

THE OCCURRENCE OF CHLOROPHYLLS C_1 AND C_2 IN THE CHRYSOPHYCEAE¹

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ABSTRACT

We analyzed 34 strains representing 25 species of Chrysophyceae for chlorophylls c_1 and c_2 using thin-layer chromatography. Most organisms had both chlorophylls c_1 and c_2 in addition to chlorophyll a but 17 strains of 9 species of *Synura* and *Mallomonas* possessed only chlorophylls a and c_1 . These are the first chlorophyll c -bearing algae which lack chlorophyll c_2 . We postulate that at least some of the silica-scaled algae including *Mallomonas* and *Synura* may be distinct from other Chrysophyceae based

upon pigmentation and other characters described in the literature.

Key index words: chlorophylls c_1 - c_2 ; chlorophyllides; Chrysophyceae; Mallomonadaceae; Synuraceae; silica-scaled algae

The class Chrysophyceae is commonly known as the golden or golden-brown algae. The carotenoid component of this golden hue was recently investigated in several genera (Withers et al. 1981) but the nature of the accessory chlorophylls remains unre-

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TABLE 1. Reports of chlorophyll *c* in species classified as members of the Chrysophyceae.

Species	Reference	Chlorophyll <i>c</i> pigments	Current classification
<i>Chromophyton rosanoffii</i> : Woronin	Seybold et al. 1941 ¹	—	Chrysophyceae
<i>Hydrurus foetidus</i> (Villars) Trevisan	Seybold et al. 1941	—	Chrysophyceae
<i>Ochromonas danica</i> Prings.	Allen et al. 1960 Gibbs 1962b Ricketts 1965 ²	— — —	Chrysophyceae
<i>Poterioochromonas malhamensis</i> (Prings.) Peterfi	Allen et al. 1960 ³	—	Chrysophyceae
<i>Pseudopedinella</i> sp.	Dales 1960	—	Chrysophyceae
<i>Pseudopedinella</i> sp.	Riley and Wilson 1967	<i>c</i>	Chrysophyceae
<i>Sphaleromantis</i> sp.	Jeffrey 1963	<i>c</i>	Chrysophyceae
<i>Synura</i> sp.	Guillard and Lorenzen 1972	<i>c</i>	Chrysophyceae
<i>Oolithodiscus luteus</i> Carter	Jeffrey 1976	<i>c</i> ₁ , <i>c</i> ₂	Chrysophyceae, Raphidophyceae, Xanthophyceae
<i>Apistonema</i> sp.	McLean 1967	—	Prymnesiophyceae
<i>Chrysochromulina chiton</i> Parke et Manton	Ricketts 1965	<i>c</i>	Prymnesiophyceae
<i>Chrysochromulina ericina</i> Parke et Manton	Dales 1960	<i>c</i>	Prymnesiophyceae
<i>Coccolithophorid</i> sp. 27	Jeffrey 1976	<i>c</i> ₁ , <i>c</i> ₂	Prymnesiophyceae
<i>Coccolithus</i> sp. 21	Jeffrey 1976	<i>c</i> ₁ , <i>c</i> ₂	Prymnesiophyceae
<i>Hymenomonas carterae</i> (Braarud et Fagerl.) Braarud	Parsons 1961 ⁴ Jeffrey 1976 ⁵	<i>c</i> <i>c</i> ₁ , <i>c</i> ₂	Prymnesiophyceae
<i>Isochrysis galbana</i> Parke	Dales 1960 Jeffrey 1963 Ricketts 1965 McLean 1967 Jeffrey 1969	<i>c</i> <i>c</i> <i>c</i> — <i>c</i> ₁ , <i>c</i> ₂	Prymnesiophyceae
<i>Monochrysis lutheri</i> Droop	Parsons 1961 Jeffrey 1969	<i>c</i> <i>c</i> ₁ , <i>c</i> ₂	Prymnesiophyceae
<i>Pavlova gyrans</i> Butcher	Dales 1960	<i>c</i>	Prymnesiophyceae
<i>Prymnesium parvum</i> Carter	Allen et al. 1960 Ricketts 1965	<i>c</i> <i>c</i>	Prymnesiophyceae

¹ Identified as *Chromulina rosanoffii* (Woronin) Butsch.

² Chlorophyll *c* was found using one method, but Ricketts concluded the pigment was absent based upon results of two other methods.

³ Identified as *Ochromonas malhamensis* Prings.

⁴ Identified as *Syracosphaera carterae* Braarud et Fagerl.

⁵ Identified as *Cricosphaera* (sic) *carterae* (Braarud et Fagerl.) Braarud.

solved. Published reports describing the chlorophylls of the Chrysophyceae are not consistent and are occasionally conflicting for a particular species (Table 1).

The problem has been complicated by two additional events, the separation of the Haptophyceae (=Prymnesiophyceae) from the Chrysophyceae (Christiansen 1962, Hibberd 1976) and the discovery that chlorophyll *c* was a mixture of two chlorophylls (chlorophyllides) (Dougherty et al. 1966). Jeffrey (1968) separated the chlorophylls using thin layer chromatography (TLC) and named them chlorophyll *c*₁ (magnesium tetradehydropeoporphyrin *a*₅ monomethyl ester) and chlorophyll *c*₂ (magnesium hexadehydropeoporphyrin *a*₅ monomethyl ester). Subsequent work has verified the presence and structure of both molecules (Dougherty et al. 1970, Wasley et al. 1970, Strain et al. 1971, Budzikiewicz and Taraz 1971).

In an extensive survey of a wide variety of chromophyte algae, Jeffrey (1976) concluded that all chlorophyll *c* bearing algae have chlorophyll *c*₂ and most have chlorophyll *c*₁. In this survey Jeffrey listed six species under the category "Chrysophyceae and Haptophyceae." Five of the species listed are now classified in the Haptophyceae (=Prymnesiophyceae) (Parke and Dixon 1976). The sixth species, *Oolithodiscus luteus* Carter, has been placed in the Xanthophyceae (Carter 1937), Chrysophyceae (Leadbeater 1969) and the Raphidophyceae (Loeblich and Fine 1977), and its current classification is in turmoil.

The recent discovery of the prokaryotic alga, *Prochloron didemni* Lewin, with chlorophyll *b* resulted in the erection of a new division, Prochlorophyta, and the presence of this accessory chlorophyll was a major factor leading to the formation of the division (Lewin 1977). Apparently chlorophyll pig-

ments have changed little over evolutionary time, and although evolutionary schemes for the algae often include chloroplast endosymbiosis (Margulis 1981, Whatley and Whatley 1981), they assume the chlorophyll pigmentation has remained stable.

Because knowledge of the accessory chlorophylls of the Chrysophyceae remains inconclusive, we examined 34 strains from 25 species that are currently classified as members of the Chrysophyceae. Most of the genera examined are regarded as the common and typical members of the class. We present here our results and a discussion of their significance, especially concerning our discovery of some algae which have chlorophyll c_1 but lack chlorophyll c_2 .

MATERIALS AND METHODS

The algae were cultured using soil-water or soil-seawater media in stationary flasks at 15° C with a 14-10 h LD regime of Cool White fluorescent light or at room temperature (22° C \pm 5° C) using light from a north window. Cells were collected on membrane or glass fiber filters. The pigments were exhaustively extracted in cold absolute methanol. Filters and cell debris were suspended in cold absolute methanol and centrifuged at 1000 \times g for 15 min (3° C). The pellet was tan colored after complete extraction. An equal volume of peroxide-free diethyl ether was added to the pigment extract and mixed with a vortex mixer with 2-3 L of cold 10% NaCl solution. The ether layer containing the pigments was collected, concentrated under N_2 to a small volume and centrifuged to remove condensed water. The pigment extract was spotted on cellulose Chromagram sheets (Eastman No. 13255) and developed in either 0.5% n-propanol in light petroleum ether (b.p. 60-80° C) or 1:3 (v/v) chloroform : petroleum ether. The chlorophyll c spot remained at the origin and was scraped from the cellulose sheets and eluted in diethylether or pyridine. This extract was spotted onto polyethylene (Polyscience No. 2719) TLC plates and developed in either 100% or 90% acetone to separate chlorophylls c_1 and c_2 . R_f values were 0.39 and 0.28, respectively, for 90% acetone and 0.50 and 0.35, respectively, for 100% acetone. All chromatograms were viewed under UV light to detect trace amounts of pigments. Identification of chlorophylls was made by spectrophotometry after extraction in pyridine from the TLC plates.

Silica scales of *Synura* and *Mallomonas* were examined by electron microscopy to identify these algae. The scales were prepared by drying cells or acid cleaned scale suspensions on formvar coated grids and were examined directly without coating or shadow casting.

RESULTS

Spectrophotometric data confirmed the TLC identifications. Absorption maxima for chlorophyll c_1 in 100% acetone (+1% pyridine) were 446, 578, 629 nm; for chlorophyll c_2 they were 445, 481, 630 nm. Absorption maxima in pyridine were 461, 593, 639 nm for chlorophyll c_1 and 467, 597, 642 nm for chlorophyll c_2 . The absorption band ratios were significantly higher for chlorophyll c_2 than for c_1 , as originally reported by Jeffrey (1972).

All species examined contained chlorophyll c_1 and many also possessed chlorophyll c_2 (Table 2), but the genera *Mallomonas* and *Synura* lacked chlorophyll c_2 . Quantitative measurements were not made for all the chlorophyll extracts but generally those species possessing both chlorophylls c_1 and c_2 had ratios of

$c_2:c_1$ which ranged from 1:1 to 6:1. The ratios of chlorophyll a to chlorophylls c_1 plus c_2 ranged from 3:1 to 30:1 with the ratio generally greater than 12:1. The chlorophyll a to chlorophyll c_1 ratios for species of *Mallomonas* and *Synura* also ranged from about 3:1 to 65:1 with the ratio generally greater than 20:1. The age of the cultures and the light and the temperature regimen changed the amounts and ratios of the chlorophyll pigments but did not affect the presence or absence of the pigments in the cultures.

DISCUSSION

Jeffrey's (1976) survey of 86 species representing at least six classes indicated that chlorophyll c_2 was present in all chlorophyll c -bearing algae. Our discovery that *Synura* and *Mallomonas* lack chlorophyll c_2 distinguishes these genera not only from other Chrysophyceae but all from chromophyte algae.

The significance of this unusual pigment composition is unclear. Most members of the Dinophyceae and Cryptophyceae lack chlorophyll c_1 (Jeffrey 1976) but there are exceptions. The presence of chlorophyll c_1 in a few members of the Dinophyceae such as *Peridinium balticum* (Levan.) Lemm. is explained by the chrysophyte-like symbionts they harbor (Tomas and Cox 1973, Withers et al. 1977). The one species of the Cryptophyceae known to possess chlorophyll c_1 , *Chroomonas mesostigmatica* Butcher (Jeffrey 1976), remains an enigma. A second enigmatic organism is the marine coccoid *Pelagococcus subviridus* Norris which has been reported to possess only chlorophyll c_2 (Lewin et al. 1977).

Should the occurrence of chlorophyll c_1 without c_2 in *Synura* and *Mallomonas* also be considered an enigma? We suggest that it should not; there are several other characters which distinguish *Mallomonas* and *Synura* (and probably the closely related genera *Mallomonopsis*, *Catinochrysis* and *Chrysodidymus*) from the other members of the Chrysophyceae.

The flagella of *Mallomonas*, *Mallomonopsis* and *Synura* have basal bodies arranged in parallel (Hibberd 1976, 1979) while other Chrysophyceae genera have basal bodies arranged perpendicular to one another (Hibberd 1976). This basal body arrangement suggests that there is a different arrangement of the flagellar anchoring structures, and this has been found to be the case (personal observations). The difference in flagellar orientation is also reflected in the structure of the photoreceptor apparatus. *Mallomonas*, *Mallomonopsis* and *Synura* lack chloroplast eyespots and do not have the swollen area at the proximal end of the shorter flagellum closely associated with the cell and chloroplast membranes (Schnepf and Deichgräber 1969, Belcher 1969, Hibberd 1976, 1978, Wujek 1978). Other members of the Chrysophyceae have a close association between the shorter flagellum swelling and the chloroplast membranes, and frequently an eyespot is present (Hibberd 1976). Finally, the transitional helix in the

TABLE 2. Distribution of chlorophylls c_1 and c_2 in the Chrysophyceae. Family classifications follow Bourrelly (1981).

Taxon	Chl		Isolate no.	Source
	c_1	c_2		
Synuraceae				
<i>Synura glabra</i> Korsh.	+	—	999	Island Lake, Illinois
<i>S. glabra</i> Korsh.	+	—	1000	Island Lake, Illinois
<i>S. glabra</i> Korsh.	+	—	7	Sandgren, Univ. Texas—Arlington
<i>S. petersenii</i> Korsh.	+	—	157	Sequoyah Resv., Arkansas
<i>S. petersenii</i> Korsh.	+	—	348	Darling Pond, Itasca, Minnesota
<i>S. petersenii</i> Korsh.	+	—	1148	Fox River, Illinois
<i>S. petersenii</i> Korsh.	+	—	1198	Winters Creek, Michigan
<i>S. spinosa</i> Korsh.	+	—	471	Roadside Ditch, Arkansas
<i>S. curtispina</i> (Pet. et Hans.) Asmund	+	—	1179	Beaver Pond, Michigan
<i>S. uvela</i> Ehr.	+	—	622	Harkins Pond, Arkansas
<i>S. uvela</i> Ehr.	+	—	1190	Tobacco R., Michigan
<i>Synura</i> sp.	+	—	1113	Volo Bog, Illinois
<i>Synura</i> sp.	+	—	1167	Volo Bog, Illinois
<i>Synura</i> sp.	+	—	1168	Volo Bog, Illinois
<i>Mallomonas cratis</i> Harris et Bradley	+	—	—	Blinn, N. Arizona Univ.
<i>M. lichenensis</i> Conrad	+	—	485	Bridge Pond, Arkansas
<i>M. papillosa</i> Harris et Bradley	+	—	929/2	Br. Cult. Coll.
Chromulinaceae				
<i>Chromulina ochromonoides</i> (?)	+	+	909/1	Br. Cult. Coll.
<i>Saccochrysis piriformis</i> Korsh.	+	+	586	Rush Creek, Arkansas
Chrysamoebaceae				
<i>Chrysamoeba</i> sp.	+	+	320	Devil's Den St. Park, Arkansas
Chrysophaeraceae				
<i>Chrysophaera magna</i> Belcher	+	+	911/2	Br. Cult. Coll.
Dinobryaceae				
<i>Dinobryon cylindricum</i> Imhof	+	+	5	Sandgren, Univ. Texas—Arlington
<i>D. cylindricum</i> Imhof	+	+	7	Sandgren, Univ. Texas—Arlington
<i>Dinobryon</i> sp.	+	+	1002	Island Lake, Illinois
<i>Dinobryon</i> sp.	+	+	1131	Lincoln Park, Illinois
<i>Epipyxis pulchra</i> Hilliard et Asmund	+	+	968	Sequoyah Pond, Arkansas
<i>E. aureus</i> Hilliard et Asmund	+	+	976	Sequoyah Pond, Arkansas
<i>Poteriochromonas malhamensis</i> (Prings.) Peterfi	+	+	933/2a	Br. Cult. Coll.
Ochromonadaceae				
<i>Ochromonas danica</i> Prings.	+	+	—	Bouck, Univ. Ill.—Chicago
<i>O. sphaerocystis</i> Matv.	+	+	419	Rush Creek, Arkansas
<i>Ochromonas</i> sp.	+	+	396	Lake Fayetteville, Arkansas
<i>Syncrypta glomerifera</i> Clarke et Pennick	+	+	958/1	Br. Cult. Coll.
Pedinellaceae				
<i>Pseudopedinella</i> sp.	+	+	947/3	Br. Cult. Coll.
Stylodococaceae				
<i>Lagynion scherffelii</i> Pascher	+	+	362	Sequoyah Pond, Arkansas

flagella has 6–8 spires in *Synura* but generally 4–5 spires in other genera of Chrysophyceae (Hibberd 1979).

Synura, *Mallomonas* and *Mallomonopsis* have, in addition to silica scales over their vegetative cells, small organic scales along the surface of one or both flagella (Bradley 1966, Hibberd 1973, Zimmerman 1977) and occasionally along the cell itself (Moes-trup 1982). Such scales have not been found on other members of the Chrysophyceae.

Although sexual reproduction is poorly known in all these organisms, *Synura* and *Mallomonas* are re-

ported to have isogamous reproduction via fusion of the posterior ends of cells (Warwick 1960, 1970, Kristiansen 1961, Bradley 1966) while others of the Chrysophyceae have fusion of the anterior ends of cells (Mack 1951, Kristiansen 1963, Sheath et al. 1975, Sandgren 1980a, 1981).

Finally, most members of the Chrysophyceae have an outer nuclear membrane continuous with the outer membrane of the chloroplast endoplasmic reticulum (Gibbs 1962a, Hibberd 1976). Belcher (1969) reports this continuum in *Mallomonas papillosa* Harris and Bradley but it is not evident in any micro-

graphs, and such a continuum is also absent in published micrographs of *Mallomonas caudata* Iwanoff (Wujek 1978). Hibberd (1978) was unable to find such a continuity in *Synura sphagnicola* Korsh. and questioned its occurrence in the genus *Synura*, although there may be a continuum of the two membranes in *Synura petersenii* Korsh. (Schnepf and Deichgräber 1969).

The only characteristic unique to both the silica-scaled algae and the other members of the Chrysophyceae is a siliceous cyst having a small pore sealed with an organic plug (Bourrelly 1957). Yet the cyst wall of *Mallomonas* (Sandgren 1980b) is structurally distinct from the cyst walls of *Chrysosphaerella* (Wujek 1966), *Ochromonas* (Hibberd 1977), *Dinobryon* and *Uroglena* (Sandgren 1980a, b). Sandgren (1980b) also showed the cysts of *Mallomonas* have a pattern of development different from that of other genera of Chrysophyceae, and he suggested these represent two distinct lines of evolution. We believe that the differences in accessory chlorophylls combined with other accumulating evidence will show that *Synura*, *Mallomonas* and at least some of the other silica-scaled algae may be more distinct than is suggested by their current classification as a family in the Ochromonadales.

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