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Edited by Jorgen Kristiansen and Robert A. Andersen

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## PART I

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### Definition and relationships

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## The Chrysophyta – a reassessment

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### Introduction

In a symposium of this nature, many problems of detail will be discussed. However, it is worth returning to some of the basic precepts of the group Chrysophyta, examining these, and raising problems that appear from modern studies of individual genera. Recently, interest is reviving in the overall classification and phylogeny of algal groups, and the “chrysophytes” play a distinctive role in these discussions. The group is traditionally one in which “protozoal” representatives have been closely allied with autotrophic forms, and the rationale of this merits consideration. In addition, the chrysophytes occupy a relatively isolated position among the algae, having apparently not developed along the usual algal lines to the same extent as other groups. This is especially true regarding the evolution of sexuality. Few other algal groups have been so fractured as have the chrysophytes and this process, involving a reassessment of the status of the widely recognized anomalous genera, will continue, although perhaps within the overall confines of a “heterokontophyte” series of organisms. Depending on whose classification one follows, the Chrysophyta can be a very restricted group with a single class Chrysophyceae or a group (Chrysophycophyta) encompassing six (Bold & Wynne 1978) or five (Ettl 1980) classes. The problems within the group are accentuated by the difficulty of obtaining reliable morphological data at the light microscopic level. Therefore, almost all decisions on critical genera rely on electron microscopy (EM). In addition, excellent EM fixation is required to determine, for example, details of the flagellar basal system. It is perhaps significant that data on the chrysophytes lags far behind the “chlorophytes” in this aspect. However, it is just these kinds of data that are leading to the exciting reevaluation of the latter series. The chrysophytes do, however, *appear* to be less complicated in terms of flagellar root structure, but this may be due only to lack of data.

### History

Historically, the chrysophytes started merely as a loose cluster of mainly flagellate species, and it was not until 1914 that Pascher drew them together as the Chrysophyceae and placed them into a division Chrysophyta. Early workers relied on careful cytological techniques, and although these data were regarded with suspicion, they did reveal the “hairy” flagella, the heterokont condition, and many interesting structural details. The peak of this activity was the superb review of chrysophyte genera by Bourrelly (1957) with its detailed classification scheme and evolutionary discussion. The genera were also described, but with less discussion, by Bourrelly in his 1968 book. Bourrelly’s detailed classification has been used as a basis by many, but, even in the 1960s, ultrastructural research was beginning to uncover additional features, resulting in the removal of the “haptophytes” (Parke 1961, Christensen 1962). The splitting of the “xanthophyte” series into two was made by Hibberd and Leedale (1972), and, in key papers, Hibberd (1976, 1980) discussed the basic structure of the chrysophyte and “prymnesiophyte” lines. Meanwhile, many details concerning the species bearing siliceous scales began to appear, starting with the classic paper by Manton (1955). The classification of these, based on scale structure, had been begun by light microscopists, but it was now put on a much firmer basis, and new species were recognized by detail that is almost only visible by electron microscopy. Throughout the history of chrysophytes, the bipartite cyst has figured prominently, but it is only in recent years that detailed studies have been made (Sheath, Hellebust, & Sawa 1975, Hibberd 1977, and most recently by Sandgren, 1980a,b). There was an exciting period when electron microscopy revealed scale types that had to be linked with whole cells and when coccoid filamentous forms were described and linked up to flagellate stages and into the classification. This process is nowhere near complete, and many groups are obviously little studied [cf. the recent description of a large number of new species of *Paraphysomonas* by Thomsen et al. (1981); Preisig & Hibberd (1982a,b, 1983)]. The outcome of these most recent studies is the realization that the type of flagellation, which was a prime feature of Bourrelly’s classification, is perhaps not applicable when electron microscopic detail is included. Another, and perhaps more unfortunate, outcome of ultrastructural work has been the emphasis placed on a few genera with anomalous features. *Olisthodiscus* and *Sphaleromantis* [“a single peculiar species of uncertain status within a group to which in fact it may not belong” (Manton & Harris 1966)] immediately spring to mind. These genera and others (e.g., *Dictyocha*, *Pterosperma*, and *Pedinella*) have been retained in the set of species with what one might term the *Ochromonas* structure, and this has led to a heterogeneous cluster that is probably misleading. Evolution is more likely to have given rise to many small sets of organisms, in this case perhaps to be loosely conceived of as a heterokont group but not as a

diversified chrysophyte group. Historically, there is a dearth of information at the biochemical/genetical level, and when this is forthcoming many of the existing problems may disappear.

Recent valuable reviews are those of Hibberd (1976, 1980) and Pienaar (1980), and it is not my intention to cover the same ground but rather to discuss some general features.

### Concepts

In many accounts and especially in textbooks, the Chrysophyta include three classes, viz., Chrysophyceae, Xanthophyceae, and Bacillariophyceae. The origin of this taxonomic treatment is Pascher (1914), and, considering Pascher's general approach, it is difficult to see the logic in the proposal since by 1931 he was proposing (Pascher 1931) that each class should have a series of life forms from flagellate through coccoid, simple filament, and branched filament to thalloid. Clearly, the diatoms (Bacillariophyceae) do not have such a range; in fact, they are purely coccoid. The Xanthophyceae do exhibit a wide range of form, although not to the same degree as some classes of algae. The Chrysophyceae are exceptional, with many flagellate and coccoid members, but relatively few with higher organization. So why were the three classes taken under the umbrella of the Chrysophyta? The usual explanation is that in some form or other there is often a bipartite wall and coupled with this a deposit of silica into the wall matrix or into discrete components (scales, valves, cysts, etc.). The flagellate stage is heterokont, but, when the amalgamation was made, the diatom motile gamete and many other flagellate forms were relatively unknown or incompletely known. In any case, the diatom motile sperm is not heterokont. (It may have been during early evolution.) Moestrup (1982) discussed the use of the term heterokont, which originally meant "unequal in length," and later described one mastigoneme-bearing flagellum and one smooth flagellum. By any criteria, the evidence for a combined series was very scant. Comparison with other well-established groups, e.g., Rhodophyta, and Phaeophyta (the latter admittedly heterokont in a loose sense), reveals a lack of consistency in the concept of the Chrysophyta; either the concept itself is incorrect or the consistency within other groups is fortuitous. Let us examine briefly each group. The "xanthophytes" in the old sense have already been fragmented by the removal of a number of genera to the Eustigmatophyceae (Hibberd & Leedale 1972; Hibberd 1981), and there have been several suggestions that the "siphonous" group might form a distinct subset – Vaucheriophyta of Maekawa (1960). Whether one leaves these as classes of the newly designated Tribophyceae [(Christensen 1979, Hibberd 1981) Xanthophyceae excl. Eustigmatophyceae] or as separate phyla is hardly relevant in the present discussion. Apart from heterokont flagellation, there are few features allying them to the Chrysophyceae or Bacillariophy-

ceae: The rarely reported “cysts” require reexamination, and the bipartite nature of some walls is not an homologous feature. Bipartite walls occur also in the “chlorophyte” series. [To designate the groups as Bivalvophyta as Hirose, quoted in Takahashi (1964), did is unnatural and has never been taken up.] The Bacillariophyceae are unique among the heterokont series in their total consistency of form, which is undoubtedly bound to the rigidity of cell structure within the confines of the multipartite siliceous wall covering that allows little scope for variation (Round 1981). There are no anomalous sections that could be split off as in the other two groups. There have been rare suggestions that they might form a coccooid order of the chrysophyte series, but there are already simple coccooid chrysophytes (e.g., in the Chrysapiales, Chrysosphaerales, and Stichogloaeales), and greater evidence of affinity would be needed to substantiate such a move. Their spore structures (auxospores) are not bipartite but multipartite. However, some of the simplest diatom resting spores do show features reminiscent of one subset within the Chrysophyceae. The Chrysophyceae in the classic sense have, like the Xanthophyceae, suffered subdivision into Prymnesiophyceae and Chrysophyceae, and this appears eminently sensible with a cluster of features characterizing the former group, e.g., organic scales, equal flagella, haptonema, calcium carbonate deposits, and a predominately marine distribution [see Hibberd (1976) for details]. However, this does not leave a homogeneous group but rather a cluster of subsets, many with rather superficial claims for inclusion in the Chrysophyceae *sensu stricto*, i.e., based on Pascher’s (1914) concept in which the endogenous cyst features as a key element. Unlike other algal phyla, there is a paucity of hard biochemical evidence to characterize the group as a whole or any of its subsets. The universal occurrence of “leucosin” is marginally permissible, but this (or very similar  $\beta$ -1,3-glycosides) occurs widely in heterokont algae. It is imperative that some of the biochemical pathways of chrysophytes be examined and compared with those of prymnesiophytes, diatoms, etc. We are left with one overwhelming feature that cannot be ignored and that is the cyst or statospore. By its mode of formation (internally in the cytoplasm) and its single, plugged aperture, the cyst is so distinctive that it must form a unifying attribute – it is possible of course, but unlikely, that this arose more than once in evolution. That the cyst unites forms with and without siliceous scales is significant and probably denotes a primitive character. Sandgren (1980b) refers to the cysts as “conserved through evolutionary time.” If this is so, are the remaining non-cyst-forming genera derived by loss of such a structure or are they out of place? We ought to ask, what is the origin of the cyst? Is it a feature of the primitive, colorless eukaryote that on the serial endosymbiotic hypothesis must have predated the pigmented derivative? If this is its origin, then ought we not to find such cysts in modern colorless flagellates? If it is not a feature of the colorless ancestor, how did it arise in the life cycle after the incorporation

of the plastids? It is not obviously sexually formed (see Sheath et al. 1975), but appears at intervals in the life cycle [see Sandgren (1980a) for details and possible sexual events after cyst formation]. That mitosis occurs prior to cyst formation in *Dinobryon* and *Uroglena* (Sheath et al. 1975; Sandgren 1980a,b) is slightly reminiscent of the necessity for nuclear division in diatoms before valve formation can occur. However, replication of the nucleus does not occur in the “*Chromulina*” type, and there is also a suggestion that in the Synuraceae other features are found (Sandgren 1980b), thus weakening this argument. Pascher (1924) referred to a filamentous chrysophyte that forms a cyst; however, the only illustration I have been able to locate is in a palmelloid piece of *Phaeotbamnion*, and this is hardly filamentous (Pascher 1925). Later (Pascher 1932), he comments that cyst formation occurs only when the filament breaks down into a palmelloid mucilage mass. In fact, this seems to be a process in which swarmers are forming (the cytoplasm contains numerous contractile vacuoles), and the arrest of these leads to cyst formation. Pascher does continue with the comment that he has also seen cysts forming inside the cells (*innerhalb behäuteter Zellen*), but this is not illustrated.

### Classification

The Chrysophyta were first treated systematically by Pascher (1914), and up to this time the diatoms (Bacillariophyceae) had always formed a well-defined taxon and indeed are one of the few groups with a completely internal consistency. The Heterokontae had been removed by Luther (1899) to become the Xanthophyceae (Allorge 1930) and most recently Tribophyceae (Hibberd 1981). Before 1914, the Chrysophyceae were simply a loose collection of phytoflagellates in the family Chrysomonadina (Klebs 1892). In 1960, Chadeaud argued in favor of clustering the chlorophyll *c*-containing algae into the Chromophycophytes [Chromophyta of Christensen (1962, 1980) and Bourrelly (1968) or Heterokontophyta of Leedale (1974)]. The latest proposal is that of Cavalier-Smith (1981), who proposes a nine-kingdom system, one of which is named Chromophyta: Phyta is not a suitable ending for such a taxon, and Round (1984) has supported this kingdom concept but suggested the name be changed to Chromoplantae. Acceptance of this idea still leaves the problem of divisions (phyla), and I believe that the concept of Heterokontophyta is too inclusive of diverse phylogenetic lines. While this name is a useful adjectival (heterokont) term, it is subsumed in the taxon Chromoplantae. I am convinced that the divergent lines (and divergence is still only hypothetical) form divisions when one takes an overall view of the organismal world. Hence, I prefer to retain the divisions Chrysophyta, Tribophyta, Bacillariophyta, and the recently separated Eustigmatophyta and Prymnesiophyta. The latter are not regarded as chrysophytes by Hibberd (1976), who earlier

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(Hibberd 1972) clearly stated that these eustigmatophytes and prymnesiophytes could not be accommodated in a heterokont division; this raises a problem in the system of Cavalier-Smith (1981) who includes them. The title of the symposium contains the term “chrysophyte,” and I am sure that this in most contributors’ minds refers to the Pascherian group of algae.

The systematic scheme of Bourrelly (1968) is one of the most detailed based on his comprehensive (Bourrelly 1957) work, but when one compares it with that generally adopted for the chlorophytes at an ordinal level, one is struck immediately by the fusion of flagellate, colonial flagellate, coccoidal, palmelloid, rhizopodial, even filamentous, and parenchymatous forms within the same order. The basis for this scheme is the form of the motile cell that is used to group orders into subclasses, and its roots lie in the variation or absence of flagellation in the genera. The only other pigmented group where such flagellar variation is prominent is the euglenophytes. Such a scheme may represent best the phylogeny – only further studies will decide this – but it is certainly a confusing system, especially in the light of new ultrastructural data. An alternative is to have a greater number of orders within the subclasses, e.g., raise some of the subordinal groups to orders. The general reluctance to do this may be related to the small number of genera in the nonflagellate clusters, although, of course, such a systematic arrangement was proposed by Pascher (1914) and has been adopted by Fritsch (1935, 1951) and Bold & Wynne (1978) with their 11 orders (10 orders if the Dictyochales are discounted and they do appear an aberrant group or a side line off the general chrysophyte evolutionary trend). A reinvestigation of the Bold and Wynne orders is required to see if some fusion of the varied series is warranted, especially when it seems that unflagellate forms are extremely rare [the only well authenticated one seems to be the *Rbizochromulina* of Hibberd & Chretiennot-Dinet (1979)] and the nonflagellate forms are surely merely life cycle variants of the various morphological series. In fact, many genera have been removed from the nonflagellate subclass (Acontochrysophycidae) as their motile stages were discovered. On the other hand, it could be argued that this approach would overemphasize gross morphology (cf. the chlorophyte series). The recent tendency in many groups has been to upgrade the importance of ultrastructural studies at the expense of the gross morphology. Ultrastructure is undoubtedly of immense value in defining a whole class (or division), as Hibberd (1976) showed for the Chrysophyceae and Prymnesiophyceae, but gross morphology/life cycle may be more important at the ordinal and familial level. Norris (1977) has, in fact, argued for the greater importance of morphology rather than flagellation in the classification of chrysophytes. Good examples of this are the loricate series, *Dinobryon* (Karim & Round 1967), *Epipyxis*, *Chrysolykos* (Kristiansen 1969), *Pseudokephyron* (Belcher 1968), *Stenocalyx*, *Bitrichia*, *Chrysopyxis* (Kristiansen 1972), and *Poterioochromonas* (Peterfi,

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1969) with their microfibrillar organization and the Synuraceae with their distinctive scales. Belcher and Swale (1972a) even recorded some microfibrils in the thecate genus *Chrysococcus*, which perhaps indicates an underlying biochemical uniformity.

The relationship of the chrysophytes to the Phaeophyceae is one that requires much further study; again, such a relationship was hinted at as early as 1914 by Pascher. On the surface, the phaeophytes seem to be very different biochemically and cytologically, and only some aspects of the flagellate cells form the main evidence for this connection – although there is no typical transitional helix (*spiralkörper*) at least in the advanced genus *Fucus*. It is clearly desirable to investigate simpler genera (Hibberd 1978). There is a general lack of simple coccoid/palmelloid genera in the Phaeophyceae and no really authenticated free-living motile forms. Several genera previously thought to be Phaeophyceae have been transferred to the Chrysophyceae [e.g., *Phaeosaccion* (Chen, McLachlan, & Craigie 1974)]. However perhaps there is still some doubt here; the sections of the flagellar base do not show a clear transitional helix that is a characteristic of the Chrysophyta. This may be due to fixation because such a structure is not clear in freshwater chrysophyte motile cells sectioned by Dop (1980), although he does refer to it. The presence of the transitional helix in 19 chrysophyte species (Hibberd 1978) and also in a number of eustigmatophyte and xanthophyte species (but not in phaeophyte or prymnesiophyte species) is clearly an important comparative feature, and it should be sought in diatom sperm and in any motile cell of doubtful affinity. Hibberd (1978) suggests it is a feature indicative of monophyly, but if this is so it will require considerable rethinking of the systematics of the heterokont series.

Gayral and Billard (1977) created a new chrysophycean order, Sarcinochrysidales, for the marine benthic chrysophytes (see also Gayral, 1972), and these certainly have many features allying them to the Phaeophyceae (see also comment in Dop 1980) or in some instances to the prymnesiophytes. There is a real need to investigate the relationships of these and simple ectocarpalean forms at the biochemical systems level, for it is indeed remarkable if no simple phaeophytes have survived from the early period of serial endosymbiosis even in such a modified form as to make recognition difficult (see comments on ecology). It is also necessary to compare Sarcinochrysidales with Prymnesiophyceae because in my view, from studying the papers of Gayral and Haas (1969), Loiseaux (1967), and Gayral and Lepailleur (1971), they may possess some haptophycean features. One cannot deny that the whole system both of Bourrelly (1957, 1968) and Bold and Wynne (1978) will need extensive revision as more genera are examined in detail. Bold and Wynne separate the Phaeophyta into a separate division and leave the remainder of the “chromophyte” series in another, as do many authors, but such disparate treatment has little



justification. Either there is a single chromophyte division (or better, a kingdom, see section on classification) or there are several.

Bold and Wynne (1978) and Pienaar (1980) use a classification based partly on Bourrelly (1968). Christensen (1980) and Kristiansen (1982) use a morphological basis, since flagellar number is a difficult criterion unless, and even if, the details are checked by electron microscopy. The various systematic treatments have been drawn together in Table 1.1.

### Morphology

The majority of Chrysophytes are unicellular, but, whereas other divisions tend to have a rather conservative form for their flagellate orders, the range in external form of chrysophytes is great. Internally, as Hibberd (1976) points out, there is greater consistency. There are, however, a number of anomalous genera included in the Chrysophyceae [e.g., *Sphaleromantis*, *Olisthodiscus* – the latter sometimes placed in Tribophyceae but recently removed to the Raphidophyceae (Chloromonadophyceae) by Loeblich and Fine (1977) – and *Dictyocha*] and all these need reassessment. If they prove to be true chrysophytes, then they should probably be allocated to new taxa at the ordinal or higher level (as indeed *Dictyocha* has in the Dictyochales) or as a subclass – Dictyochophycidae – by Kristiansen (1982). The most consistent group is the one possessing siliceous scales [*Mallomonas*, *Mallomonopsis* [only a variant on flagellar form (?)] *Synura*, possibly *Catenochrysis*], and they probably form a distinctive evolutionary line (but see comments on cysts). *Chryso-sphaerella* cannot be included in this line and is now separated from *Synura* and *Mallomonas* in the Paraphysomonadaceae (Preisig & Hibberd 1983). The scales do have a distinct ordered heteromorphy, with the most complex occurring at the flagella pole, a main mass of body scales, and a number of simplified antapical scales (cf. the numerous publications on these genera). Only very rarely have additional structures been found on the scales, e.g., the flask-shaped structures on *Mallomonas cyathbellata* (Wujek & Asmund 1979). It is only members of this group (=Synuraceae) Mallomonadaceae that have siliceous structures that might conceivably relate the whole series to the Bacillariophyceae. Scales of a different type are recorded in *Syncrypta*. These seem to be hollow discs, the outer part of which is irregularly microfibrillar (Clarke & Pennick 1975). The origin of scales varies in genera commonly placed in the Chrysophyceae [e.g., those of the Synuraceae are associated with the chloroplast membrane, but those of *Paraphysomonas* and *Sphaleromantis* are possibly Golgi–endoplasmic reticulum (ER) associated].

The existence of rhizopodial forms in the Chrysophyceae is a striking feature as Pascher originally pointed out, and it is a feature almost confined to this group of algae. Pascher also pointed out the parallels in morphology

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between this group and the green algae, but such a feature should be placed more in context since in the Chrysophyceae there is a vast base of variability at the monad level declining to a few filaments at the more complex level whereas the reverse is true of the Chlorophyta.

The so-called benthic chrysophytes mostly have a coccoid/palmelloid form (especially those living in fresh water) and only rarely are truly filamentous, e.g., *Phaeothamnion* (see Dop 1980). The marine forms, on the other hand, seem to require further study; the growth of some species from a basal cup seems rather distinctive.

**Cysts**

Cysts (or stomatocysts, statospores, or endocysts) are generally considered a feature of the Chrysophyta, and indeed in genera such as *Ochromonas*, *Dinobryon*, *Mallomonas*, *Synura*, and *Uroglena* they are conspicuous. The cyst wall is very variable from smooth in some *Dinobryon* and *Synura* species to ornamented with stellate spines in *Mallomonas torquata* (Asmund & Cronberg 1979). In *Hydrurus*, the cyst has a winglike structure (Bourrelly 1957). In spite of their occasional occurrence or even absence in many chrysophycean genera, it was the cyst above all that Pascher (1914) considered the characteristic feature of the group. In fact, if one checks back into the early literature, many species were described together with their cysts (e.g., by Doflein 1923 and Conrad 1926). Has its significance and the attempt to fit cysts of other groups into the evolutionary framework been overdone? Although Pascher (1914 and 1932) wrote at length concerning cysts, it was Scherffel in 1911 who first quite clearly stated that the endogenous origin and the presence of a “plug” were the characteristic features. Both Cienkowsky (1870) and Prowazek (1903) had investigated the cysts before Pascher. Are the various cyst forms homologous structures? This topic is not new, and the argument was aired 60 years ago between Scherffel (1924) and Pascher (1924). In xanthophyte genera, cysts are less obvious and consist of two equal (subequal?) halves, although there is very little detail of these in the literature apart from the scattered illustrations in Pascher’s early publications and a series of figures in his introductory remarks to the Heterokontae (Pascher 1939). The superficial resemblance of the diatom resting spore (common only in *Chaetoceros*) is only coincidence in that the two halves are a result of the bipartite mode of cell growth of this group. Diatom resting spores can resemble heavily silicified vegetative cells or depart considerably from this (e.g., *Leptocylindrus*), but they are still composed of two valves (Hargraves 1976). Pascher comments on at least one cyst with equal halves in the Chrysophyceae, but I have been unable to locate this. The cysts in the filaments of *Giraudyopsis* (Loiseaux 1967; Gayral & Haas 1969) really do not resemble the “plugged” chryso-