban, Honda et Chihara. *In* T. Hori (ed.) An Illustrated Atlas of the Life History of Algae. Volume 3. Unicellular and Flagellated Algae, pp. 74–75. Uchida Rokakuho Publishing, Tokyo.

Honda, D. & I. Inouye. 1995. Ultrastructure and reconstruction of the flagellar apparatus architecture in *Ankylochrysis lutea* (Chrysophyceae, Sarcinochrysidales). Phycologia 33:215–227.

Lewis, I. F. & H. F. Bryan. 1941. A new protophyte from the Dry Tortugas. American Journal of Botany 28:343–348.

Nemoto, Y., S. Kawano, S. Nakamura, T. Mita, T. Nagata & T. Kuroiwa. 1988. Studies on plastid-nuclei (nucleoids) in *Nicotiana tabacum* L. I. Isolation of proplastid-nuclei from cultured cells and identification of proplastid nuclear proteins. Plant & Cell Physiology 29:167–77.

O'Kelly, C. J. 1989. The evolutionary origin of the brown algae: information from studies of motile cell ultrastructure. *In* J. C. Green, B. S. C. Leadbeater & W. L. Diver (eds) The Chromophyte Algae: Problems and Perspectives. Clarendon Press, Oxford. pp. 255–78.

O'Kelly, C. J. & G. L. Floyd. 1985. Absolute configuration analysis of the flagellar apparatus in *Giraudyopsis stellifer* (Chrysophyceae, Sarcinochrysidales) zoospres and its significance in the evolution of the Phaeophyceae. Phycologia 24:263–274.

Taylor, W. R. 1951. Structure and reproduction of *Chrysophaeum lewisii.* Hydrobiologica, 3:122–130.

Taylor, W. R. 1952. The algal genus *Chrysophaeum.* Bulletin of the Torrey Botanical Club. 79:79.

Taylor, W. R. 1960. Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas. University of Michigan Press, Ann Arbor.

Watanabe, M. M. & F. Kasai. 1985. NIES-Collection List of Strains First Edition 1985 Microalgae. The Microbial Culture Collection, National Institute for Environmental Studies, Tsukuba, Japan, 116 pp.

West, J. A. 1969. Observations on four rare marine microalgae from Hawaii. Phycologia 8:187–192.