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THE TAXONOMY OF THE CHLOROPHYTA

by

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The green pigmented algae have long been an established taxonomic entity, but in almost every textbook, different groups have been included or excluded and the number of orders and allocation of genera to orders has varied. The early removal of the "heterokont" green algae on the basis of flagellation, wall structure and reserve products, now confirmed by electron microscope and biochemical studies, left a large heterogenous collection of algae—the Chlorophyta*. Recent works by Fott (1959), Chadefaud (1960), and Christensen (1962) have revived old and introduced new concepts into this group.

The taxonomic problem can be divided into four parts:—(1) Into how many phyla should the green algae be divided? (2) How many classes may be recognised? (3) What is the best subdivision of these classes into orders? (4) What genera belong in each order? (There is perhaps less argument on this point than others and it will hardly be discussed here.)

These are problems both for the herbarium taxonomist and the experimentalist and it is the experimental approach which has recently been providing the most exciting results. The greatest value which might derive from a consideration of the taxonomic status of the green algae is not the mere redistribution of the genera, but the stimulation that this provides to the biochemical and electron microscopic approach, by focusing attention on possible differences in the groups.

An outline of some of the major systems of classification of the green algae is given in Table I.

The separation into divisions must be based upon fundamental morphological or biochemical features and the system used by Christensen (1962), using the presence or absence of normal nuclei, presence or absence of flagellate stages and the supplementation of chlorophyll a by other pigments, appears to meet such a requirement although creating groups (Procaryota, Eucaryota, Aconta, Contophora) larger than divisions. The green algae fall into the section Eucaryota–Contophora, which is divided into two divisions Chromophyta and Chlorophyta (see review of Christensen's book by Round, 1963), the latter characterised by the presence of chlorophyll b which is absent from the Chromophyta. If the presence of chlorophyll b unites these algae (Euglenophyceae, Loxophyceae, Prasinophyceae, Chlorophyceae), into a single division, the question arises as to whether the next lowest taxonomic grouping should be the class, as suggested by most authors, thus placing the "euglenoids", with their characteristic flagellation, alongside the "isokont" green algae. Should not the three divisions of earlier authors, Euglenophyta, Chlorophyta and particularly Charophyta be retained in some way? At this level, as with

^{*}The term Chlorophycophyta proposed by Papenfuss (1946) has not been generally accepted, although the ending—phycophyta has been applied by Chapman (1962) to groups of classes (divisions?).

TABLE 1. THE MAJOR SUBDIVISIONS OF THE GREEN ALGAE

	Воным (1901)	BLACKMAN and TANSLEY (1902)	Oltmanns (1904)	WILE (1909)
Division or Phylum [Abteilung]				
Classes (Klasse)	Chlorophyceae	Chlorophyceae	Chlorophyceae Akontae (Heterokontae)	Chlorophyceae Conjugatae
Orders Orders, Orden) of Chlorophyceae excluding classes split off by various authors	Protococcoideae Incl. Volvocincae and Tetrasporaceae) Ulotrichales (Incl. Ulvaceae and Claetophoracean Algae) Microsporales Srephanokontae (= Oedogoniaceae) Siphoneae (Incl. Cladophoraceae and Sphaeropleaceae)	Isokontae Protococcales (Incl. Volvocacea and Tetrasporaceae) Ulotrichales (Incl. Prasiolaceae and Chaetophoracean Algae) Ulvales Siphonales (Incl. Siphonocladiaceae containing Cladophoraceae) Siphonales (Ancl. Siphonocladiaceae containing Cladophoraceae) Siphonales Continuation Cladophoraceae Containing Cladophoraceae	Volvocales (Incl. Tetrasporaceae) Protococales Ulotrichales (Incl. Ulvaceae, Prasiolaceae and Chaetophoracean Algae) Siphonocladises (Incl. Cladophoraceae and Sphaeropleales) Siphonales	Protococcales (Incl. Volvocaccae and Tetrasporaceae) Chactophorales (Incl. Ulvaceae, Ulotrichaceae) Siphonocladiales (Incl. Cladophoraceae and Sphaeropleaceae)

TABLE 1. THE MAJOR SUBDIVISIONS OF THE GREEN ALGAE-continued

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TABLE 1. THE MAJOR SUBDIVISIONS OF THE GREEN ALGAE—continued

Su.va (1963)*	Euglenophyta Chlorophyta Charophyta		Volvocales (Incl. Tetrasporineae) Chlorococales Siphonocladales Codiales Derbesiales Davoladales Davoladaes Unorrichales Ulotrichales Ulotrichales and Sphaeropleaceae) Ulyales Schizogoniales Cladophorales Cladophorales Cladophorales Cladophorales Capennatales
Christensen (1962)	Eucaryota–Contophora (in Part) Chlorophyta	1. Euglenophyceae 2. Loxophyceae 3. Prasinophyceae 4. Chlorophyceae	Volvocale; (Incl. Tetrasporaceae) Chlorococcales Prasiolales Ulotrichales (Incl. Ulvaceae, Sphaeropheraceae and Sphaeropheraceae) Zygnematales Ocdogoniales Cladophorales Siphonocladales Caulerpales Dasycladales Charales
CHAPMAN (1962)	Euphycophyta (in Part)	Chlorophyceae Charophyceae	Volvocales Chlorococcales Ulotrichales (Incl. Sphaeroplea) Ocdogoniales Chaetophorales Siphonocladales Incl. Cladophoraceae) Dasycladales Siphonales Conjugales Conjugales
CHADEFAUD (1960)	Eucaryotes Euglénophycinées (Within Pyrrophycées) Chlorophycophytes	Three sub-phyla:— 1. Zygophycées (3 orders) 2. Buchlorophycées split into two classes a. Prasinophycinées b. Euchlorophycinées 3. Charophycées	(Prasinococcales) (Prasinovolvocales) Euchlorovolvocales Euchlorovoccales Ulotrichales (Incl. Chaetophorales and Ulvales) Oedogoniales Microsporales Trentepobliales Prasiolales Prasiolales Pleurococcales Sphaeropleales Cladophorales Chlorochytriales Siphonocladales Dasycladales
	Division or Phylum [.4bteilung]	Classes (Klasse)	Orders CReine, Ordnung, Orden) of Chlorophycae excluding classes split off by various authors

*This may not include all the orders recognised by Silva, since only orders containing genera mentioned in Lewin (1963) are quoted.

the separation into divisions, fundamental morphological and biochemical criteria must be considered. Thus in the "euglenoids", there is no rigid cell wall and the cell undergoes metaboly and/or is spirally striate (rigid cell walls are not present in all "isokont" green algae, but these are not as metabolic nor are they spirally striate), the two flagella are very unequal, the longer one at least has unilateral appendages running in a spiral manner, the flagella are inserted in an anterior invagination, the eyespot lies free in the cytoplasm (and not in the chloroplast as in "isokont" green algae), the polysaccharide reserve product is formed in a particular manner although it is only a glucose polymer, there are strong heterotrophic tendencies and sexual reproduction or the asexual production of zoospores is extremely rare or absent in most species. At the opposite end of the scale are the "charophytes", characterised by a very precise mode of cell division and differentiation, the division into "root, stem and leaves," the complex protection of the egg cell, the formation of a sterile "wall" around the spermatozoid mother cell which is not found in any other group of algae and approaches a Bryophyte status, the form of the spermatozoid (more like that of a Bryophyte or Pteridophyte than the more usual "Chlamydomonas-like" or "Protosiphon-like" gamete of the green algae) and finally the "protonemal" germination of the oospore. These and other features were sufficient for earlier workers to create divisions for the "euglenoids" and "charophytes" and are still amply sufficient evidence for their separation from the main mass of green algae, if not into divisions, then into subdivisions and thus I suggest that this secondary split of the green algae be into Euglenophytina, Charophytina and Chlorophytina (cf. the use of subdivisions in the fungi-Alexopoulos, 1962). The first two subdivisions or subphyla contain the single classes Euglenophyceae and Charophyceae and will not be discussed further since they contain well defined orders (excluding the colourless "Euglenoids").

The Chlorophytina is a large group and includes Christensen's classes Loxophyceae, Prasinophyceae (first recognised by Chadefaud in 1950 and containing the order Pyramidomonadales) and Chlorophyceae. The Loxophyceae contain a mixed group of flagellates with varied flagellation (Bipedimonas, Thalassomonas, Pedinomonas, Micromonas and possibly Nephroselmis and Mesostigma); the number of genera will obviously increase as further studies are made and will need continual taxonomic revision, if indeed they form a coherent class. The Prasinophyceae are better defined, since the two or four flagella arise from an apical pit surrounded by four projections. Christensen places the Polyblepharidaceae, Tetraselmidaceae, Chlorodendraceae and Halosphaeraceae in this class, thus removing a controversial group (Chlorodendraceae) from the Volvocales where they always appeared out of place. Chadefaud (1960) recognised two orders Prasinovolvocales and Prasinococcales, containing the motile and predominantly non-motile genera (e.g. Halosphaera) respectively. I consider that the inclusion of the third group of branching forms (Prasinocladus and Chlorodendron) warrants a further order, the Prasinodendrales. Chadefaud suggested over a decade ago that the flagellates of this group occupied an intermediate position; this is borne out by Parke & Adams (1961), who clearly illustrate the basal reservoir connected to the exterior via the canal which passes up between the four apical lobes in the Pyramimonas stage of Halosphaera (cf. the canal-reservoir system in the Euglenoids and Cryptomonads). Of even greater importance is the recent discovery by Manton, Oates & Parke (1963) of the presence of scales in at least two layers on the body and along the flagellum of the *Pyramimonas* stage of *Halosphaera* and in three species of *Pyramimonas*. In view of these important discoveries it appears that the Prasinophyceae must be regarded as a group differing from those in the Chlorophytina (e.g. the Volvocalean series is without reservoir and scales) and the evidence points to the status of a subdivision for this group—the Prasinophytina.

The Chlorophyceae is split into 11 orders by Christensen (1962), whilst Chapman (1962) recognises 9, Chadefaud (1960) 19 and Fott (1959) only 6. Some of this variation is due to the removal by some of the authors of the "charophytes" and "conjugate" algae from the Chlorophyta and their upgrading to separate classes. The recognition of the Charophyceae and its elevation to a sub-division I have discussed above, whilst the removal of the "conjugate" algae into a class Conjugatophyceae appears equally desirable. In making this latter change, both negative and positive reproductive features are used; thus there are no flagellate stages and the sexual reproduction is of a particular type (conjugation). Essentially this is the only feature which justifies the creation of a class, since morphologically they contain simple filaments (cf. the Ulothricales) and complex, unconstricted or constricted unicells composed of two distinct halves; admittedly this feature is not found in any other order of the Chlorophyta, but it may not in itself justify raising the group to a class. This illustrates how a single over-riding feature (in this case the reproductive process) can legitimately be used to define a taxonomic group. Similarly a single dominant feature (true vegetative division into non-filamentous thalli) was used by Herndon (1958) to characterise a new order, the Chlorosphaerales.

The acceptance of the Conjugatophyceae as a class, although not a new concept (see Table I), focuses attention on two other groups, the Oedogoniales and the Siphonaceous algae. Both have been controversial groups since the early taxonomic treatments of the green algae and, if one accepts the reasons for elevating the Conjugatophyceae, then equally valid arguments can be advanced for thse groups. Oedogoniales are characterised by a unique method of cell division; theis is a feature of both the simple filaments of Oedogonium and the branching filaments of Bulbochaetae and Oedocladium, as are the formation of "stephanokont" type zoospores, androspores and male gametes, the distinctive orgamy and perhaps most striking the production of dwarf male plants in some species of all three genera. To these characters may be added the reticulate chloroplast, the morphology of the chromosomes which are long threadlike structures according to Kretschmer (1930), and the characteristic differentiation of the antheridium, within which only two spermatozoids are formed. Such a combination of characters, even more striking than those of the Conjugatophyceae, and much more fundamental than those separating some orders of the Chlorophyta, are I suggest, ample grounds for re-instituting the old "Stephanokontae" group and bringing it into line with modern nomenclature by elevating it to a class, the Oedogoniophyceae. Fritsch (1935) points out similarities between this group and the Chaetophorales, whilst at the same time maintaining that they "have few points of contact with other filamentous Chlorophyceae". To place them in the Ulotrichales, as does Fott (1959), would seem to confuse the taxonomy of the green algae and to use this order as a refuse dump for filamentous types which do not belong in the Conjugatophyceae.

The two remaining large groups are the siphonaceous/siphonocladial algae and the

flagellate/coccoid/filamentous series. These differ not only morphologically but also in their reproduction. The latter series basically form gametangia from any cell, although slight differentiation has occurred in some groups e.g. some Volvocineae and Coleochaetaceae, whilst the siphonaceous/siphonocladial algae convert segments of the thallus into gametangia or in the more highly differentiated group, either form distinct gametangia as specialised branches or form multinucleate cysts from which gametes are released. These three reproductive types are used by Chadefaud (1960) to split the latter group into Hémisiphonées (Sphaeropleales, Cladophorales), Eusiphonées cystosiphonées (Chlorochytriales, Siphonocladales, Dasvcladales) and Eusiphonées typiques (Derbesiales, Codiales, Caulerpales, Dichotomosiphonales). This system groups algae with similar characteristics into three ordinal series, the first being the simplest with walls dividing the thallus up into multinucleate units, the second comprising those forming cysts and/or having segregative division and the third series lacking these characters but with additional characteristic carotenoid pigments (siphonein and siphonoxanthin) and with cell walls containing polysaccharides other than cellulose (i.e. mannans in all that have been studied except Halicystis which has a mixture of xylans and glucans (Kreger, 1963; Iriki & Miwa, 1960). Other authors present slight variations on this system e.g. Christensen (1962) places the Siphonocladales close to the Cladophorales; there are certain definite features which link these groups (e.g. the presence of cellulose I) and indeed Fott (1959) fuses them into a single order. There is a tendency to link the remaining orders of Chadefaud's scheme into one or two groupings usually involving the recognition that the Dasycladales differ somewhat from the others. The inclusion of the Sphaeropleales and the Chlorochytriales (Phyllobium, Chlorochytrium, Endosphaera) has removed two anomalous groups from the Chlorophyceae. A study of the biochemistry of the wall of these genera may help to establish the validity of the changes.

Fott's (1959) nomenclatural change from Siphonales to Bryopsidales is valid but I would extend this name to cover the three series and elevate the group to a class, the Bryopsidophyceae, for surely these algae form as distinct a taxonomic unit as do the Conjugatophyceae and Chlorophyceae, from which they differ in their multinucleate nature and numerous other morphological and biochemical details. Finally the three series designated by Chadefaud are in fact groups or orders, i.e. cohorts, and the proper ending for these is—iidae and therefore I propose that they be named Hemisiphoniidae, Cystosiphoniidae and Eusiphoniidae.

The remaining green algae have sufficient in common to warrant their inclusion in a single class, the Chlorophyceac. Since the early part of the century the flagellate and coccoid groups have been separated into Volvocales and Chlorococcales, even when placed as separate lines in a single order; for the last thirty years they have been firmly separated and indeed the Chlorococcalean series forms one of the most well defined groups of algae, albeit with their own problems such as the relationship between the autosporic and zoosporic series and the status of the multinucleate forms. The Volvocales were a much less uniform group, but the removal of the Chlorodendraceae to the Prasinophyceae and the tetrasporal forms to the Tetrasporales (e.g. Smith, 1955; Fott, 1959) leaves a compact group of unicellular and colonial flagellates. The Chlorococcales are a relatively clear cut group except for the occurrence of multinucleate genera in the Hydrodictyaceae; the

Prasinophyceae Prasinovolvocales Prasinococcales Prasinodendrales Chlorophyceae Prasinophytina Derbesiales Codiales Caulerpales Dichotomosiphonales (Chromophyta) Charophyceae Charales Charophytina Loxophyceae Eusiphoniidae Eucaryota—Contophora Chlorochytriales Siphonocladales Dasycladales Bryopsidophyceae Cystosiphoniidae Chlorophytina Chlorophyta Oedogoniophyceae Oedogoniales Hemisiphoniidae Euglenophyceae Euglenales Euglenophytina Cladophorales Sphaeropleales Conjugatophyceae Mesotaeniales Zygnematales Gonatozygales Desmidiales

Subphylum

Class Order

Class Order

232

Phylum

Ulvellales
Chaetophorales
Trentepohliales
Coleochaetales
Pleurococcales

Volvocales Tetrasporales Chlorococcales Chlorosphaerales Ulotrichales

Ulvales Prasiolales Microsporales

Chaetophorales

TABLE 2. A SCHEME OF CLASSIFICATION OF THE GREEN ALGAE

genus Hydrodictyon has a wall composed of mannose and glucose (Frei & Preston, 1961) and in this respect differs from other Chlorophyceae. Likewise Pediastrum appears to be in some way anomalous, since its wall structure is not destroyed in lake sediments whereas other Chlorophyceae disappear completely. Both genera also have unusual chloroplast structures and form cysts in the life history. They are worthy of further biochemical study to ascertain their correct position, for they have characteristics of a "Coccosiphonaceous" group. These features have indeed been used to indicate a connection with siphonaceous algae e.g. the Protosiphonaceae of some authors has been removed from the Chlorococcales and placed in the Siphonocladales (Chadefaud 1960) and Chlorochytrium in the Chlorochytriales of the Cystosiphoniidae. In 1958, Herndon removed some genera of unicellular algae capable of vegetative division out of the Chlorococcales into a new order, the Chlorosphaerales. This was based on an admirable, detailed study of their life history which fully warrants the introduction of a new order, but it is doubtful whether it has really any affinities with the siphonaceous algae as is suggested by placing it close to the Dasycladales in Silva's (1963) scheme.

The filamentous and thalloid algae of the Chlorophytina are assigned to families on the basis of external morphology, chromatophore type, presence or absence of pyrenoids, mode of cell division, reserve products, life cycle, type of swarmer, gametes and reproduction and are grouped into a single order (the Ulotrichales of Fott) or into several orders (see Table I). To group these all into one order appears to me to defy general taxonomic concepts, in that groups with grossly different features are placed together and if similar treatment were applied to the Phaeophyta, then all the orders usually grouped below the Laminariales would be united-indeed there are fewer points of differences between the orders of the Phaeophyta than the groups included in the Ulotrichales sensu lato. As suggested above the Oedogoniales should form a class and the Cladophorales be removed to the Bryopsidophyceae, whilst the other orders have sufficient common characteristics and few if any non-Chlorophycean characters to maintain their position in the Chlorophyceae. These remaining orders fall into two groups, the first comprising the Ulotrichales, Ulvales, Microsporales, Prasiolales (perhaps forming a cohort—Ulotrichiidae) and the second the Chaetophorales, or the orders recognised by Chadefaud (1960) i.e. the Trentepohliales and Pleurococcales, to which I would add the Chaetophorales to form a second cohort the Chaetophoriidae. The fundamental distinction recognised by Fritsch (1935) between the uniseriate filaments of the Ulotrichales sensu stricta and the branched heterotrichous system of the Chaetophorales is, I believe, valid. To combine these two orders it is necessary to present a convincing set of common characters strong enough to overcome this basic difference in morphology. Surprisingly, although Fritsch considered that separation into orders was warranted by the possession of simple or branched filaments, he did not apply the same criteria to the status of simple filaments or thalloid expanses which would result in the separation of the Ulvales from the Ulotrichales; this is equally fundamental. The fact that the Ulvales start as a uniseriate filament is not necessarily evidence of their affinity with the simple filamentous Ulotrichales (even the Laminariales develop in this manner). Also the Ulvales have parietal, cup-shaped chromatophores, not interrupted rings as in the Ulotrichales sensu stricta and in addition a high degree of branching in some species (see the photographs of type specimens in

Papenfuss, 1960). It is implied by Papenfuss that the isomorphic alternation of generations (some may be heteromorphic), is comparable to the rarely recorded alternation in the Ulotrichales sensu lato, but it would seem that the different genera in the Chlorophyceae can exhibit a considerable range of life history and this should not deter us from separating groups which are morphologically dissimilar. The Prasiolales as distinguished by Chadefaud (1960) and Christensen (1962) also form a vegetatively distinct group with single stellate chromatophores, a thallus one cell thick and division of cells into packets of four (inclusion of the Cylindrocapsales is debatable). By 1954, Fritsch had also begun to consider the Prasiolales as a definite order. The Microsporales contain the single genus Microspora which has an unusual wall structure composed of overlapping H-pieces, between which a further H-piece is intercalated at cell division; it also has a much lobed parietal chloroplast often covering the whole cell wall and devoid of pyrenoids. Another genus placed in the Ulotrichales sensu lato by many authorities is Sphaeroplea which has been removed to the Bryopsidophyceae and made into a separate order, the Sphaeropleales (see above).

Many of the above points are arguable but what is really needed is a considerable comparative study of cell wall, chloroplast and pyrenoid structure (preferably on an electron-microscopic scale), of biochemical systems, life histories etc. The plasticity of some forms, e.g. Enteromorpha, makes this lengthy and difficult, but not impossible. Fragmentation into orders and the grouping of these into cohorts does at least point out some differences and may stimulate research, whereas assimilation tends to disguise the problems. Finally the Chaetophorales comprises a group in which there has obviously been considerable plasticity in the way that the branching filamentous thalli have been developed; also, according to Beger (1954), the Chaetophoraceae produce starch and the Trentepohliaceae, Coleochaetaceae, Chaetosphaeridiaceae, Pleurococcaceae and Microthamnieae store oil and glycogen. Further work is required to show how fundamental this distinction iscertainly the groups do appear divergent and the latter five each have their peculiarities e.g. the formation of aplanospores and the possession of numerous chromatophores in each cell in the Trentepohliaceae and the advanced oogamy of the Coleochaetaceae. I am inclined to think that the cohort of orders forming the Chaetophoriidae as suggested above may need to be enlarged to do justice to the taxonomic entities e.g. to include the Chaetophorales, Ulvellales, Coleochaetales, Trentepohliales and Pleurococcales.

A final summation of these ideas, many of them reintroductions from the excellent work of early phycologists, is now possible (Table 2).

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