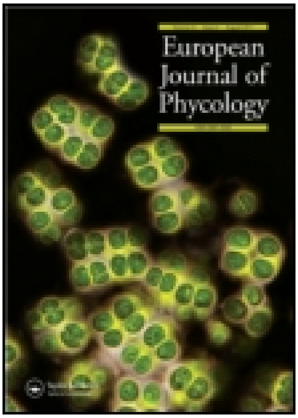

British Phycological Journal
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tejp19

# The taxonomy of the Chlorophyta. II

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To cite this article: F.E. Round (1971): The taxonomy of the Chlorophyta. II, British Phycological Journal, 6:2, 235-264

To link to this article: http://dx.doi.org/10.1080/00071617100650261

*Br. phycol. J.* (1971) **6** (2) 235–264
October 31, 1971

# THE TAXONOMY OF THE CHLOROPHYTA. II

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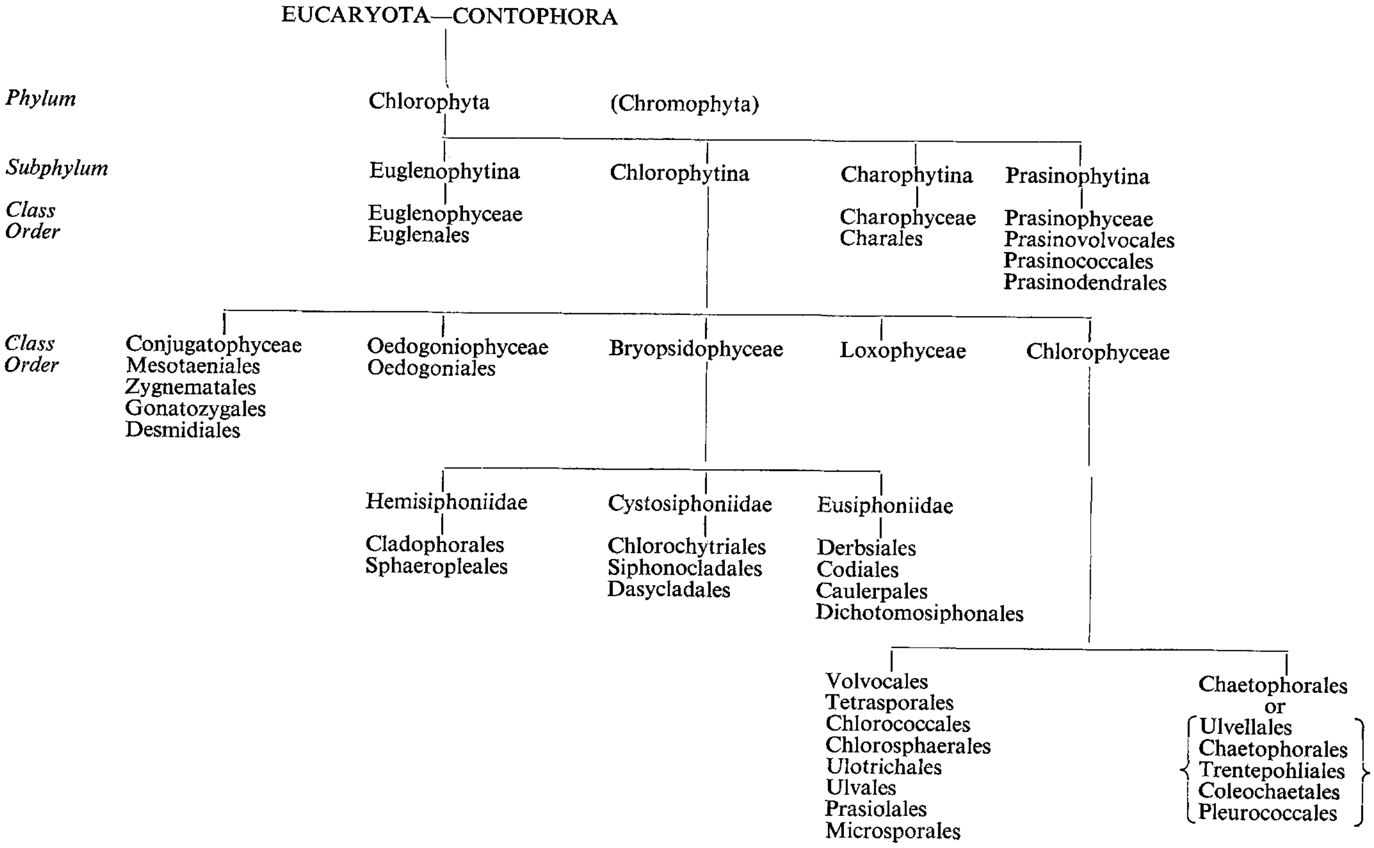
The taxonomy of all the algal groups possessing both chlorophyll *a* and *b* is discussed for the levels above that of the family. Much of the discussion is related to previously conceived taxa but some new combinations are proposed. The subdivision of 'green' algae into Euglenophyta, Prasinophyta, Charophyta and Chlorophyta is discussed in the light of recent publications. The problem of further subdivision in the Chlorophyta is reviewed and the need stressed for more extensive electron microscopical and biochemical evidence. Until such data are available the author favours maintaining a large number of orders but also the rejection of those based on single characters.

> 'The appearance of new systems of classification does not at all signify the destruction of everything old for much from the old systems enters into the new ones as component elements.'
>
> Armon Takhtajan, 1968
>
> 'We are seeking a "natural" classification. The test for such a "natural" classification is its internal consistency: the accuracy by which one can predict unknown features of an organism when one knows its assigned taxonomic position.'
>
> Ralph A. Lewin, 1968

There have been eight years of intense work in phycology since I attempted a tentative discussion of some problems in the taxonomy of the green algae (Round, 1963). This work yields an even clearer picture of the group and I am encouraged to attempt a re-evaluation since many phycologists have commented to me on the 1963 paper; some have found it useful as a basis for teaching the group (which is encouraging since, as Koch (1960) remarks, one of the important applications of taxonomy is its usefulness to students) and, as I hoped, others have applied new techniques to test the hypotheses. Table I, taken directly from the 1963 publication, summarises the groupings which then appeared to me to be emerging. It was in many ways a cautious approach and evidence has now accumulated which, although not altering the basic entities, warrants the upgrading of some to a higher status. The points listed in 1963 are still worthy of consideration: (1) How many phyla (divisions) are involved? (2) How many classes should be recognised? (3) What is the best subdivision of these classes into orders? (4) What genera belong in each order? This latter question cannot be dealt with in detail here; only certain critical genera can be discussed. The size of the problem is obvious when one considers that Bourrelly (1966) lists 565 freshwater genera alone. As in 1963, many of the schemes have been proposed at various times by other phycologists and I am merely attempting to draw these together and hope that this will stimulate and point the way to further work to test the hypotheses.

TABLE I. The scheme of classification of the 'green' algae proposed in Round (1963).



## PHYLA

I now believe my caution over the first question was unnecessary and we can return to the much earlier concept of several phyla rather than subphyla. It is interesting that Banks (1968) in a stimulating paper on the early history of land plants also uses sub-divisions (sub-phyla) for groups which other workers would regard as divisions (e.g. Rhyniophyta, Lycophyta, Sphenophyta, etc.; see also Cronquist, Takhtajan and Zimmermann, 1966) and maintains a single division Tracheophyta, for all vascular plants above the bryophyte level. Surely a division should be based on more than the possession of vascular strands! This is, I believe, directly comparable to maintaining the phylum Chlorophyta for all green algae. It is difficult to find a characteristic other than the possession of both chlorophyll *a* and *b* to embrace this series of algae and, though Christensen (1962) used this to segregate his Chlorophyta from the Chromophyta, it is surely neither a sufficient criterion to hold such a varied assemblage together as a single phylum nor sufficient to embrace all green plants which logically it should (see also Bold, 1956; Fott, 1965). In fact, Bold (1957) did bring all the divisions of plants containing chlorophyll *a* into a sub-kingdom, Chlorota. Three other characters of the chloroplast, namely, absence of girdle bands (groups of thylakoids passing around the ends of the main series of longitudinally running bands), tight apposition of the thylakoids, and evaginations or invaginations of the thylakoids, are common to the ‘chlorophyte’ and tend to be absent from most or all ‘chromophyte’ algae (Gibbs, 1970); however, on similar criteria the ‘chromophyte’ series itself does not form an entity. Indeed, although the ‘chromophyte’ series is a valuable concept in that it distinguishes the ‘non-green’ algae (including, however, the Xanthophyceae) from others and has stimulated much work, the algal groups contained within it no more constitute a single phylum than those in Christensen’s Chlorophyta. Equally it is unsatisfactory to group all algae together in the same division, Phycophyta, as Koch (1960) proposed and as used by Mägdefrau in Strasburger (1967). Whittaker (1969) uses the term Euchlorophyta for a sub-kingdom of the kingdom Plantales; the Chlorophycophyta forms a branch of the Euchlorophyta and contains the Chlorophyta and Charophyta. Whilst this may be a useful concept it is exceedingly confusing to use -phyta for three different classificatory levels.

The literature on algae is virtually devoid of philosophical discussion on the concept of phyla and indeed of most taxonomic entities. The concept of a phylum is derived from a consideration of the major vegetative and reproductive characteristics of a number of genera all showing a similar manifestation of these characteristics. Without denying that phyla may be derived from one another at some stage in their evolutionary development they appear to be lines with long independent fossil histories. The vegetative and reproductive basis is most clearly recognised in the plants with more complex anatomy from the Bryophyta upwards and in most of the more complex animal phyla. Thus in at least 99 % of cases anyone encountering a new leafy or thalloid non-vascular plant with archegonia, antheridia or sporogonia immediately assigns it to the correct phylum or one of two phyla if one follows Bold (1956).* Clearly a phylum such as

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* The fact that a very small number of genera cannot be classified easily and are the subject of controversy, e.g. the genus *Psilotum*, does not in any way detract since these genera often require further detailed studies.

Bryophyta has some characters common to other phyla (and, indeed, phyla have certain features, particularly nuclear characteristics, in common), but superimposed on these are certain well defined biochemical, morphological and reproductive characters which recur throughout the genera thus collected together. If, however, a single genus or a small number of genera possess equally distinctive but different characters then they must constitute a phylum; the reluctance to elevate such groups has been common amongst phycologists and I was still reluctant to accept the concept in my 1963 paper. The reason for this unwillingness to regard these groups as phyla is probably completely illogical and rests merely on the feeling that, since phyla are major taxonomic entities and usually contain a large number of genera, then small groups of anomalous genera must be found a place in the large phyla (the same reasoning is often applied to subsidiary groupings too and it adds unnecessary confusion, particularly in the minds of students—see below). The definition of the phylum must be clear and based on a number of distinctive characters which recur throughout the genera. Once these have been recognised and shown to contrast with another set of equally characteristic features in another group of genera then one can constitute the phylum irrespective of the number of genera involved. Such discrete groupings are constituted by the 'euglenoid' and 'charophyte' algae which require classification into the phyla Euglenophyta and Charophyta, though the latter has only 6 living genera (Wood and Imahori, 1965). However, amongst certain groups of genera the characters are less well defined, often owing to lack of study, but it is still necessary to classify them into a phylum and state its characteristics, e.g. the larger grouping of algal genera in the Chlorophyta (see below). If this is a properly constituted phylum then the characters of flagellation of the motile cell, structure of reproductive organs, life cycles, etc., will all have a basic similarity. The degree of similarity, however, appears to decrease in this group as it does in the unicellular group of the animal kingdom and this makes a precise definition more difficult; this variability must not however be an excuse to embrace those groups of genera which are more clearly defined (e.g. Euglenophyta and Charophyta). As Walters (1962) points out in an article on higher plant taxonomy, history cannot be ignored. In the algae, three kinds are historically recognised, 'green', 'brown' and 'red', and the latter two emerged as eminently discrete entities in the last century and have remained so ever since as the Phaeophyta and Rhodophyta; thus by extension the Chlorophyta had to include all green algae and also be a discrete group. But even an elementary study shows that it cannot be regarded as such.

## 1. EUGLENOPHYTA

The work of Leedale (1958, 1964, 1967), Walne and Arnott (1966, 1967), Mignot (1965, 1967) and Buetow (1968) has clearly revealed that the 'euglenoid' algae possess a most distinctive series of characters unknown in any other section of the green algae and, as Leedale (1970) says, 'emerge as an old and taxonomically isolated group showing possible affinities with the lower fungi and certain zooflagellates'. The possession of a complex, proteinaceous, pellicular strip periplast combined with helical symmetry of other cytological structure; the occurrence of the plasma membrane outside this periplast; the sub-apical anterior invagination from which the two flagella arise, unequal in most forms, the longer with a single row of hairs and a para-flagellar swelling towards the the base, the shorter without any hairs; predominately 3-thylakoid chloroplast lamellae, absence of grana (Gibbs 1970), and chloroplasts surrounded by complete layers of endoplasmic reticulum; the stigma (eyespot) free in the cytoplasmic matrix and composed of groups of carotenoid droplets each surrounded by a unit membrane (Walne and Arnott, 1967); the characteristic mitochondria with basally constricted cristae; the peculiar mode of nuclear division (including the retention of the nuclear membrane and the characteristic separation pattern of the chromatids); the absence of sexual stages and of zoospore formation; the occurrence of paramylum, a $\beta$-1,3 linked glucan with helical substructure, formed outside the chloroplast envelope but adjacent to the pyrenoid (Ueda, 1961; Konitz, 1965; Leedale, 1967, 1969); formation of ergosterol (Aaronsen and Baker, 1961); the unusual pathway of lysine synthesis via $\alpha$-amino adipic acid (Vogel, 1965); and the characteristic contractile vacuole, discharging into the anterior invagination, are all highly characteristic. All these contrast with features of the remaining green algal groups and fully merit the status of a phylum for this group of plants, the Euglenophyta. Recently, however, a new class the Eustigmatophyceae, has also been found to have a free eyespot (Hibberd and Leedale, 1970, 1971). The erection of this new class is based almost entirely on ultrastructure and is an admirable illustration of the use of such micromorphological detail in classification. The phylum Euglenophyta has been divided into six orders (three with chloroplasts) by Leedale (1967), the reader is referred to the latter for further details. One final point of interest, however, is that the Euglenophyta seem to have only the possession of chlorophyll *a* and *b* to associate them with other 'chlorophyte' algae whilst, as Gibbs (1970) points out, the 'euglenoid' chloroplast is surrounded by a complete envelope of endoplasmic reticulum which is a 'chromophyte' rather than 'chlorophyte' character.

### 2. CHAROPHYTA

The 'charophyte' series has now been further typified in detail from electron microscope studies (Chamber and Mercer, 1964; Pickett-Heaps, 1967a, 1967b, 1968a, 1968b) and further information added to their gross anatomy (Kausik and Bhattacharva, 1971; Sundaralingam, 1954, 1959, 1962a, 1962b, 1963, 1966). The early anatomical studies revealed a complex and precise segmentation system unknown in any other green alga and this is now shown to be even more complex (see, especially, Sundaralingam, 1954, 1966). Equally complex and precise is the morphogenesis of the antheridia and oogonia (Sundaralingam, 1954, 1966). In some ways the development of both plants and reproductive structures resembles that of the Bryophyta and some Pteridophyta, with a high degree of morphogenetic precision which runs throughout the group and back to the fossil forms. The compound, complex organisation of the antheridia and oogonia is well known and so unlike any other algae that this alone points to divisional status, a view propounded by Desikachary and Sundaralingam (1962). There is no reproduction via zoospores and meiosis is generally believed to occur at germination of the zygote. Chromosome number is based on 5 in *Tolypella*, 6 in *Nitella* and 7 in *Chara* (Hotchkiss, 1964, 1965; Tindall and Sawa, 1964; Guerlesquin, 1967; Sinha and Noor, 1967). Of even greater significance is the recent confirmation that the 'unchlorophycean' male gamete is even more distinctive in having small square scales arranged in diagonal rows on the flagella (Pickett-Heaps, 1968; Turner, 1968) whilst there are somewhat larger scales on the body (Moestrup, 1970). The arrangement of head, mid and tail region of the male gamete together with the characteristic microtubule system and origin of the flagella are most distinctive (Sato, 1954; Pickett-Heaps, 1968; Moestrup, 1970). An eyespot seems to be absent from the motile cell. *Chara* is reported to contain lycopene and to lack carotene which is present in Chlorophyta (Hill and Whittingham, 1958), special organelles (termed *charosomes*) have been found associated with the plasmalemma and the cross walls are penetrated by plasmodesmata (Barton, 1965; Crawley, 1965). Set these distinctive characters alongside those of the Euglenophyta and clearly the 'charophytes' are as precisely and unequivocally designated and fully warrant their status as a phylum.

### 3. PRASINOPHYTA

In 1963 the 'prasinophyte' series formed a less well characterised group than they do now, largely owing to the lack of previous study and the necessity to use electron microscopy to determine the details. Nevertheless, even then they were known to possess features found in no other group and it was considered reasonable to align them alongside the 'euglenoids' and 'charophytes' and tentatively suggest that they were of similar stature. Even in 1966, however, Bourrelly maintained them in families of the Volvocales and Klein and Cronquist (1967) were against separating this group from the Volvocales. But Parke and Rayns (1964) had already placed the 'prasinophyte' genera in a separate class, the Prasinophyceae. Boney (1970) reviews some aspects of their biology and relates this to that of other scaly flagellates. In 1963, only the *Pyramimonas* stage of *Halosphaera* (Manton, Oates and Parke, 1963) had been adequately studied. Now, however, *Platymonas* (Manton and Parke, 1965; McLachlan and Parke, 1967), *Prasinocladus* (Parke and Manton, 1965), *Mesostigma* (Manton and Ettl, 1965), *Heteromastix* (Manton, Rayns, Ettl and Parke, 1965), *Nephroselmis* (Parke and Rayns, 1962), *Micromonas* (Manton and Parke 1960), *Monomastix* (Manton, 1967, where she comments on the tentative position of this genus), *Pachysphaera* (Parke, 1966), *Pedinomonas* (Ettl and Manton, 1964; Belcher, 1968), *Scourfieldia* (Throndsen, 1969) *Spermatozoopsis* and *Asteromonas* (possibly to be included here, see Peterfi and Manton, 1968) have all been investigated in both the light and electron microscope in a splendid series of papers. Ettl (1966) reviews the previous taxonomic position of some of these genera. The following characters are common to the majority. The four flagella (a few genera are known with fewer flagella) of the motile cells tend to arise from an apical pit; the flagella have a coating of scales and also hairs (but not of the 'Flimmer' type); the body of the motile cell is covered with one to several layers of scales, each layer with its own peculiar characteristics; a special type of fibrous band joins the flagellar bases to the plastid and nuclear surfaces; cytoplasmic extensions (sometimes even the nuclear envelope) penetrate the pyrenoid; two apical contractile vacuoles empty into the apical pit, two prominent dictyosomes are sited above the nucleus and on either side of the flagellar bases; flagellar scales and hairs are formed in a scale reservoir, and body scales in vesicles of the Golgi apparatus; the eyespot is contained within the chloroplast; some genera have pigments similar to Chlorophyceae but others have additional pigments, e.g.

magnesium 2, 4, divinylphaeoporphyin $a_5$ monomethylester (this even occurs in *Micromonas pusilla* (Butcher) Manton et Parke which does not have scales on its flagella), a new xanthophyll (micronone) in *Micromonas squamata* Manton et Parke and even siphonein, in *Heteromastix* and *Pyraminonas amylifera* Conrad (Ricketts, 1967); starch is formed within the chloroplast of some species though this starch is of a different form to that of the 'chlorophytes'; lipid bodies readily form in some species (particularly in the 'cyst' stages); mannitol is also formed as a characteristic soluble product of photosynthesis (McLachlan and Craigie, 1967); dimethyl-$\beta$-propiothetin is present in some genera, but is generally absent from Chlorophyceae (Achman, Tocher and McLachlan, 1966); zoospores tend to be formed in pairs and often at 180° to one another (*Prasinocladus*, *Platymonas*), whilst the motile cells can also divide longitudinally; sexual reproduction is unknown in almost all genera but there is a tendency to the formation of non-motile 'cyst' stages. Thus the group has emerged steadily as a distinct green algal series the equal of the previous groups and undoubtedly warrants the status of a phylum. At least two genera, *Monomastix* and *Pyramimonas*, have trichocysts (Belcher, 1965; Manton, 1969), structures which are absent from the Chlorophyta, and in these genera seem to be unlike the trichocysts of other groups. Manton (in Ettl and Manton, 1964), in a discussion of one of the simplest genera of this group (*Pedinomonas*), comments that 'the sum of evidence points to a phyletic separation (of *Pedinomonas*) from the Volvocales almost as great as in the cognate case of the euglenoids which also possess chlorophyll *b* but are not members of the Volvocales'. The later study of the even more distinctive genera amply bears this out, and Ackman, Addison, Prakash and Hooper (1970) comment on the increasing biochemical evidence for the separation. The genus *Pedinomonas* is, however, still somewhat problematical and requires further detailed study of as many species as can be isolated to establish whether or not the general cellular organisation is characteristic of the prasinophytes.

Unlike the previous two phyla, the Prasinophyta includes orders which are motile (Pyramimonadales), coccoid (Halosphaerales) and tetrasporal (Prasinocladales; Prasinodendrales of Round, 1963, but renamed after the genus *Prasinocladus*). The formation of the thecae in *Platymonas* and *Prasinocladus* is very similar and quite unlike the scale formation in other genera. This, plus the fact that Ricketts (1967) found that the carotenoids of these two genera are similar and contrast with those of the other genera suggests that *Platymonas* should be removed from the Pyramimonadales and placed alongside *Prasinocladus* in the Prasinocladales. Parke and Dixon (1968) place *Prasinocladus* in the Chlorodendraceae derived from 'a no doubt artificial group—Chlorodendrineae' of Fritsch (1935). Since other genera of this 'chlorodendroid' group have been placed in other orders and some may have to remain in a 'dendroid' group of the Chlorophyceae it is better to use a new name based on a genus, hence Prasinocladales.

It is perhaps worth noting that in these first three phyla there is a relatively small number of genera and they all conform closely to the generalised descriptions which can be written for the phylum, a situation which is not quite so well exemplified by the remaining green algal group.

The impressive work of the last decade has served to separate and distinguish the above three algal phyla and none has given any suggestion of 'convergence', thus warranting the early workers' recognition of their separation.

## 4. CHLOROPHYTA

This leaves the group which in 1963 was classified as the Chlorophytina and such a diverse group may not warrant a uniform treatment on a par with the above three phyla. The evidence just quoted shows quite remarkable uniformity within the first three phyla (cf. similar uniformity in some other algal phyla, e.g. Cyanophyta, Bacillariophyta, Rhodophyta, and even higher phyla, e.g. Bryophyta, Sphenophyta, Lycophyta, etc.). There certainly is less uniformity in this remaining 'chlorophyte' series. Indeed no other algal phylum shows such a range! Should this greater dissimilarity be acceptable within a single phylum or is more than one phylum involved?

Almost the only important unifying factor between the previous three phyla and this remainder is pigmentation and, whilst only a few genera have been investigated, they all tend to have both chlorophyll *a* and *b*, $\beta$-carotene as the principal carotenoid pigment (with the exception of some siphonous genera, Strain, 1965), lutein as the principal xanthophyll and neoxanthin and violoxanthin present. From the brief discussion of the first three phyla one might reasonably expect the following characteristics to be relatively constant: the structure and chemical nature of the cell wall; chemical nature of the reserve substances; place of formation of the reserves (e.g. within the chloroplast in these remaining groups, Ueda, 1961); structure of the chloroplast and pyrenoid; position of eyespot, contractile vacuoles, dictyosomes and mitochondria; formation of zoospores in zoosporangia (as opposed to vegetative cleavage in Prasinophyta and Euglenophyta, a distinction made by Schussnig, 1960, and Lund, 1962, and one which is probably important at several different levels of classification); ploidy of the vegetative phase; the point at which meiosis occurs in the life cycle; and flagellation of the motile cells. Features one would not expect to be constant in comparison with other phyla (e.g. Phaeophyta) are possession of motility; type of life history (Kornmann, 1965a, comments that, in general, life histories and presence of isogamy or anisogamy, are not significant for the characterisation of units higher than genera; see also the discussion of the Ulotrichales, Ulvales and Acrosiphoniales below); vegetative morphology; and chromosome number or form. Some of these features are however of great importance in designating orders of algae. In addition, it must be accepted that owing to the large number of genera (Bourrelly, 1966, lists over 500 freshwater genera alone in this remaining group) a greater spread of characters must be expected, and therefore fewer common criteria with which to characterise the phylum.

The 'chlorophyte' series have isokont flagella (wherever motile stages occur), without 'flimmer' or scales but sometimes with a flocculent coating; these arise from the apex of the motile cells, often emerging through lateral pores in the wall; simple contractile vacuoles occur; the stigma is immersed in the chloroplast; starch is formed within the chloroplast; the walls are composed of polysaccharides often of microfibrillar nature. A few genera are recorded which have somewhat unequal flagella (Starr, 1955; Bold, 1970) but these in no way approach the normally accepted heterokont state. Looked at from a negative aspect, there are perhaps no groups of algae within this remaining series which have a sufficient number of characteristic features (such as have the 'euglenoid', 'charophyte' and 'prasinophyte' series) to warrant their separation at the moment.

Cronquist, Takhtajan and Zimmerman (1966) proposed that divisions should have names based on types, i.e. genera, rather than names based on morphological characters. This had also been suggested earlier (Rickett and Camp, 1950) and it seems to me an admirable suggestion though one which may take a long time to become generally acceptable. Fortunately, of the above phyla, three are based on genera (*Euglena*, *Chara* and *Prasinocladus* or others commencing with *Prasino*-) but the Chlorophyta is not (*Chlorophyton* being an angiosperm).

## CLASSES

In the first three phyla the division into classes is simple and need not concern us further. Thus in the Euglenophyta there is only the Euglenophyceae (Leedale, 1967), in the Charophyta only the Charophyceae and in the Prasinophyta only the Prasinophyceae.

The Chlorophyta however are too varied to contain a single class and four classes as defined in Round (1963) still appear to me to be valid entities. The artificial group Loxophyceae, which was the convenience group erected by Christensen to contain genera on which further work was required, can now be omitted as its genera have been transferred elsewhere.

### ZYGNEMAPHYCEAE (CONJUGATOPHYCEAE)

Since it is preferable to have class names based on genera I propose that the conjugate algae be grouped in the class Zygnemaphyceae; this is entirely synonymous with the earlier Conjugatophyceae (Fott, 1959; Meyer, 1962; Round, 1963) and the Zygophycées (Bourrelly, 1966). In spite of the occurrence of numerous papers on cytological aspects and species descriptions since 1962, I am not aware of any studies to change my view, supported by Sarma (1964) on cytological grounds, that this is an extremely discrete class of the Chlorophyta. Fowke and Pickett-Heaps (1969) added another distinctive feature in that in *Spirogyra* both cleavage and the formation of a phragmoplast contribute to cell division. The distinctive ultra-structural characters of the cell walls of desmids has been used to elucidate some classificatory problems (Mix, 1967; Gerrath, 1969, 1970) and it is clear from such studies that the Zygnemaphyceae is a distinct class within the Chlorophyta.

### OEDOGONIOPHYCEAE

Further electron microscope studies (Hoffman and Manton, 1963; Hoffman, 1967; Hill and Machlis, 1968; Fraser and Gunning, 1969; Pickett-Heaps and Fowke, 1969; Fowke and Pickett-Heaps, 1969; Retallack and Butler, 1970) have added other characteristics to this already highly distinctive class. Manton (1964) comments on the rather greater differences than expected between the ultrastructure of the motile cells of *Oedogonium* and those of *Stigeoclonium*. The presence of microtubules in the chloroplast (Hoffman, 1967) has been recorded only rarely in other green algae (e.g. in developing chloroplasts of *Fritschiella*, McBride, 1970). The peculiar process of cell division (Hill and Machlis, 1968; Pickett-Heaps and Fowke, 1969) appears even more distinctive now its electron microscope detail is revealed. The presence of prominent plasmodesmata between cells of *Oedogonium* (Hill and Machlis, 1968) and of *Bulbochaete* (Fraser and Gunning, 1969) has not been recorded in other Chlorophyta *sensu stricto*. Sarma (1964), comparing the chromosome morphology with that of the Ulotrichales, came to the conclusion that the Oedogoniophyceae had distinctive karyological features warranting their separation as a class. Leedale (1970) points out that mitotic variations set *Oedogonium* (and also *Spirogyra*) somewhat apart from other green algae; obviously the details of many other genera are needed before firm conclusions are drawn. Pascher (1931) recognised that their status was higher than that of an order of the Chlorophyta but only raised them to a sub-class.

### BRYOPSIDOPHYCEAE

There still seem to be good reasons for maintaining this class as an entity though recognising that there are rather striking differences between the orders (see below). Ettl (1958) also obviously thought of the siphonous forms as a class (Siphonophyceen) but his designation is not based on a genus and therefore I prefer to retain the name Bryopsidophyceae based on the genus *Bryopsis*. The motile cells require more detailed study and I am inclined to regard the occurrence of 'lateral fusion' of gametes (Köhler, 1957; Neumann, 1969a, 1969b) as significantly different to that in 'volvocalean' type gametes. A detailed study of the ultrastructure of the gametes and zoospores, and comparison of these with those of the Chlorophyceae, is needed since the very interesting papers of Goldstein and Morrall (1970) on *Caulerpa* and of Burr and West (1970) on *Bryopsis* show somewhat unusual features (compare also the interesting removal of part of the Xanthophyceae as an isolated new class by Hibberd and Leedale (1970, 1971) based on ultramicroscopic features of the motile and vegetative cells, where the arrangement of some organelles was similar in both types of cell, thus adding confidence to comparisons between motile and non-motile genera). The gametes appear to fuse without the formation of a cytoplasmic bridge such as is found in Volvocales and electron micrographs indicate a lack of contractile vacuoles, a characteristic feature of Volvocales (see below). Goldstein and Morrall (1970) report that the gametes of *Caulerpa* sp. are naked and fusion occur in various ways after pairing. Only the female gametes have eyespots in the chloroplasts whereas in Chlorophyceae both gametes have eyespots. The published electron micrographs of genera of this class (e.g. *Acetabularia*, Crawley, 1963) do not show dictyosomes associated with 'amplexi' type outgrowths of endoplasmic reticulum from the nucleus in either vegetative cells or gametes, such as is common in some species of Volvocales, Chlorococcales, Chlorosarcinales, etc. The importance of biochemical features, e.g. pigment complement ($\alpha$-carotene is the predominant carotenoid as opposed to $\beta$-carotene in the Chlorophyceae, Strain, 1965; Kleinig, 1969; Ricketts, 1971), wall polysaccharides (Iriki and Miwa, 1960; Frei and Preston, 1964; Parker, 1970) and cytological detail, e.g. chloroplast/leucoplast structure (Hori and Ueda, 1967), are of overwhelming importance in this group and features of these separate the Bryopsidophyceae from the Chlorophyceae, but, unfortunately, none are all embracing for the class as a whole.

### *Remaining class or classes*

In some features the remaining green algal genera are more discrete than those in the preceding class in that characters such as wall polysaccharides, pigments, chloroplast type, nuclear organisation, etc., are relatively conservative; on the other hand, their morphological development is diverse.

Bourrelly (1966) groups these remaining orders into two classes, Euchlorophycées and Ulotricophycées. These stand alongside his Charophycées (which have been dealt with above in a separate phylum) and his Zygophycées which are synonymous with the Zygnemaphyceae. However, Bourrelly's Ulotrichophycées still contain the siphonous orders and Oedogoniales in an unnatural grouping; with these removed, the classes of Bourrelly are more acceptable. The term Euchlorophycineae had been used earlier by Skuja (1938) to embrace the Volvocales, whereas Bourrelly's Euchlorophycées contain the orders Volvocales, Tetrasporales and Chlorococcales, i.e. the solitary and colonial but non-filamentous and non-thalloid forms, whilst the Ulothricophycées contain the filamentous and thalloid genera. This is a convenient grouping (it was earlier used by Pascher, 1931; Volvocineae and Ulotrichineae) but it could be argued that it is artificial, being based solely on morphology; this criticism can be removed only if other criteria can be correlated with the morphological features. One characteristic which does seem to unite the volvocalean, tetrasporal and coccoid groups is the fact that daughter cells are formed inside the mother cell wall which then disrupts (Fott, 1965).

This issue is, however, further complicated in that, in an excellent study by Ettl (1958a), inadvertently overlooked in my earlier paper, a group of flagellate orders (Pyramimonadales, but see p. 245, Raciborskiellales, Chlamydomonadales, Volvocales and Pedinomonadales) were elevated to the status of a class (Volvophyceae); this concept is in fact derived from Pascher (1931), see above, but enlarged from later studies. Further he also elevated the tetrasporal series to the Tetrasporophyceae (containing the Chlorangiales, Characiales and Characiosiphonales) and the coccoid series to the Chlorococcophyceae (Ettl, 1958b). Again these can both be traced back to Pascher's Tetrasporineae and Protococcineae and Ettl obviously also recognised a filamentous class, Ulotrichophyceae.

The choice then is between a single class, Chlorophyceae, as in my original article in which two series were recognised but not raised in status, equal to the two classes Euchlorophycées and Ulothrichophycées of Bourrelly (1966), or the four classes, Volvophyceae, Tetrasporophyceae, Chlorococcophyceae and Ulotrichophyceae of Ettl (1958a, 1958b). If one rejects such subdivided systems then, by comparison with classes in other phyla, e.g. Bangiophyceae and Florideophyceae (Cronquist, 1960) of the Rhodophyta, Centrobacillariophyceae and Pennatibacillariophyceae of the Bacillariophyta (Silva, 1962), the Chlorophyceae (*sensu* Round, 1963) contrasts as a vastly diverse group on morphological, reproductive, biochemical and cytogenetical grounds. Even considering Ettl's four classes, each encompasses a range of morphology (e.g. unicellular and colonial organisation in the case of the Volvophyceae) but each also has its distinctive morphological features (e.g. the vegetative cell is always flagellate in the Volvophyceae). On the other hand, characteristics of the motile cells are remarkably similar in the volvocalean, tetrasporalean, coccoid and even filamentous genera. Fott, Novakova and Kalina (1965) clearly consider the tetrasporal series as 'an evolutionary step between two grades of algal phylogeny' and if this is so, then retention at the ordinal level seems to be preferable.

Contractile vacuoles were regarded as important phylogenetic and systematic characteristics of flagellates as early as 1926 by Korschikov (1926 and 1932) and by Pascher and recently their importance has been stressed by Ettl (1961), and Lund (1962). Hence the name Vacuolatae was used by Korschikov (1932) for the tetrasporal series of algae, but such vacuoles occur regularly in the orders up to and including the Chaetophorales (even rarely in the Zygnematales) and therefore perhaps cannot be such important diagnostic features. Their occurrence in the Bryopsidophyceae requires verification since they may prove important criteria in this class.

Apical fusion of gametes with the formation of a 'connecting bridge' is common in some Volvocales, e.g. *Volvulina pringsheimii* Starr (Starr, 1962), *Volvulina steinii* Playfair (Stein, 1958), *Chlamydomonas moewusii* Gerloff (Lewin and Meinhart, 1953; Gibbs, Lewin and Philpott, 1958; Brown, Johnson and Bold, 1968) and *C. reinhardtii* Dangeard (Friedman, Colwin and Colwin, 1968). *C. reinhardtii*, however, is also reported to fuse laterally after pairing by flagellar agglutination, followed by release of the gametes from the cell wall (Jones, 1970). This latter type of fusion may be facilitated by the loss of a cell wall and so the occurrence of apical, lateral or basal fusion may merely be a reflection of this; nevertheless it could be a useful feature of classification. Another criterion which might cautiously be used in distinguishing classes is the occurrence of dictyosomes in 'amplexi' alongside the nucleus, e.g. *Pediastrum* (Moner and Chapman, 1960), *Astrophomene* (Lang, 1963), *Tetracystis* (Brown and Bold, 1964); *Haematococcus* (Lang, 1968), possibly similar in *Chlorogonium* (Ueda, 1966), and *Eudorina* (Hobbs, 1971). Caution is needed because this arrangement is not even constant throughout a genus (e.g. *Tetracystis*) or is absent from closely related genera (e.g. absent from *Carteria* but present in *Chlamydomonas*), but its total absence may add to the characterisation of a group. In *Chlamydomonas reinhardtii*, Johnson and Porter (1968) show the dictyosomes in partial amplexi-like segments of endoplasmic reticulum extending from the nucleus and here they are located at the base of the nucleus, quite the opposite to their position in the Prasinophyta. So far this perinuclear arrangement seems to have been found fairly frequently in Volvocales, Chlorosarcinales, Chlorococcales and also in zoospores of *Stigeoclonium* (Manton, 1964). If not in 'amplexi', dictyosomes are commonly found adjacent to the nuclei in these groups, e.g. in *Carteria* (Joyon and Fott, 1964) and in *Chlorella* (Griffiths and Griffiths, 1969).

In 1962, Meyer proposed a subdivision of the green algae into two classes (Centroplastophyceae and Parietoplastophyceae) based on the presence of either an axile or parietal chloroplast, but such a system based on consideration of a single characteristic is unacceptable. The class Loxophyceae of Christensen (1962) no longer appears to be necessary, since any genera which cannot be included in any of the above classes are best unallocated until their position is clarified.

In the present state of knowledge I consider it prudent to retain a single class, Chlorophyceae, for these remaining algae.

## ORDERS

How the genera are to be grouped into orders is still as much a problem as it was in 1963 but some progress has been made. In the Charophyceae, the single order Charales is valid and in the Euglenophyceae, Leedale (1967) distinguished the Eutreptiales, Euglenales, Rhabdomonadales, Sphenomonadales, Heteronematales and Euglenomorphales. The Prasinophyceae contain the three orders Pyramimonadales (= Prasinovolvocales of Chadefaud and Emberger, 1960; Round, 1963), Prasinocladales (= Prasinodendrales of Round, 1963) and Halosphaerales (=Prasinococcales of Chadefaud and Emberger, 1960; Round, 1963). In the Oedogoniophyceae the single order Oedogoniales remains and in the Zygnemaphyceae the four orders Mesotaeniales, Zygnematales, Gonatozygales and Desmidiales require no emendation. Bourrelly (1966) recognises only a single order, Zygnematales, and places into this order all the above orders but reduced to families. The Ulotrichales of Fott (1959) or Chadefaud or Chaetophorales of Printz (1964) or Ulotrichineae of Pascher (1931) are all groups I would consider artificial in that they embrace all the filamentous and in some schemes even siphonous orders. Even with the removal of siphonous groups, the Ulotrichophycées would contain the orders Ulotrichales, Ulvales, Chaetophorales and Trentepohliales of Bourrelly (1966), to which I would add the Microsporales, Cylindrocapsales and Coleochaetales. I cannot support Bourrelly in distinguishing these filamentous green algae as a class but would, however, maintain for the time being two cohorts within this filamentous group as tentatively suggested in 1963. The first is the Ulotrichiidae, containing the Ulotrichales, Ulvales, Microsporales, Cylindrocapsales and Prasiolales, and the second is the cohort of branching filamentous green algae, the Chaetophoriidae, containing the Chaetophorales, Pleurococcales, Trentepohliales and Coleochaetales. The reason for not elevating this section to a class and at the same time separating it from the flagellate/tetrasporal/coccoid series (Bourrelly's Euchlorophycées), is based on comparison with the Zygnemaphyceae/Oedogoniophyceae/Bryopsidophyceae, each of which is clearly characterised by well defined cytological, morphological, reproductive, life cycle, biochemical and even ecological criteria. Consideration of any of these numerous factors throughout the orders from the Volvocales to the Coleochaetales reveals no striking discontinuities, e.g. cellulose is the commonest wall component throughout; biflagellate gametes fuse usually by their apices; chloroplasts vary from cup shaped, band shaped to stellate; the pyrenoid is embedded in the chloroplast; isomorphic to heteromorphic alternation of generation is scattered throughout the group; the zoospores tend to be quadriflagellate; etc. At the ordinal level the problems which remain in the Chlorophyceae can be conveniently brushed aside by merging the orders. On the other hand, I believe that maintaining them separate is more likely to stimulate individual studies of genera which otherwise might be neglected. Numerous orders have been established or merged during the history of the 'green' algae, but the criteria used for establishment of an order have rarely been defined and equally rarely have these criteria been applied to the others within a class. To some extent the criteria differ in different algal groups. Thus in the Rhodophyta the emphasis is on the female reproductive branch system, in the Bacillariophyta it is on the morphology of the siliceous wall components of the vegetative cell. Morphology was used as a keystone of the ordinal systems of Pascher (1931 and earlier papers) applied not only to the Chlorophyceae but also to the Xanthophyceae, Chrysophyceae, etc. and it 'is still the major criterion for taxonomic discrimination' (Dixon, 1970). Fott (1965) obviously considers that morphological features are important since he comments that orders contain genera of the same morphological habit. There is nothing to be ashamed about in using morphology; it is obvious from the inadequate morphological detail in the literature that this is a most *difficult* subject and as Dixon and Richardson (1970) point out the phenotypic plasticity of most aquatic species adds acute problems. That morphology can be used within some of the most difficult genera is shown in the excellent study of *Chlorella* by Fott and Novakova (1969). Orders should surely provide a valuable test of the concept in the quotation from Lewin (1968) at the head of this article. Within reasonable limits any genus of an order should contain the information necessary to define the order and the converse also should apply. This test applies to genera such as *Cosmarium* (Desmidiales), *Spirogyra* (Zygnematales) and *Oedogonium* (Oedogoniales) but it is inapplicable, for example, to the Chaetophorales of Printz (1964) or the genera within this order. Starting from a basis of morphology it is often found that biochemical characteristics correlate, e.g. in the siphonous orders. If such biochemical characteristics were available for many more genera then the ordinal system could be based on these as Aaronson and Hutner (1966) and Margulis (1968) suggested. If, then, morphology is to be used (and I mean in its widest sense drawing on ultrastructural detail) it should be applied consistently and, bearing in mind the concept in the quotation from Lewin (1968), students who may at first be confused will find the quotation from Takhtajan (1968) is entirely applicable. At the ordinal, generic and species levels the large number of characteristics required for sorting the taxa will require the application of numerical taxonomy such as has been so admirably applied to *Flexibacteria* (Fager, 1969; Lewin, 1969) where 84 characteristics were utilised for 85 strains. However, until sufficient comparable data are available for the majority of genera the older approach must be used. It is almost impossible to keep up with the vast literature and I have undoubtedly missed some important contributions but below is a summary of orders which have been recognised at various times in the Chlorophyceae; taxa in square brackets are considered superfluous. It is not easy to find the authority for each order but where this is known I have quoted it.

[PEDINOMONADALES, PROTOCHLORIDALES = CHLOROCHYTRIDIALES; Korschikov, 1923, 1938 as Protochlorinae]. Ettl (1966) united the Pyramimonadineae and Pedinomonadineae within this order and Manton (1967) considered that some genera may have to be retained in a grouping similiar to this. This order was used by Ettl (1966) for Korschikov's (1923) Protochlorineae. All the genera of these groups have been transferred *en bloc* to the Prasinophyceae by Parke and Dixon (1968).

POLYBLEPHARIDALES. Ettl (1966) admits that this order is one of the most problematical. The family Polyblepharidaceae has in fact been transferred to the Prasinophyceae (see Christensen, 1966; Parke and Dixon, 1968). This still leaves some unicellular naked forms (e.g. *Dunaliella*) and the colonial Raciborskiellaceae; Parke and Dixon (1968), however, retain the Dunaliellaceae in the Volvocales. Maintaining a separate order may at least stimulate further studies.

[RACIBORSKIELLALES; Ettl, 1958]. This designation was used by Ettl for colonial flagellates without cell walls. Later (1966) he submerged these in the Polyblepharidales as a family (Raciborskiellaceae).

CHLAMYDOMONADALES; Fritsch in West (1927). Ettl (1958a, 1966) maintained the unicellular *Chlamydomonas*-like species in a separate order. This is not new since Pascher (1931) also used this system. Establishing a separate group for the unicellular forms is in line with a policy of maintaining as far as possible only a single vegetative morphology in an order. Wall structure is generally regarded as being based on cellulose microfibrils but Schlösser (1966) reported galactose and arabinose in *Chlamydomonas reinhardtii.* Ettl (1970) uses ultrastructural features to separate the species without pyrenoids from those of *Chlamydomonas* and places them in the separate genus *Chloromonas.*

[CENTROMONADALES; Meyer, 1962]. This order is unacceptable since it is based upon a single characteristic.

VOLVOCALES; Oltmans (1904), Pascher (1931), Ettl (1966). This order embraces the colonial flagellate genera some of which are admittedly very close morphologically to genera of the Chlamydomonadales whilst others, e.g. *Volvox*, would hardly be placed adjacent if the series from *Gonium* through *Pandorina, Eudorina,* etc., was not so firmly entrenched. Lang (1963) and Parker (1964) comment on the lack of a compact cell wall in this group compared with the *Chlamydomonas* group and Parker suggests this may be of some evolutionary significance. However, Olson and Kochert (1970) report that the flagellum-kinetosome complex is similar in the two groups. Ettl (1966) includes *Spondylomorum* and *Corone* within this order and this may be valid, but the structure of these colonial genera is quite unlike the former ones, e.g. in their polarity, physiology, at least of *Uva* (= *Chlamydobotrys* and *Pyrobotrys* according to Bourrelly, 1966), formation of bridges between the cells and somewhat different organisation of the thylakoids in *Uva* (Merrett, 1969). I suspect that when further details, especially of ultrastructure, are available this latter group may have to be reassessed.

TETRASPORALES; Lemmermann in Pascher (1915). This order has been misunderstood by many phycologists but Ettl (1966) points out the importance of polarity and the presence of contractile vacuoles. The cells tend to have the characters of the flagellate series minus the flagella, though in some, e.g. *Tetraspora*, the flagella bases are retained (Lembi and Herndon, 1966). The formation of embedding mucilage and mucilaginous pseudoflagella is an incidental character of some genera.

[PALMELLALES; Chadefaud and Emberger, 1960 & earlier]. Synonymous with Tetrasporales.

CHLORODENDRALES; Fritsch in West (1927). Genera placed in this order require reinvestigation. It should not be merged until this has been undertaken.

[CHLORANGIALES; Pascher, 1931; Ettl, 1958b]. Merged into Tetrasporales by Ettl (1966).

[CHARASIOSIPHONALES; Ettl, 1958]. Merged into Tetrasporales by Ettl (1966).

[CENTROPALMELLALES; Meyer, 1962]. See remarks on Centromonadales.

CHLOROSARCINALES; Groover and Bold (1969) [= Chlorosphaerales, Herndon, 1958]. The extensive studies of the group working under Bold have steadily refined the characteristics of this difficult order. Its inclusion in the Chaetophorales as a family (Chlorosarcinées) by Bourrelly (1966) is, I think, untenable since the genera never form filaments even in culture; the form of the chloroplast and zoospore type and behaviour (Bold, 1970) are also unlike those of the Chaetophorales. The ultrastructure of the region of flagellar insertion in *Tetracystis* is very similar to that of *Chlamydomonas* (Arnott and Brown, 1967).

CHLOROCOCCALES; Marchand (1895). This order remains on the whole a distinctive one and the numerous excellent biochemical/microbiological studies of the Texas group under Bold, and the morphological studies of the Prague group under Fott, are succeeding in defining the group. But it is one of the largest orders of green algae and much remains to be achieved in the reorganisation of the families. Trainor (1970 & earlier work) and Swale (1965, 1967) have shown the extreme pleomorphism of some genera. The wall composition is variable in the group, e.g. cellulose in many but a mixture of glucans and mannans in *Hydrodictyon* and *Pediastrum* (Parker, 1964; Gawlik and Millington, 1969). This suggests that the group is perhaps in need of further detailed study and subdivision.

[CENTROCOCCALES; Meyer, 1962]. See remarks on Centromonadales.

[PROTOCOCCALES]. Synonymous with Chlorococcales. Printz (1927) used Protococcales to include volvocalean, tetrasporalean and coccoid series.

ULOTRICHALES; Borzi (1895). This is maintained as a small order of algae by Kornmann (1963, 1965c) in which the filamentous stage alternates with a cyst-like (*Codiolum*) stage in many species. The genus *Monostroma* has been investigated by several workers (Tatewaki, 1969; Kornmann, 1963; Gayral, 1965; Dube, 1967; Bliding, 1968). Kornmann (1963) and Gayral (1965) place *Monostroma* in the Ulotrichales whilst Bliding (1968) and Kida (1967) include it in the Ulvales. Dube (1967) found that *M. fuscum* (Postels et Ruprecht) Wittrock and *M. obscurum* (Kütz.) J. Ag. are distinct from other *Monostroma* species, in fact, Bliding (1968) transferred these species to *Ulvaria* within the Ulvales (see below). There seem therefore to be monostromatic thalli in both orders, with heteromorphic life cycle in the Ulotrichales and isomorphic in the Ulvales. The germling stage of *Monostroma* is a system of branching filaments and as such fits in with other genera of the Ulotrichales although in some *Ulothrix* species this stage can be very reduced. On the other hand, *Ulvaria* forms a monosiphonous filament which enlarges into the blade and should probably be maintained in the Ulvales. *Stichococcus* and the morphologically very similar *Nannochloris* have been shown to be rather unusual members of the Chlorophyceae in that they form mannitol (Craigie, McLachlan, Ackman and Tocher, 1967) and also have a similar reaction to surfactants (Ukeles, 1965), and therefore probably require further study. Christensen (1966) includes the Acrosiphoniaceae, Codiolaceae and Sphaeropleaceae here but I prefer to maintain these groups as separate orders.

CODIOLALES; Kornmann (1965a). Kornmann transferred *Urospora* (presumably *U. wormskioldii* (Mertens) Rosenvinge) from the Acrosiphoniales to the Ulotrichales since it has a heteromorphic life cycle, though in another paper (Kornmann, 1965b) he comments that life cycles may not be significant for characterisation of taxa above genera. In the same paper Kornmann created a new order, Codiolales, containing this *Urospora* but without specifying any further details for the order. *U. wormskioldii* has a single nucleus and a band-shaped chloroplast whilst other *Urospora* spp. are multinucleate and with a netlike chloroplast (Hanic, 1965; Scagel, 1966) which suggests that, as in *Monostroma*, two or more genera are being confused here. There is little doubt that intensive studies are needed on many species before this order is settled and a serious attempt should be made to include biochemical studies to add to the morphological and life history data.

ULVALES; Blackman and Tansley, 1902. Bliding (1963, 1968) includes here a group of genera with isomorphic alternation of generations (male, female and zoosporic plants in some species; Chihara, 1968), cup-shaped chloroplasts, multicellular rhizoidal development, filamentous young stages (though often arising from basal discs, see Gayral, 1967), and a high degree of polarity of the cells and thalli. Papenfuss (1960) thought they might be reduced to a family of the Ulotrichales but I can see few arguments for this merger though undoubtedly further detailed studies are highly desirable. The gametes are said to fuse laterally and this needs to be compared with fusion of gametes in the Ulotrichales using electron microscope techniques such as those already used so successfully for *Chlamydomonas* and *Prasiola*.

PRASIOLALES; Fritsch in West (1927). [= SCHIZOGONALES, West, 1904; and CENTROSTROMATALES, Meyer, 1962]. These remain an isolated group in which the form of the thallus, chloroplast structure and the unusual method of fertilisation (Friedmann, 1960; Manton, 1960) places this group apart from other green algae. The fact that ultrastructure of the gametes (attachment of flagellar bases to the tip of the male nucleus, simplicity of thylakoids, stellate chloroplast, etc.) and the submergence of one male flagellum in the egg at fertilisation are regarded as important criteria in this group encourages the view that a study of similar criteria in other genera will assist the classification.

MICROSPORALES; Bohlin (1901). These have been maintained separately (Prescott, 1969) but Sarma (1964) found little to distinguish them from the Ulotrichales on cytological grounds. Maintenance of a separate order may stimulate biochemical and ultrastructural studies leading to a reappraisal.

[CENTROTRICHALES; Meyer, 1962]. See remarks on Centromonadales.

CYLINDROCAPSALES; Prescott (1951). A small order requiring further investigation.

CHAETOPHORALES; West (1904). This order is still often included within the Ulotrichales but, apart from similarity in chromosome morphology and number (Sarma, 1964; Abbas and Godward, 1964) which led these authors to suggest that the orders should be united, there seems little reason to combine them. Other workers have gone further and split them into Chaetophorales, Coleochaetales and Trentepohliales (Chadefaud and Emberger, 1960; Prescott, 1969). Certainly by comparison with other orders this is valid on the basis of morphology, reproduction and some biochemical features. Much has been made of the occurrence of a ring-like chloroplast in both Ulotrichales and Chaetophorales but this is one of the few similarities. South (1968) comments that whilst cultural studies have proved invaluable in some groups, e.g. Chlorococcales, they have to be used cautiously in the Chaetophorales.

COLEOCHAETALES; Chadefaud and Emberger (1960). Prescott (1969) recognises this order and includes not only *Coleochaete* but also the Aphanochaetaceae and part of the Chaetonemaceae within it. This is undesirable and these families should remain in the Chaetophorales until further detailed studies have been made. I think it better to retain only *Coleochaete* with its most characteristic features in the order. Abbas and Godward (1964) pointed out that *Coleochaete* was quite distinct from other filamentous genera and McBride (1967) reported that *Coleochaete* possesses distinct chloroplast grana, surprisingly complex setae at the ultrastructural level and a pattern of columnar protrusions on the outer cell wall. Adding these to the highly distinctive reproductive system suggests a most distinctive order.

TRENTEPOHLIALES; Chadefaud and Emberger (1960). Again a small highly specialised order of mainly terrestrial epiphytic algae. Zoospores are produced in specialised sporangia which absciss and are wind dispersed. The early report (Heilbron, 1942) that *Trentepohlia* completely lacks sterols requires rechecking since Hegnauer (1962) reports the presence of erythrotol.

PLEUROCOCCALES; Chodat (1909). This small group requires further study.

ULVELLALES. Again further studies are required on this order.

In the Bryopsidophyceae the problem of the number of orders and the distribution of genera amongst them is now somewhat clearer since further pigment (Kleinig, 1969) and cell wall studies (Parker, 1970) have been made. The orders can still be allocated to three cohorts, as follows:

*HEMISIPHONIIDAE*; Chadefaud (1960).

CLADOPHORALES; West (1904). By 1964 the work on structure of the walls by Frei and Preston (1964) had provided ample evidence for the uniformity and distinctness of this group and subsequent contributions have emphasised this. Sarma (1964) concluded that the nuclear detail with a basic chromosome number of 6 established the discreteness of the group on cytological grounds. Then Hori and Ueda (1967) found that the ultrastructure of the chloroplasts differed from that in other siphonous forms with numerous closely packed thylakoids (discs) and 'bilenticular' pyrenoids. Parker (1970) discussing the evidence from biochemistry of the wall microfibrils again stresses the unity of the group. The cross walls are formed by annulus-like ingrowth (van den Hoek, 1963) but since Fowke and Pickett-Heaps (1969) found a combination of an ingrowing septum and a phragmoplast in *Spirogyra* the whole question of cross wall formation in filamentous genera requires reinvestigation. The occasional occurrence of heteromorphic life cycles (Archer and Burrows, 1960) does not detract from the discreteness of the order since such life cycles have been reported scattered in various green algal groups. Van den Hoek (1963) in an excellent study of the genus *Cladophora* considered that only the structure of cell wall, chloroplast and pyrenoid, allied with cell division, should be used to distinguish *Cladophora* from other genera. The Cladophorales have an inoperculate exit pore for the zoospores and gametes and this differs from the Acrosiphoniales. Christensen (1966) combined the Cladophorales with the Siphonocladales.

SPHAEROPLEALES; Fritsch in West (1927). These are still aligned with the filamentous Chlorophyceae by many authors though their multinucleate nature, annular growth of the cross wall, etc., really place them in the Bryopsidophyceae. This problem will not be solved until detailed biochemical criteria and ultrastructure of the walls can be added to the morphological features. Klein and Cronquist (1967) place this order close to the siphonous line based on the structure of the photosynthetic apparatus.

ACROSIPHONIALES; Kornmann (1965b). Parker (1970) comments on the isolation of this group from the Cladophorales in that cellulose has not yet been completely and adequately demonstrated whilst even the mucilages differ. The cells are strongly polarised with apical branching, branches often curved and rhizoids arising at the base of the cells. The germling forms a basal branching disc in which the cell row tends to adhere. Hanic (1965) showed that the *Codiolum* stage had a pectin wall. The wall of *Spongomorpha* differs from that in *Cladophora* and *Chaetomorpha* (Hanic and Craigie, 1969), forming another criterion for separation of the orders. There seems to be some confusion over the number of nuclei per cell in the various species; Kornmann (1965b) considers that the operculate opening of the sporangia is a characteristic of this group. In *Acrosiphonia* and *Spongomorpha* only the apical cells increase in length (Kornmann, 1965b, 1967) and it would be interesting to compare this with the situation in the genera of the Cladophorales. Hori and Ueda (1967) studied the ultrastructure of the chloroplast and pyrenoid and concluded that details of these supported a separate order. Jónsson (1963), however, did not support the establishment of this order.

*CYSTOSIPHONIIDAE*; Chadefaud (1960). Hori and Ueda (1967) add substance to the view that the Siphonocladales and Dasycladales are in the same group since they have features of chloroplast ultrastructure in common.

DASYCLADALES; Pascher (1931). This is perhaps the easiest group to define. All the genera have radial symmetry, the vegetative thallus is uninucleate with a massive nucleus in the rhizoidal portion, the multinucleate state occurs prior to reproduction, operculate cysts arise in specialised gametangia and these open to release the gametes; there is also a strong tendency to deposit calcium carbonate. According to Merac (1955), Hegnauer (1962) and Meuse (1962, 1963) this order does not store glucosans or oil but fructosans. Inulin has been recorded in *Acetabularia* (Merac, 1953) but noted as early as 1863 by Naegeli according to Meuse (1963) who also found it in *Batophora* but not in *Dasycladus*. Neither siphonoxanthin nor siphonein have been recorded (Kleinig, 1969) and $\beta$, 1–4 mannan is the chief wall polysaccharide with lesser and varying amounts of galactose (Werz, 1963), though as Parker (1970) points out the whole order needs to be surveyed. In the cap region of *Acetabularia*, however, the proportions of glucose and galactose increase and only in this region is rhamnose found (Zetsche, Grieninger and Anders, 1970), indicating that when comparative biochemical studies of wall material are made the exact origin of the material should be stated. Hori and Ueda (1967) showed that the chloroplasts have no pyrenoid though starch is present in both the chloroplast and cytoplasmic matrix and in some species the thylakoids have a distinctive grana-like structure (Werz, 1966; Bouloukhère, 1970).

SIPHONOCLADALES; Blackman and Tansley (1902). This order is characterised by cellulose walls (Parker, 1970; Dawes, 1966; Stewart, Dawes, Dickens and Nicholls, 1969) and segregative division. Dawes (1969) records a microfibrillar wall in *Apjohnia* with the fibrils running in three directions and centripetally formed cross walls. There is slight evidence of ‘segregative division’ when rhizoids form. Fritsch describes the method of ‘segregative division’ in such a clearly defined way that it seems to be a good criterion for separation from the Cladophorales. Nizamuddin (1964) confirmed the distinctive types of division in the two orders. However, neither *Anadyomene* nor *Microdictyon* show distinctive segregative division and Fritsch (1954), Egerod (1952) and Papenfuss (1955) suggested their removal to the Cladophorales. However on morphological criteria they are better left in the Siphonocladales. Christensen (1964) considered that this order and the Cladophorales were very close but the segregative division was fundamentally different from the septation in the Cladophorales. Hori and Ueda (1967) found that large numbers of chloroplast thylakoids were aggregated to form bands and, though this state was approached by some species of the Cladophorales, it is an added criterion to separate these from the Siphonocladales. It may be significant that Kleinig (1969) found siphonoxanthin in three genera (*Boodlea*, *Valonia* and *Blastophysa*; he places the latter genus in this order), whereas this pigment is recorded only in a few species of *Cladophora*. It is desirable to check the identity of these *Cladophora* species.

[VALONIALES; Pascher, 1931]. This is synonymous with Siphonocladales.

CHLOROCHYTRIALES. This small order requires further study—recently one symbiotic genus *Ostreobium* has been shown to possess both siphonein and siphonoxanthin (Jeffrey, 1968). *Ostreobium* is placed in the Chlorococcales by Parke and Dixon (1968) and is obviously a genus requiring further study. The genus *Chlorochytrium* itself is the sporophytic generation of *Spongomorpha* (Chihara, 1969). *Blastophysa* may belong here but I agree with Parker (1970) that it may have to be in a separate order, Chaetosiphonales.

*EUSIPHONIIDAE*; Chadefaud (1960). This grouping still has value since it brings together genera all possessing siphonein and siphonoxanthin (except Dichotomosiphonales) and $\beta$, 1–3 xylan as the commonest wall component (Iriki and Miwa, 1960; Frei and Preston, 1964; Parker, 1970). *Halicystis* requires further study (Parker, 1970) but glucose and xylose residues are present. *Derbesia* and *Codium* however have $\beta$, 1–4 mannan. *Codium* is also exceptional in that both lutein and lutein epoxide are absent (Kleinig, 1969). However, some genera have a single type of plastid (*Codium*, *Derbesia*, *Bryopsis*, *Pseudodichotomosiphon*) whilst others have both chloroplasts and amyloplasts and also the 'concentric lamella system' found by Hori and Ueda (1967) and also by Sabnis (1969) who termed these structures 'terminal bodies'. These appear as areas of coiled thylakoids at the apices of the chloroplasts. *Chlorodesmis*, *Halimeda*, *Udotea*, *Caulerpa*, *Avrainvillea* and *Dichotomosiphon* lack the 'concentric lamella' system. Thus some of the features cut across the system of orders (see below). This suggests that further work is needed on a whole range of characters in order to typify the groups more satisfactorily.

DICHOTOMOSIPHONALES. Two features recently added to those distinguishing *Dichotomosiphon* are absence of siphonoxanthin (Kleinig, 1969) and the absence of amyloplasts (Hori and Ueda, 1967). Frei and Preston (1964) and Maeda, Kuroda, Iriki, Chihara, Nisizawa and Miwa (1966) analysed the wall structure of *Dichotomosiphon* and found it consisted of $\beta$, 1–3 xylan. *Pseudodichotomosiphon* however has only chloroplasts. The order requires further detailed study.

CODIALES; Setchell (1929). *Bryopsis* has now been shown to have a giant nucleus with a long sinuous nucleolus (cf. *Acetabularia*) in its protonemal stage and only becomes multinucleate prior to formation of the plumose habit (Neumann, 1969b). *Bryopsis hypnoides* Lamour. undergoes lateral fusion of gametes ('seitliche verschmelzung'). Kleinig (1969) found that lutein and lutein epoxide were absent from *Codium* and lutein epoxide absent from *Bryopsis*; they were, however, both present in *Pseudobryopsis* and *Avrainvillea*. Hori and Ueda (1967) first reported bands composed of 4–5 thylakoids in the chloroplast of *Bryopsis* and this has recently been confirmed by Burr and West (1970). As pointed out by Parker (1970) this whole order requires detailed studies and I would add that submicroscopic studies of the thalli and gametes, including the process of fusion, are required, to reinforce the biochemical studies of cell walls where both xylans and mannans have been recorded. Burr and West (1970) show the very distinctive male gamete with its degenerate chloroplast and massive mitochondria, also the unusual angle of insertion of the flagella. The female gamete on the other hand has a large chloroplast, a very extensive eyespot and, unlike the male gamete, it has layers of endoplasmic reticulum around the nucleus (Urban, 1969).

[EUSIPHONALES; Feldmann, 1946]. This order was created by Feldmann for the siphonous genera with a single type of plastid as opposed to those with chloroplasts and amyloplasts. The earlier taxon, Codiales, is preferable since it is based on a genus.

CAULERPALES; Setchell (1929). There is little to add to the characterisation of this order, the algae within which have walls of β, 1–3 xylan.

DERBESIALES. Parker (1970) confirmed that on wall structure this order is probably distinct but again more detail is needed. The *Derbesia* stage probably contains glucose and xylose and the *Halicystis* stage has β, 1–4 mannan. Kleinig's (1969) study confirmed the presence of the typical pigments siphonein and siphonoxanthin. Neumann (1969a) showed that the gametes of *Derbesia* fuse in a manner similar to that in *Bryopsis*.

[SIPHONALES; Willie in Warming, 1894]. The previous siphonaceous orders were formerly united in this order.

PHYLLOSIPHONALES. This order requires reinvestigation. According to Chadefaud and Emberger (1960), *Phyllosiphon* may belong to the Xanthophyceae.

A summary of the above orders is presented in Table II.

TABLE II. A summary of the scheme of classification of the 'green' algae.

EUCARYOTA—CONTOPHORA

| | | | | |
|---|---|---|---|---|
| *Phylum* | Euglenophyta | Charophyta | Chlorophyta | Prasinophyta |
| *Class* | Euglenophyceae | Charophyceae | | Prasinophyceae |
| *Order* | Eutreptiales<br>Euglenales<br>Euglenamorphales | Charales | | Pyramimonadales<br>Prasinocladales<br>Halosphaerales |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Class* | Zygnemaphyceae | Oedogoniophyceae | Bryopsidophyceae | | | Chlorophyceae | | |
| | | | [Hemisiphoniidae] | [Cystosiphoniidae] | [Eusiphoniidae] | | | |
| *Order* | Mesotaeniales<br>Zygnematales<br>Gonatozygales<br>Desmidiales | Oedogoniales | Cladophorales<br>Sphaeropleales<br>Acrosiphoniales | Dasycladales<br>Siphonocladales<br>Chlorochytriales | Derbesiales<br>Codiales<br>Caulerpales<br>Dichotomosiphonales<br>Phyllosiphonales | Chlamydomonadales<br>Volvocales<br>Polyblepharidales<br>Tetrasporales<br>Chlorodendrales<br>Chlorosarcinales<br>Chlorococcales | Ulotrichales<br>Codiolales<br>Ulvales<br>Prasiolales<br>Cylindrocapsales<br>Microsporales | Chaetophorales<br>Coleochaetales<br>Trentepohliales<br>Pleurococcales<br>Ulvellales |

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Note added in proof: Dr M. Parke has kindly brought to my notice a paper I had overlooked in which Kornmann (KORNMANN, P., 1970. Advances in marine phycology on the basis of cultivation. *Helgol. wiss. Meeresunters.*, **20,** 39–61) proposes a new family Codiolophyceae to embrace the Ulotrichales, Codiolales and Acrosiphoniales. This is an interesting concept but it will require a very detailed re-survey of the genera in each order to determine what other characters are common to the three orders apart from the occurrence of the *Codiolum* stage.