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SYSTEMATICS OF THE GREEN ALGAE

Edited by
D. E. G. IRVINE
D. M. JOHN

THE SYSTEMATICS ASSOCIATION
SPECIAL VOLUME No. 27

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Preface

Interest in the systematics of the well-defined assemblage of chlorophyll *a*– and *b*–containing algae commonly known as the "Green Algae" has been rekindled in recent years by the rapid accumulation of new descriptive information on details of their ultrastructure. This has all come from a repeat of the superb light microscopical studies of the nineteenth and earlier twentieth centuries by a new generation of researchers now using the electron microscope and interference light microscopy in conjunction with a vast array of equipment recently available to the cell biologist. The synthesis and evaluation of this newly acquired cytological data are leading to attempts to reorganize fundamentally the traditional classification of the green algae and to the creation of what might be termed a "new taxonomy". Furthermore, there has been a revival of interest in the phylogeny of this group, which has long been appreciated as standing nearer than any other to the main line of evolution of the higher plants.

Given the new wave of interest in green algal systematics it was decided to approach several eminent specialists in the field to see whether the time was right to hold a symposium on this topic. We received an unequivocally enthusiastic response to our suggestion and have been gratified by the support we have been given in formulating and arranging this Symposium. Naturally opinions differ as to the algae to be designated as "Green Algae", and for the purposes of this Symposium we decided to exclude the Euglenophyta (-phyceae) but to include the Charophyta (-phyceae *sensu stricto*) even though in some conservative treatments the latter are classified separately. In this Symposial Volume little attempt has been made to standardize the taxonomic level used by the authors for the major divisions of the green algae as this is unlikely to cause any confusion or misunderstanding.

The Symposium provided a forum in which specialists reviewed the current status of the systematics of green algal taxa, both extant and fossil, at all levels, and showed how the systematics of the higher groupings (families, orders, classes) and their suggested phylogenetic relationships with others are affected by newly acquired ultrastructural and, to a lesser extent, cultural and biochemical information. We believe that the Symposium achieved all its objectives and that this resulting volume makes a useful contribution to green algal systematics by bringing together in a single work much of our current thinking concerning this group.

We wish to thank Academic Press for their willing cooperation with us as editors at all times, the chairmen of the sessions, and those contributors who kept to the space allocated to them. It was unfortunately necessary to edit valuable material from some manuscripts, and to those authors we apologize, and to limit the index drastically because of the strict restraints imposed upon us concerning the length of the published volume. Despite our strenuous efforts in this direction it still exceeded the page limit generally applied to symposial volumes in the series, but the Systematics Association decided to make an exception in this case and to allow us to exceed this limit as the volume covered the whole group and dealt with important new classificatory proposals. Much of the success of this international Symposium was due in no small part to the assistance given us by many helpers, but those deserving of special mention are Mrs O. E. J. Etherington of the Department of Geography and Geology, Polytechnic of North London, Mrs J. A. Moore and Dr L. R. Johnson of the Department of Botany, British Museum (Natural History), and Dr P. F. Brandon, Head of the Department of Geography and Geology, Polytechnic of North London, who kindly allowed this Symposium to be held in his Department. We give special thanks to Mr D. R. Croome, Deputy Director of the Polytechnic of North London, for his opening address to the Symposium. Finally, we are most grateful for the financial support given us by our sponsors, the Systematics Association, and for support and guarantees provided by the Royal Society, the British Council and the British Phycological Society, as well as from various sources to many of our contributors.

September 1984

D. E. G. Irvine
D. M. John

SYSTEMATICS OF THE GREEN ALGAE

Contents

1 | The Systematics of the Chlorophyta: An Historical Review Leading to some Modern Concepts [Taxonomy of the Chlorophyta III]

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Abstract: A brief historical outline traces the development of systematic studies on the green algae from the earliest valid descriptions of genera to the latest organization into classes. The problem of dealing with one of the most complex and diverse groups of algae is discussed and the criteria for subdivision involving both gross and ultrastructural detail are outlined. Classification in an overall system of green plants (Viridiplantae of Cavalier-Smith) is proposed. The major orders are placed into classes and a number of divisions suggested. The importance of attempting to reconstruct phyletic lineages back to unicellular flagellate ancestors, placing the discussion on an earlier basis, is stressed.

Evolution is the essence of systematics
(WHITTAKER AND MARGULIS, 1978)

INTRODUCTION

An historical perspective is desirable when any subject is discussed, and for the green algae it is helpful to understand the conflicts which have punctuated the writings and coloured the scientific approaches of the last two centuries and are raging even today. There has been and still is much confusion; some of this may be resolved if we invoke a second historical perspec-

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tive and consider the possible lines of early evolutionary history of these green algae. This duality is well within the definition of systematics; many definitions have been proposed, and two suitable ones are "the scientific study of the kinds and diversity of organisms and of any and all relationships among them" (Simpson, 1961) and "systematics, which is concerned primarily with form (in the broad sense) and secondarily with time" (Nelson and Platnick, 1981). It may be easier to discern relationships if we take an evolutionary stance which involves time, form and diversity. A systematic treatment of the green algae must indicate which clusters have sufficient features in common to form discrete groups and also indicate any genera or clusters which, although allied to others, nevertheless have peculiar features and thus form problematic entities. Often these entities have been squeezed into larger taxa and concealed, whereas in my view the "splitting" approach highlights these anomalous groups and points the way to new lines of research. One problem I have encountered, especially in reading the modern literature, is the situation in which some specific attribute is discussed as though it were a feature of all green algae when clearly it is only a feature of a subset. It is a difficulty which may cause problems of communication in this symposium. In the botanical vernacular "green algae" refers to organisms possessing chlorophyll *a* and *b*—often grouped as Chlorophyta(phyceae), Charophyta(phyceae) and Prasinophyta(phyceae) in a conservative sense and including the Euglenophyta(phyceae) and Prochlorophyta(phyceae) in the broadest sense, though of course the latter are prokaryotic algae and the euglenoids belong in a quite separate position. But there are yet other taxa (see below), and confusion results if it is not clear exactly what a taxon includes or excludes.

The main thrust of work on the green algae has been along morphological/cytological/life history paths, but these approaches when pursued in isolation tell us little of the inter-relationships. Their comparative study does allow us to distinguish similar clusters, but the relative evolutionary distances cannot be discerned. In fact, no detailed studies along biochemical lines have been undertaken on green algae, such as those used by Schwartz and Dayhoff (1978) working on genera from different groups of organisms and by numerous workers considering, for example, the inter-relationships of primates. However, it must never be forgotten that these studies are based on samples from the tips of the evolutionary series; the information may be presented as a phenogram, but this must not be interpreted as a phylogeny (Cavalier-Smith, 1980). It will be more difficult, if not impossible, to get comparable biochemical information from fossils, although it is surprising how many data have been obtained from some fossils (King, 1974). If the existing morphological data can be used to define an evolutionary series, then subsequent biochemical studies will not be quite as random or based on laboratory "weeds" as are Schwartz and Dayhoff's data. This is

not to decry the value of that work in any way but, as Mattox and Stewart (1977) commented, it is desirable that biochemical studies be extended "from a few 'standard' organisms to a carefully selected variety", even if the results, as for the primates, tend to confirm the predictions from gross anatomical detail (Cherfas, 1981). I write "gross" intentionally, since there is a recent tendency in green algal studies to neglect the overall morphological features—ultrastructural studies must take their place with all other attributes and should not over-balance the systematics of the green algae.

Although the systematics of the green algae has been confused, this has not prevented their use in studying many biological problems; in fact they have been used more than any algae from any group with the following five green algae providing a vast range of biological data: *Chlamydomonas* (genetics), *Chlorella* (biochemistry), *Acetabularia* (morphogenetics), *Nitella* (biophysics/salt uptake) and *Euglena* (general biochemistry and rhythms). It is time we sorted out the systematics.

EARLY HISTORY

Before Linnaeus's time algae had figured in various publications (early Chinese, Greek and Roman); the earliest mention in a systematic sense is probably that in Bauhin (1620).

In the *Species Plantarum* of Linnaeus (1753), green algae were recognised in the class Cryptogamia only as *Ulva, Conferva, Chara* and *Volvox* (the last excusably as an animal, but can we excuse the modern biologists who still place "chlamydomonads" in the animal kingdom?). In 1758 Linnaeus also mentioned *Acetabularia* and *Codium,* but not as algae. *Chara* was allocated to several plant groups before coming to rest as an alga where, in spite of its unique features, it must surely remain. *Volvox* was probably the earliest recorded green flagellate since it is mentioned in a letter from Leeuwenhoek to the Royal Society in 1700. Lamouroux (1813) established an "ordre" Ulvacées and he was perhaps the first to conceive a green group of algae (of macroscopic form—*Ulva, Bryopsis, Caulerpa*). Agardh in 1817 added to the Lamouroux system a new subset, the Confervoideae, which included filamentous green algae. Gray (1821) established the Characeae and Dumortier (1822) the Conjugataceae. The 1750–1825 period was one of pioneer description of algae and the crude beginning of systematic clustering. Some workers placed algae in clusters which are totally outside modern concepts and need not be considered here.

Green algae as a natural assemblage, separate from other algae, were first recognised by Harvey (1836) and named Chlorospermeae. Blue-green algae were included in Harvey's Chlorospermeae, but not the desmids which

were placed within the Diatomaceae. By 1838 Kützing had separated the desmids into a group termed Chamaephyceae (dwarf algae). Already in this period Kützing (1843) could record a very impressive range of green algae which he split into a whole range of families, many of which are recognised entities even today: Desmideae, Palmelleae, Hormideae, Ulotricheae, Conferveae, Zygnemeae, *Hydrodictyon* (as a family), Protonemeae (including *Gongrosira*), Draparnaldieae, Ulvaceae, Enteromorpheae, Vaucherieae (not now a green set), Caulerpeae, Codieae, Anadyomeneae, Dasycladeae and Chareae; the last six are clustered in a sub-order Coeloblaste. The term "zönoblastische" was used by Ettl and Komárek (1982) for algae with numerous nuclei and is presumably a modern form of the old Coeloblaste. In 1845 Kützing changed the name Chlorospermeae to Chlorophyceae, though as a discrete group it was marred by the inclusion of genera from bacteria, fungi, and red and brown algae, a not entirely surprising feature considering the optics of the time; even today students confuse groups when observing only pigmentation. He also termed them Gymnospermeae and commented on the fact that the "seeds" were on the surface and not surrounded by a fruit body—a feature of modern definitions (cf. the definition in Bold and Wynne, 1978). Macroscopic forms such as *Fucus* he had in a section called the Angiospermeae. At this time the groups Palmellaceae and Protococcaceae were established for colonial and unicellular green algae and we find considerable discussion of their status in this early literature (cf. the present discussion, e.g. Ettl and Komárek, 1982).

In these early years the conjugate green algae often appeared as a distinct entity, although other groups were often linked with them. Running through the whole of the nineteenth century is the concept of five clusters of green algae: a protococcoid, a palmelloid, a confervoid (Chlorophycean), a conjugate (Zygnematophycean) and a macroscopic-multicellular (Charophycean) cluster. The "chlamydomonads" were given further status (Volvocaceae) by Cohn (1856), and then Rabenhorst (1863) grouped the Volvocaceae, Palmellaceae and Protococcaceae into the Coccophyceae [cf. the modern Volvocophyceae of Schoenischen (1925) and Volvocineae of Pascher (1931)]. Even the siphonaceous group was recognised around this time by Greville (1830) as "orders" Siphoneae (*Codium, Bryopsis, Vaucheria, Botrydrium*), and Kützing (1849) distinguished the groups Sphaeropleaceae, Cladophoraceae, Valoniaceae, Caulerpaceae and Dasycladaceae; Stitzenberger (1860) placed the three last clusters into the Siphonophyceae. Thus these early workers established a precedent for the multiplicity of classes which have now been described*.

*These are listed by Silva (1980), but it might be advantageous to mention here the number of classes which have been established by various authors: some merely descriptive, some valid

About this time De Bary (1858) united the filamentous Zygnemataceae and Desmidiaceae into Conjugatae and thus by 1868 Rabenhorst could distinguish the Coccophyceae, Zygophyceae (=Conjugatae), Siphophyceae (Botrydiaceae and Vaucheriaceae) and the filamentous Nematophyceae (Ulvaceae, Sphaeropleaceae, Confervaceae, Oedogoniaceae, Ulothrichaceae, Chroolepidaceae (=Trentepohliaceae), and Chaetophoraceae)—almost a twentieth-century grouping. Wille (1890–1891) turned the clock back in that he had only two major sections, one containing the coccoid/colonial forms (Protococcoideae) and one the filamentous (Confervoideae) and siphonaceous (Siphoneae) forms. An unfortunate piece of terminology (the Thallophyta) became common in the latter half of the nineteenth century to include both algae and fungi and regrettably still appears in some student texts. In 1895 Borzi elevated the simple filamentous series to the Ulotrichales. This 1825–1900 period was one of intense activity, describing algae and clustering them into families, classes, etc. Many other interesting problems were discussed in the literature (e.g. fertilisation, alternation of generations, animal/plant distinctions, pigment complement) and cultural/physiological work commenced, often using green unicells.

At the turn of the century, Blackman (1900), building on earlier, scattered work, crystallised the concept of motile, coccoid ("a heterogeneous remainder of primitive forms"), tetrasporine and stephanokont lines of development. His writing enabled workers to grasp something of the phylogenetic relations of what once seemed a chaos of forms and he came to the conclusion that they are all derived from a *Chlamydomonas*-like organism. His concept of "volvocine" forms reproducing by means of a set number of divisions (coenobial), and of tetrasporine forms in which vegetative cell division can be continuous (though not always), is an interesting one. Blackman did, however, consider that some of the genera were out of place and that separation into tetrasporine and confervoid lines was not defensible. He also conceived a line of development from coccoid to siphonaceous forms. In 1901, Willie separated the branching filamentous genera into the Chaetophorales. A key paper by Bohlin (1901) appeared between Blackman's (1900) discussion of evolutionary lines and the systematic treatment of Blackman and Tansley (1902). Bohlin's contribution was to suggest that

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and some invalid, viz. Akontae, Bryopsidophyceae, Chaetophorophyceae, Chlorococcophyceae, Codiolophyceae, Coleochaetophyceae, Confervophyceae, Conjugatophyceae, Euchlorophyceae, Glaucophyceae [these possess many exceptional features, some of which may yet ally them with the chlorophyll *b* series (Moestrup, 1982), though Cavalier-Smith (1981) places them alongside the red algae]; Isokontae, Oedogoniophyceae, Placodermae, Protococcophyceae, Saccodermae, Siphoneae, Siphonocladophyceae, Stephanokontae, Tetrasporophyceae, Ulotrichophyceae, Ulvophyceae, Volvocophyceae, Zygophyceae and Zygnematophyceae.

the Confervoid group be split, with the Confervales in the newly described Heterokontae (Luther, 1899) and the Ulotrichales, Microsporales and Stephanokontae (=Oedogoniales; he suggested this term be used) left in the Chlorophyceae as three equal groups. He also discussed many of the propositions which today are being re-investigated, e.g. he stated quite clearly that (I paraphrase), "zoospores must be considered as embryonic forms of great importance in systematics. . . . within algal systematics the zoospores provide the first and foremost basis for subdivision ("indelningsgrunden"). . . . when there are no zoospores, then the characters of the spermatozooids are of importance for systematics". Bohlin also pointed to the value of pigments and considered that the pigmented forms were developed from colourless forms and could not change from one into another. He was not sure that all "protococcoid" algae (certainly not the conjugate algae) were derived from the same flagellate, i.e. he saw the possibility of multiple origins.

Blackman and Tansley (1902) porposed the term "isokont" to apply to algae with equally developed flagella, but it can apply to other groups (see also discussion in Moestrup, 1982). They also incorporated Bohlin's (1901) concepts into the first overall scheme, which incidentally appears to have been devised largely because "it fell to their lot" to deliver an advanced course of lectures to students in Cambridge and London. They were not primarily phycologists, but they proposed the Ulvales as a separate entity and maintained the Ulotrichales for the unbranched and branched filamentous forms. Although their work is much quoted it is mainly a catalogue of genera. The major lines of algal morphological advance were elaborated by Pascher (1914, 1931), who also elevated the classes to divisions and in his later paper presented what now appear to be rather modern subdivisions. He used the ending *-ineae* but termed them classes: Volvocineae, Tetrasporineae, Protococcineae, Ulotrichineae, Siphonineae, and Siphonocladineae. He also commented perceptively that it was not possible to find connections between Chlorophyceae and other algal groups (thus pre-empting the Chlorophyte/Chromophyte series in the multi-divisional system of Cavalier-Smith, 1982) and also that the charophytes could not be drawn into the Chlorophyta—a view echoed by many workers since. After Pascher, green algal systematics tended to rest on Fritsch's (1935) monumental and apparently logical and simplified nine-order system, which most modern phycologists have had instilled into them. But Fritsch was careful to distinguish those genera which were anomalous and to discuss these somewhere in his treatment of each order. During the last 25 years many of these "out-of-place genera" have been re-studied and re-allocated, though some are still awaiting systematic evaluation. This period from 1900 to 1950 was a

stable one with few major advances—a period when systematic studies were rather out of favour.

From 1950 onwards, three different approaches have revitalised systematic studies of the green algae; one is the re-birth of "cytology" using electron microscopy, a second is the stimulus arising from Margulis' writing on endosymbiosis, and the third is the intense study of biochemical/molecular genetic systems. All these approaches require integration and are to a great degree dependent on one another. Out of them is emerging a new systematics and a new phylogeny. This present period may be termed the "Age of Ultrastructure" in green algal systematics, just as Corliss (1979) termed it in the Protozoa, where also it has led to a proliferation of groupings above the family level.

SYSTEMATIC CONCEPTS

The repeated attempts at sub-division and re-clustering in the early studies gave a sure indication that something was amiss in the conceptual framework of the classification. Almost no other algal group has suffered such vicissitude, e.g. the limits of the Phaeophyta and Rhodophyta (see Boney, 1978) have never been really questioned and indeed they seem to form very discrete entities in spite of numerous internal conflicts which do not disturb the overall consistency. Compare this with the green group, where there is anything but consistency*, although attempts have been made to impose consistency by lumping groups together. To quote the extremely perceptive G. S. West (1916), "in no other group of plants are there such wide differences in form and cytological structure: or such varied life histories as can be found in one section of the Green Algae"; he continued, "the most important result of this recent work is the recognition by the more experienced of algological investigators that the various groups of the green algae have originated by a progressive evolution, either directly or indirectly from flagellated ancestors and that the cytological structure of the motile zoogonidia funishes a reliable key to phylogenetic relationships". Carried through to the present day, Moestrup (1982), commenting on the ultrastructure of the transition region of the flagella, writes "the impression is that of variation in the primitive groups [of green algae] more so, in fact, than in any of the 'chromophyte' algal classes that have been examined carefully". Of course there are common features of biochemistry (e.g. pigmentation, photosynthetic products, starch (α-1,4-glucose) contained with-

*". . . diversity of habit and habitat is very striking and in this respect the Chlorophyceae surpass any other algal class" (Fritsch, 1935).