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THE SPIHONOCLADALES

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In recent years there has been some discussion about the validity or otherwise of the order Siphonocladales (Feldmann 1938, Fritsch 1947, Egerod 1952). Much of this has been summarized in the last of these contributions. The only justification the present writer has for entering this discussion arises from information obtained during a revision of the New Zealand marine Chlorophyceae (Chapman in press, Chapman 1952, Chapman 1953). In this revision a new species of *Microdictyon* came to light (Dellow 1950) and it was also necessary to study local species of *Cladophoropsis*.

The present writer agrees with Feldmann and Egerod in recognizing the order Siphonocladales, and is unable to subscribe to Fritsch's view that the Siphonocladaceae, Valoniaceae, Dasycladaceae, Boodleaceae and Anadyomenaceae should be classed as septate Siphonales. He also agrees with Feldmann and Egerod in excluding the Dasycladaceae from the Siphonocladales and putting them in a separate order, the Dasycladales. As Egerod points out, the Dascyladales differ from the Siphonocladales in possessing discoid plastids, a uninucleate vegetative thallus (where studied) and in many cases special reproductive cysts.

Feldmann and Egerod, however, differ in their concept of the Siphonocladales in that the former includes the Cladophoraceae, whereas the latter accepts the viewpoint of Fritsch (1947) and Boergesen (1948) that the Cladophoraceae should be placed in a separate order, the Cladophorales. The present author is of the opinion that Feldmann's viewpoint is the more correct. On this basis the Siphonocladales can be characterized broadly as an order in which all genera are septate at some stage of their existence, the cells or segments being multinucleate and possessing reticulate chloroplasts. Fritsch (1947) has suggested that the plastids of the Valoniaceae can be regarded as discs joined by delicate threads, and that in this respect they bear some resemblance to the Siphonales. On the other hand Nicolai and Preston (1952) have shown that the cell wall structure of *Valonia* is similar to that of species of *Cladophora*.

The Siphonocladales as presently understood by the writer include the following five families: Cladophoraceae, Anadyomenaceae, Boodleaceae, Siphonocladaceae and Valoniaceae.

The exclusion of the Cladophoraceae from the order by other writers is based upon their lack of the typical initial stage of development, namely the existence of an erect, tubular, primary vesicle. However, it is not difficult to envisage slight elaboration of the basal cell of species of *Chaetomorpha* (fig. 1), especially *C. darwinii*, to the condition found in *Microdictyon* and *Cladophoropsis* (fig. 2). Further development of the condition found in

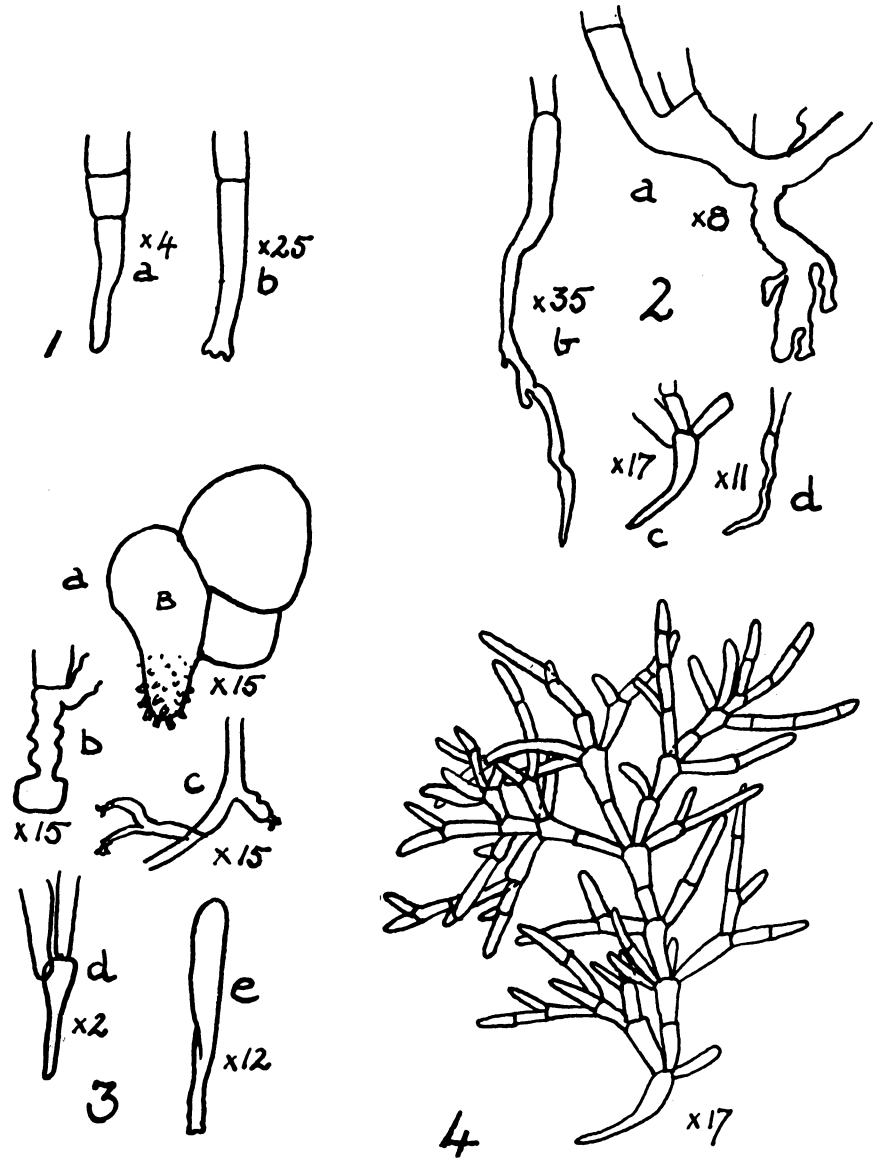


FIG. 1. Basal cells: a) *Chaetomorpha darwinii.* b) *C. aerea.* FIG. 2. Basal cells: a) *Cladophoropsis membranacea.* b) *Microdictyon japonicum.* c) *M. mutabile,* spongiose plant. d) *M. mutabile,* sporeling. (a, b, after Egerod; c, d, after Dellow). FIG. 3. Basal cells: a) *Dictyosphaeria favulosa.* b) *Siphonocladus tropicus.* c) *Boodlea siamensis.* d) *Valonia trabeculata.* e) *Siphonocladus tropicus,* young plant. (a–c, after Borgesen; d, e, after Egerod). FIG. 4. *Microdictyon mutabile*: Portion of spongiose thallus. (After Dellow.)

these genera would lead to the vesicles found in *Boodlea, Siphonocladus, Dictyosphaeria* and *Valonia* (fig. 3). Apart from this issue there is, however, the remarkable similarity between the *Cladophora* type of thallus and the thallus of *Microdictyon mutabile* and species of *Cladophoropsis.* There is also the similarity in wall structure between *Valonia, Siphonocladus, Dictyosphaeria* and species of *Cladophora* (Nicolai and Preston, 1952).

M. mutabile described by Dellow (1950) is a remarkable species found in New Zealand. Two distinct forms exist: one is markedly spongiose and the threads have relatively few anastomoses, so that on casual examination it can easily be mistaken for a coarse species of *Cladophora* (fig. 4). The other form, which under certain conditions develops from the spongiose form, has the typical habit of *Microdictyon.*

The genus, *Cladophoropsis,* has had a chequered history. Founded by Boergesen in 1905 it was originally placed in the Cladophoraceae. Later (1913) he transferred it to the Boodleaceae and more recently (1948) to the Siphonocladaceae. There is therefore justification for a close relationship to both Cladophoraceae and Siphonocladaceae. *Cladophoropsis membranacea* is the type member of the genus, but there are other species in which some of the lateral branches do not remain in open connection with the mother cell, thus resembling *Cladophora.* This is particularly true of *C. membranacea* var. *repens, C. herpestica* and *C. lyallii,* all species found in New Zealand (Chapman in press).

It would seem therefore that the justification for excluding the Cladophoraceae from the Siphonocladales cannot be completely sustained, and if one includes the Cladophoraceae within the Siphonocladales one has an orderly sequence of phylogenetic development. It is worth noting that Egerod (loc. cit.) admits that the Anadyomenaceae (which includes *Microdictyon*) represents a distinct difficulty if one accepts both Cladophorales and Siphonocladales. The above solution eliminates this problem.

Another issue raised by Egerod (loc. cit.) is concerned with the origin of the Siphonocladales. Her argument is that the ancestral type may have been a plant akin to *Protosiphon,* which she places in the Chlorococcales. Her main points refer to the nature of the vesicle and method of cleavage in *Protosiphon,* and it is suggested that it is not difficult to derive a plant such as *Valonia ventricosa* from a Protosiphon-like alga. If this viewpoint is accepted, one must also accept the view that the Valoniaceae form the most primitive family, and that the Siphonocladaceae and Anadyomenaceae are secondarily septate. It should be noted that recently Nicolai and Preston (1952) have hinted that the Protosiphoneae have an alliance with *Halicystis* (Siphonales) rather than *Valonia* in so far as wall structure is concerned.

The present writer considers that there are the following serious objections to Egerod's view and that it cannot be upheld:

1. The Chlorococcales, to which *Protosiphon* is assigned (including *Protosiphon* in this case) are practically all fresh water or terrestrial forms.

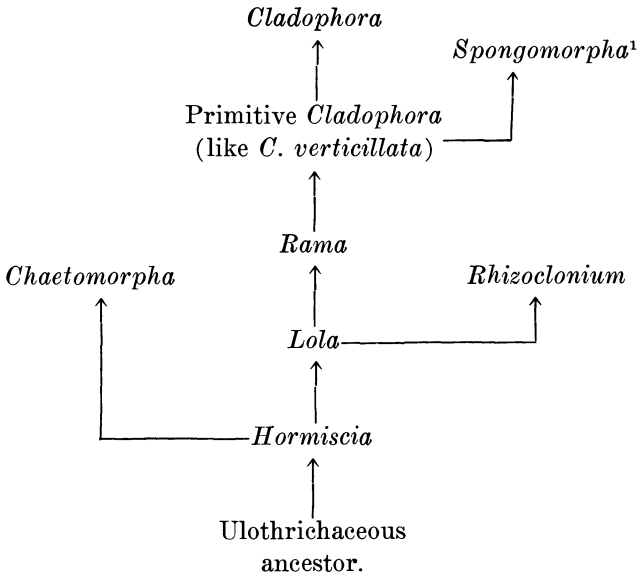
The Siphonocladales, on the other hand, are almost wholly marine, though there are some fresh water species in the Cladophoraceae. Whilst it may be argued that the primitive siphonocladaceous ancestor may have lived in relatively fresh or wholly fresh waters, and that over the course of years the descendants have gradually become more or less restricted to salt water, one could legitimately expect that some of the simpler members of the Siphonocladales would at least live in brackish waters. The Valoniaceae (the primitive family according to Egerod) are, however, strictly marine.

2. Work that has been carried out on the life cycle of *Valonia* (Schechner-Fries 1934, Schussnig 1938) has shown that the species investigated are wholly diploid, reduction division taking place at gametogenesis. This is the type of life cycle typically associated with the more advanced (Siphonales) rather than the more primitive members of the Chlorophyceae. *Protosiphon,* from which it is suggested the Valoniaceae may have been derived, almost certainly has a wholly haploid life cycle, reduction division taking place at zygote germination. It would be necessary to assume, therefore, that at some intervening period a whole series of forms must have arisen in which a diploid phase was introduced into the life cycle and the haploid phase subsequently lost. One could expect that one or more of such forms might well have survived.

3. Work that has been carried out on the life cycle of *Microdictyon* (Iyengar and Ramanathan 1940) and *Anadyomene* (Iyengar and Ramanathan 1941) has shown that there is a regular alternation of generations in the life cycle of species of these two genera. It is probable that most workers would consider the wholly haploid type of life cycle as being the most primitive, though recently Feldmann (1952) has argued that the life cycle with regular alternation of generations is the most primitive. Unless reduction or an abnormality can be clearly established, either of these two types of life cycle must be regarded as primitive to the wholly diploid type. There seems no reason for regarding *Microdictyon* or *Anadyomene* as reduced forms in the Siphonocladales, so that if the Valoniaceae are regarded as the primitive family it would imply that the Anadyomenaceae would have to be removed from the Siphonocladales.

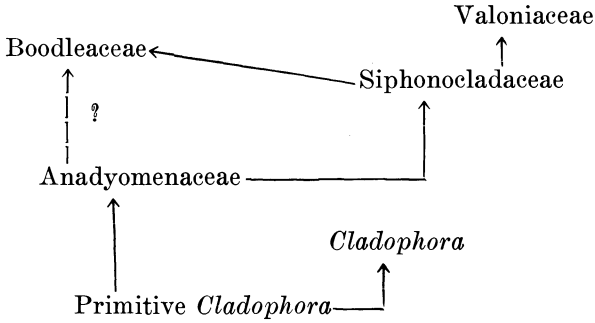
At this point an alternative interpretation of the situation in the Siphonocladales may be presented. In this alternative it is suggested that the primitive family is the Cladophoraceae and that the Valoniaceae represent the final stages in reduction and elimination of septae within the order.

On this basis we start with a family in which there is either a haploid generation only in the life cycle or else alternation of generations in the life cycle, with only one certain case of a wholly diploid life cycle (*Cladophora glomerata*). As a result of studies of the New Zealand marine Chlorophyceae (Chapman 1952 and in press), the present author has considered the course of development within the Cladophoraceae (Chapman 1953) and has proposed the schema below:

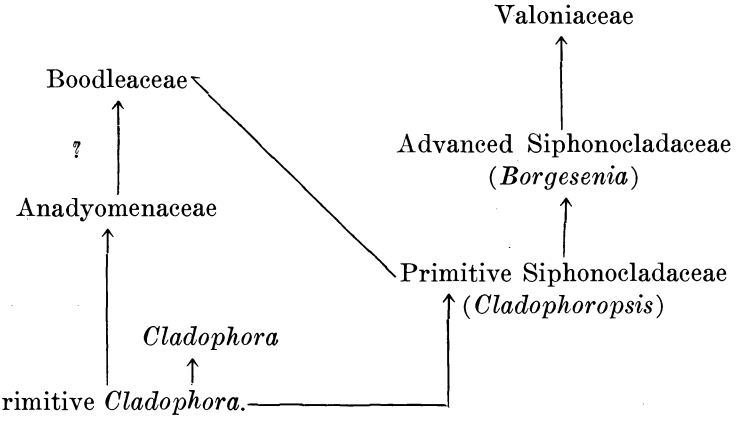


On this basis it would seem that one can build the remainder of the Siphonocladales according to one or other of the two schemas below:

A.



B.



[1] Nicolai and Preston (1952) present arguments for separating *Spongomorpha* completely from *Cladophora*.

Fritsch (1947) argues that the genus *Cladophora* represents the most advanced type in the Cladophoraceae and that any affinities with other families must lie in genera such as *Rhizoclonium, Lola* and *Chaetomorpha.* If this view is accepted, then it is indeed difficult to find forms bridging the gap between the Cladophoraceae and any of the other families of the Siphonocladales. The argument presented by me stresses the relationship between *Cladophora* and *Microdictyon* on the one hand and *Cladophora* and *Cladophoropsis* on the other: on this basis there would seem to be no justification for excluding the Cladophoraceae from the Siphonocladales.

The relationship of the Boodleaceae raises a problem, because on the one hand *Microdictyon* provides a link with the Anadyomenaceae and on the other hand *Cladophoropsis* provides a link with the Siphonocladaceae. However, acceptance of the first view would also involve acceptance of a dual origin of segregative cell division, which is apparently absent in the Anadyomenaceae. Whilst there is no reason why this type of cell division should not have arisen on more than one occasion, it would seem more likely that such a special mode of cell division only arose once. Under these circumstances the origin of the Boodleaceae from the Siphonocladaceae would seem the more probable. The other and less likely alternative is therefore represented in the schemas by a dotted line.

Of the two schemas put forward the present author favours B, because the net type of thallus (Anadyomenaceae) is in most cases well developed, and would seem to represent an end line in evolution as indicated in scheme B. In either scheme *Microdictyon mutabile* is regarded as possibly the most primitive member of the Anadyomenaceae, and in scheme A would be the point from which the Siphonocladaceae would have to be derived.

In conclusion the present author believes that Scheme B, superimposed on the schema for the Cladophoraceae (Chapman 1953), represents most satisfactorily, in our existing state of knowledge, the relationships and status of the Siphonocladales.

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