

Phylogenetic systematics of the freshwater red algal order Batrachospermales

Timothy J. Entwisle* and Orlando Necchi Jr.**

*National Herbarium of Victoria, Birdwood Ave, South Yarra, Victoria 3141, Australia.

**Instituto de Biociências, Letras e Ciências Exatas, Universidade Estadual Paulista, Departamento de Botânica, Caixa Postal 136, 15001—São José do Rio Preto, SP, Brasil.

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The order Batrachospermales is a well-defined, almost certainly monophyletic group. The five constituent genera have been arranged in three families: the Batrachospermaceae (including *Batrachospermum* sensu Necchi & Entwisle), the Lemaneaceae (*Lemanea*, *Psilosiphon*) and the Thoreaceae (*Nemalionopsis*, *Thorea*). Our cladistic analyses of the five genera support the current familial arrangement, although further information about the reproductive morphologies of *Psilosiphon*, *Nemalionopsis* and *Thorea*, and a better understanding of the relationships of Batrachospermales to the other Rhodophyta (i.e. what is its sister group?) are needed to verify this result. A key is provided to the currently accepted families and genera in the Batrachospermales on the basis of vegetative characters.

Key Index Words: Batrachospermum—Batrachospermales—cladistics—classification—freshwater—Lemanea—Nemalionopsis—phylogenetics—Psilosiphon—Thorea.

The Batrachospermales is a clearly delimited order with at least two good synapomorphies—a heterotrichous life-history without tetrasporic meiosis, and pit-connections with an enlarged outer cap-layer (the latter possibly, but unlikely, to be homologous with the pit-connections of the Corallinales). Members of this order also have discoid to laminate chloroplasts, determinate lateral filaments in prominent phase, no auxillary cells and are known only from freshwater habitats (Sheath 1984).

The Batrachospermales includes three families, Batrachospermaceae, Lemaneaceae and Thoreaceae, which until recently (Pueschel and Cole 1982) were included in Nemaliales. The Batrachospermaceae and Lemaneaceae have always formed a tight knit group due to their uniaxial construction and distinctive life history. The genus *Thorea*, placed in the Thoreaceae, has recently been shown to have a similar life history to that found in the Batrachospermaceae and Lemaneaceae (Yoshizaki 1986; Necchi

1987a). So, in spite of the multiaxial construction of the Thoreaceae, the three families seem to be closely related and monophyletic.

Phylogenetic (or cladistic) analysis has not been a widely used tool for studying relationships in the red algae (Gabrielson and Garbary 1987), but it is proving to be a useful companion for both the older morphological approaches and the newer biochemical techniques of modern systematics (Lindstrom 1988). We believe cladistics reasoning is desirable for the study of pattern among living organisms.

Our recent subjugation (Necchi and Entwisle 1990) of four Batrachospermacean genera (*Batrachospermum*, *Nothocladus*, *Sirodotia* and *Tuomeya*) into one (*Batrachospermum*), the discovery of sexual reproduction in *Thorea* (Yoshizaki 1986, Necchi 1987a), and the description of the new genus *Psilosiphon* (Entwisle 1989) makes a reassessment of the relationships between the genera in Batrachospermales and an evaluation of the current familial classification opportune.

Table 1. Comparative features of genera in the Batrachospermales and Liagoraceae.

Character	<i>Batrachospermum</i> ¹ ROTH	<i>Lemanea</i> BORY	<i>Nemalionopsis</i> SKUJA	<i>Psilosiphon</i> ENTWISLE	<i>Thorea</i> BORY emend. NECCHI	Liagoraceae
Information (other sources as indicated)	NECCHI & ENTWISLE (1990); and unpubl. observations	ATKINSON (1890); FRITSCH (1935); MULLAHY (1952)	SWALE (1963); HOWARD & PARKER (1979)	ENTWISLE (1989); and unpubl. observations	BISCHOFF (1965); YOSHIZAKI (1986); NECCHI (1987a)	FRITSCH (1935); BOLD & WYNNE (1985); KRAFT (1989)
No. of species	c. 150	20	1	1	12	—
Distribution throughout the world	Tropical to temperate, widespread	Temperate, northern hemisphere ²	Tropical to temperate, northern hemisphere	Temperate, south-eastern Australia	Tropical to temperate, widespread	Tropical to temperate [marine]
Morphology of diploid stage of life history	Prostrate crust or erect tufts (VON STOSCH & THEIL 1979; BALAKRISHNAN & CHAUGULE 1980)	Prostrate crust & in some species also erect tufts	Prostrate crust	Prostrate crust and some erect tufts	Prostrate crust and erect tufts	Free-living diploid phase erect tufts
Number of axial filaments in prominent phase	1	1	>1	1	>1	>1
Thallus apex pseudo-parenchymatous?	No	Yes	No	Yes	No	No
Axial filaments sheathed by rhizoidal filaments?	Yes	Yes or no	No	No	No	?No
Number of periaxial cells cut off axial cell if thallus uniaxial	4-7	4	Not applicable	4	Not applicable	Not applicable
Interlaced medullary filaments present?	No	No	Yes	Yes	Yes	Yes
Outer cortical cells forming cohesive outer rind?	No ³	Yes	No	Yes	No	No

Number of plastids/cell	1-3	4-10	several	> 6	several	1
Plastid shape	Discoid	Discoid	Discoid (HARA & CHIHARA 1974) or laminate	Discoid	Laminate	Laminate, reticulate, or stellate
Diameter of thylakoids (nm) (BERGFELD 1970; THIRB & BENSON-EVANS 1983; BISCHOFF 1965; and unpubl. observations)	35-80	c. 14-17	Not known	c. 14	c. 12	?
Propagation by adventitious plantlets?	No	No	No	Yes	No	No
Ability to produce monosporangia?	Some species	No	No ⁵	Not known	No ⁵	?No
Spermatangia arising from specialized filaments?	No	Yes	Not known	Not known	No	In three genera
Spermatangia in superficial sori?	No	Yes	Not known	Not known	No	No
Shape of spermatangia	Spherical to obovoid	Oblong to ellipsoid	Not known	Not known	Ellipsoid to Obovoid	Ellipsoid to obovoid
Carpogonial branch accessory?	No	Yes	Not known	Not known	No	In seven genera
Number of cells in carpogonial branch	1-30	3-10	Not known	Not known	1-2	usually 3 or 4
Trichogyne inflated?	Yes	No	Not known	Not known	No	No
Trichogyne persisting after fertilization?	Yes	No	Not known	Not known	No	No
First gonimoblast initial cut from fertilized carpogonium	Longitudinal, or rarely transverse (see KUMANO & RATNASABAPATHY 1982)	Oblique distal	Not known	Not known	Oblique distal	Transverse, oblique or longitudinal

Table 1. Continued.

Fusion cell in primary gonimoblast?	No ⁴	Yes	Not known	Not known	No	In nine genera
Gonimoblast filament growth	Limited, unlimited or both	Limited	Not known	Not known	Unlimited	Limited or unlimited
Cells of gonimoblast forming carposporangia	Terminal	Nearly all	Not known	Not known	Terminal	Terminal or chains of terminal cells
Spore germination	Unipolar	Bipolar	Not known	Not known	Unipolar	?unipolar
Effect of MgCl ₂ on alcian blue staining (SHEATH & COLE 1990)	Elimination, same or less	Elimination	Same	Not known	Same	Not known

¹ *Batrachospermum* includes *Notholadus* Skuja, *Sirodotia* Kylin and *Tuomeya* Harvey (see Necchi & Entwisle 1990).

² There is only one literature record of the genus from the southern hemisphere (KLEERKOPER 1955) and two additional herbarium specimens, both from Argentina (JOHN BLUM pers. comm. and observations of the second author).

³ *Batrachospermum americanum* (Harvey) Necchi & Entwisle (previously *Tuomeya americana* Harvey) has a more cohesive outer cortex than most species of *Batrachospermum*, but it is not separated from the medullary region as is found in *Lemanea* and *Psilosphon*.

⁴ Report of a fusion cell in *Tuomeya* by Webster (1958) has yet to be confirmed.

⁵ Structures described as 'monosporangia' in these genera are probably misinterpreted spermatangia or carposporangia (Yoshizaki 1986, Necchi 1987a). The real occurrence of monosporangia in Thorea and Nemaionopsis has yet to be confirmed in light of the new information concerning sexual reproduction.

This higher level phylogeny can then be used to examine the pattern of relationships within these genera and families.

Methods

Character data matrices obtained from published and original observations were run through both PAUP (Swofford 1990) and Henning 86 (Farris 1988) programs using exhaustive search options. In the data matrix (Table 2), a code of 9 indicates that the character was either inapplicable, unreported or known to be both present and absent in the taxon (polymorphic). Characters coded as 9 were not used for that particular taxon in the cladistic analyses. The shortest trees were rooted by either: (1) using Liagoraceae as an outgroup, or (2) by hypothesizing plesiomorphic states in selected characters and using Lundberg rooting (see Discussion for rationale behind these alternatives).

Results

From a compilation of 25 comparative features derived from published descriptions and our own observations (Table 1) we extracted 18 characters suitable for cladistic analysis (Table 2). The following features could not be adequately tabulated but require some explanation:

a) Tubular lamellae in chloroplasts were suggested by Hara and Chihara (1974) to be characteristic of the Batrachospermaceae, but Sheath et al. (1979) have shown that their formation is more likely to be environmentally and developmentally controlled in a range of taxa.

b) The life history features suggested by Von Stosch and Theil (1979) and Balakrishnan and Chaugule (1980) are not yet well enough documented (Sheath 1984) to be used in this analysis, but may eventually proved a means of producing a more natural classification.

c) The absence of phycobilisomes in scanning electron micrographs was considered by Bergfeld (1970) to be characteristic of

Batrachospermum, but Duckett and Peel (1978) argue that it is not clear whether the absence of phycobilisomes from some species is 'a real taxonomic feature or merely the result of poor fixation'.

d) Chromosome number has not yet been documented for enough taxa (Sheath 1984, Cole 1990) but may eventually prove to be a powerful tool for phylogenetic analysis.

e) The position of the 'elimination cells' after occurrence of meiosis in early stages of gametophytic development (Magne 1967, Balakrishnan and Chaugule 1975, 1980, Von Stosch and Theil 1979, Necchi 1987b) may also hold promise of a good character in future, but still require further documentation.

f) Although the cell walls of Batrachospermales seem to be distinguished from those of the marine red algae by their production of an acidic rather than sulfated polysaccharides, the comparison of a few *Batrachospermum* species and *Lemanea annulata* Kützing has shown some generic (or familial) differences in cell wall composition may exist (Gretz *et al.* 1991).

g) The long hair-like filaments that characterize *Thorea* are certainly not analogous with the hairs found in many species of *Batrachospermum*. The difficulty in scoring this character in genera other than *Thorea* and *Nemalionopsis* necessitated our leaving it out of the table. Nevertheless, it remains a useful diagnostic character within the Thoreaceae.

Eighteen features were considered suitable for inclusion in the cladistic character set (Table 2). The rationale for coding and (in some cases) *a priori* polarizing of these characters is outlined below. Probable autapomorphies have been included in the analysis since polarity of characters is somewhat nebulous (and apparent autapomorphs may well be plesiomorphic states in terms of global parsimony).

1 Gametophyte uniaxial (1) or multiaxial (0).

NOTES: A cladistic analysis of the Dumontieae (Rhodophyta) by Lindstrom (1988) resulted in the multiaxial condition being considered plesiomorphic for that group. This character was polarized *a priori* concordant with that result.

2 Thallus apex pseudoparenchymatous (1) or not (0).

NOTES: The early development at the thallus apex of *Lemanea* and *Psilosiphon* is quite distinctive and unlike that found in the other genera (although *Batrachospermum puiggarianum* is superficially similar). Not polarized.

3 Axial filaments sheathed by rhizoidal filaments (1) or not (0).

NOTES: Presumably an autapomorph for *Psilosiphon*. Not polarized.

4 Number of periaxial cells cut off axial cell

Comparative features and characters scored

Table 2. Data matrix of Batrachospermales used in cladistic analyses. The presence of an * beneath the character number indicates that the zero score was assumed to be plesiomorphic for the Lundberg rooting.

Taxa	Characters																		
	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	
	*			*	*			*			*	*	*						
Ingroup																			
BAT	1	0	1	0	0	0	1	0	0	0	0	0	1	0	9	0	1	9	
LEM	1	1	9	1	1	1	1	0	1	1	1	0	0	1	1	1	0	1	
NEM	0	0	0	9	0	1	9	0	9	0	9	9	9	9	9	9	9	0	
PSI	1	1	0	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9	
THO	0	0	0	9	0	1	0	0	0	0	0	1	0	0	0	0	1	0	
Outgroup																			
LIA	0	0	0	9	0	0	0	0	9	0	9	1	0	9	9	9	9	9	

(if thallus uniaxial) always 4 (1) or variable 4-7 (0).

NOTES: A fixed number of periaxial cells could be considered homologous to what occurs in the Rhodomelaceae (Ceramiaceae), a highly derived group of red algae (Gabrielson and Garbary 1987). Polarized with fixed number apomorphic.

5 Outer cortical cells forming cohesive outer rind (1) or not (0).

NOTES: A cohesive outer rind is likely to be derived feature since it is difficult to imagine how it could proceed an open fascicle structure in evolutionary terms. Polarized with cohesive outer rind apomorphic.

6 Number of plastids per cell: 1-3 (0) or >4 (1).

NOTES: Not polarized.

7 Plastids discoid (1) or laminate (0).

NOTES: Not polarized.

8 Propagation by adventitious plantlets (1) or not (0).

NOTES: Adventitious plantlets appear to be unique to the genus *Psilosiphon*. Such propagules are also found in the Ceramiaceae, but are not necessarily homologous. The production of adventitious plantlets is treated as an apomorphic character.

9 Spermatangia on specialized filaments (1) or not (0).

NOTES: This feature needs to be further evaluated, particularly in the genus *Batrachospermum*, where species in a number of sections are described as having specialized spermatangial filaments (but presumably not homologous with those described from *Lemanea*). Not polarized.

10 Spermatangia in superficial sori (1) or distributed throughout whorl (0).

NOTES: Likely apomorphy for *Lemanea* (or Lemaneaceae). Not polarized.

11 Carpogonial branches accessory (1) or

not (0).

NOTES: Lindstrom (1988) regarded the more advanced taxa of Dumontiaceae as having a strongly recurved (accessory) carpogonial branch, as did Kraft (1989) in the Liagoraceae. We have polarized this character likewise.

12 Number of cells in carpogonial branches: constant or little variable (1) or highly variable (0).

NOTES: Kraft (1989) found a major disjunction between those genera with low and relatively consistent numbers of cells in carpogonial branches, and those with higher, more indeterminate, numbers. A similar split can be used in the Batrachospermales. The latter state was considered by Kraft (1989) to be plesiomorphic, and this polarization is followed here.

13 Trichogyne inflated and persistent (1) or not (0).

NOTES: Sheath (1984) pointed out that the occurrence of inflated and persistent trichogynes is a feature of the life history of most species of the Batrachospermales and that it appears to be an adaptation for growth in the unidirectional flow of rivers and streams (the larger and more persistent surface area could enhance the probability of spermatangial contact). As a unique evolutionary novelty among the Rhodophyta, the inflated and persistent trichogyne is considered to be an apomorphy.

14 Fusion cell in primary gonimoblast present (1) or absent (0).

NOTES: Not polarized.

15 Gonimoblast filaments growth at least partly unlimited (0) or entirely limited (1).

NOTES: The continuum between loosely constructed carposporophytes and compact gonimoblasts is paralleled in the Liagoraceae (Kraft 1989). Not polarized.

16 Carposporangia single terminal cell (1) or in chains (0).

NOTES: Pairs of chains of carposporangia are reported from only two genera of the Liagoraceae, but arise in parallel in the cladograms illustrated by Kraft (1989). Not polarized.

17 Spore germination unipolar (1) or bipolar (0).

NOTES: Although included in the analysis, more material needs to be examined to confirm the consistency of this character. Not polarized.

18 $MgCl_2$ when added to alcian blue staining eliminating or reducing staining (1) or having no effect (0).

NOTES: Extremely variable within *Batrachospermum sensu lat.* and may provide a useful phylogenetic marker within that genus (Sheath and Cole 1990). Not polarized.

The other features tabulated (Table 1) were not used in the cladistic analysis for the following reasons.

(a) Morphology of diploid stage of life history: no suitable disjunctions found.

(b) Interlaced medullary filaments present or absent: the medullary filaments in *Psilosiphon* are not homologous with those of *Thorea* and *Nemalionopsis* since they develop in very different ways (the latter two genera are multiaxial while the medullary filaments of *Psilosiphon* are derived from the periaxial filaments of a single axial filament).

(c) Diameter of thylakoids: more specimens and species of each genus need to be examined.

(d) Monosporangia present or absent: variable within *Batrachospermum* and uncertain in *Thorea* and *Nemalionopsis* (see note 5 of Table 1).

(e) Spermatangial shape: no clear disjunction found.

(f) Orientation of first gonimoblast initial: no clear disjunction found and more information needed to properly assess.

Cladograms

Using either Liagoraceae as an outgroup,

or by polarizing selected characters, we obtained three equally parsimonious trees (Figs. 1, 2). The node giving rise to *Batrachospermum*, *Lemanea* and *Psilosiphon* was always well resolved, as was the nested node of *Lemanea* and *Psilosiphon*. There is insufficient evidence to decide between the three alternative arrangements for *Thorea*, *Nemalionopsis* and the *Batrachospermum-Lemanea-Psilosiphon* node: *Thorea* and *Nemalionopsis* together could be either monophyletic or paraphyletic.

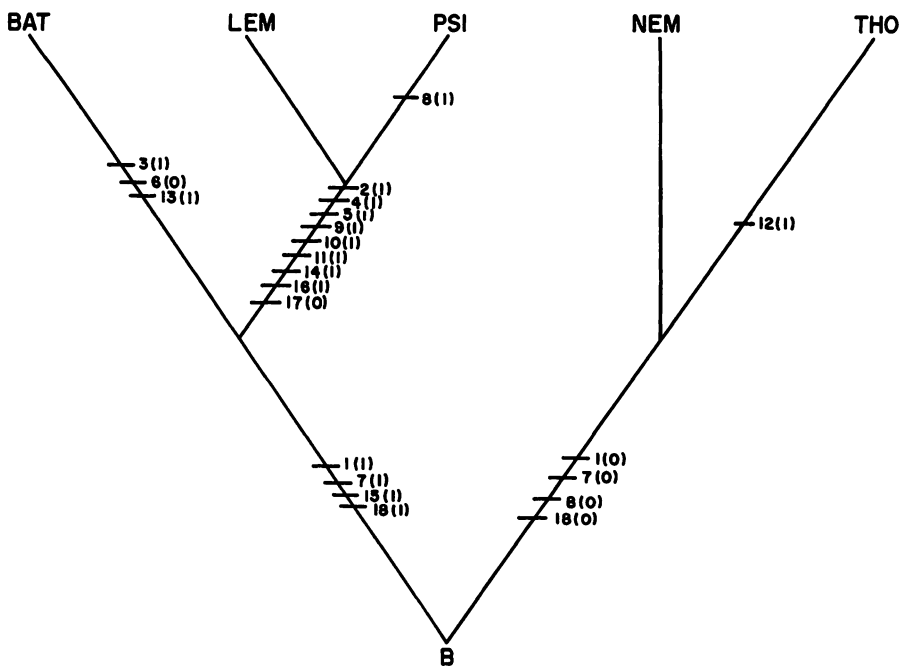
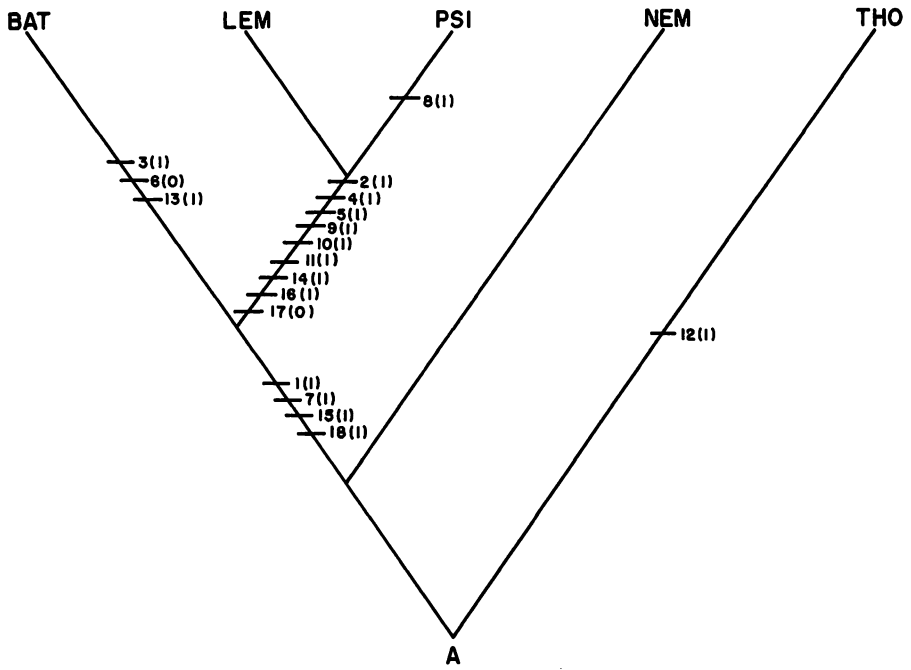
The node shared by the Batrachospermaceae (*Batrachospermum*) and the Lemaneaaceae (*Lemanea* and *Psilosiphon*) is defined by at least one apparently reliable synapomorphy [uniaxial gametophytes (character 1)], the Lemaneaaceae node by two [pseudoparenchymatous thallus apex (2), cohesive outer rind (5)] and the Batrachospermaceae node by one [only 1-3 plastids per cell (6); although if Liagoraceae included as outgroup, this character is a homoplasy]. All other characters supporting these nodes are either unknown in one or more taxa or vary within a taxon.

If a multiaxial gametophyte is considered plesiomorphic to a uniaxial gametophyte, the node supporting the Thoreaceae is poorly supported. More information is needed about sexual reproduction in *Nemalionopsis* before this part of the cladogram can be resolved. From the information we have to date, it appears that *Nemalionopsis* and *Thorea* have either evolved separately or together, but that other genera in the Batrachospermales share a distinct common ancestry.

Discussion

Polarity of Characters

The Batrachospermales are described by Gabrielson and Garbary (1986 p. 357, 1987 p. 134) as 'clearly a monophyletic order', due the characteristic life history (*Lemanea* type) with absence of tetrasporangia and their restriction to freshwater. In addition, the presence of an enlarged outer cap layer on the pit plug is found only in Batrachospermales, Corallinales and some species of Acrochetiales (Pueschel 1989). This combi-



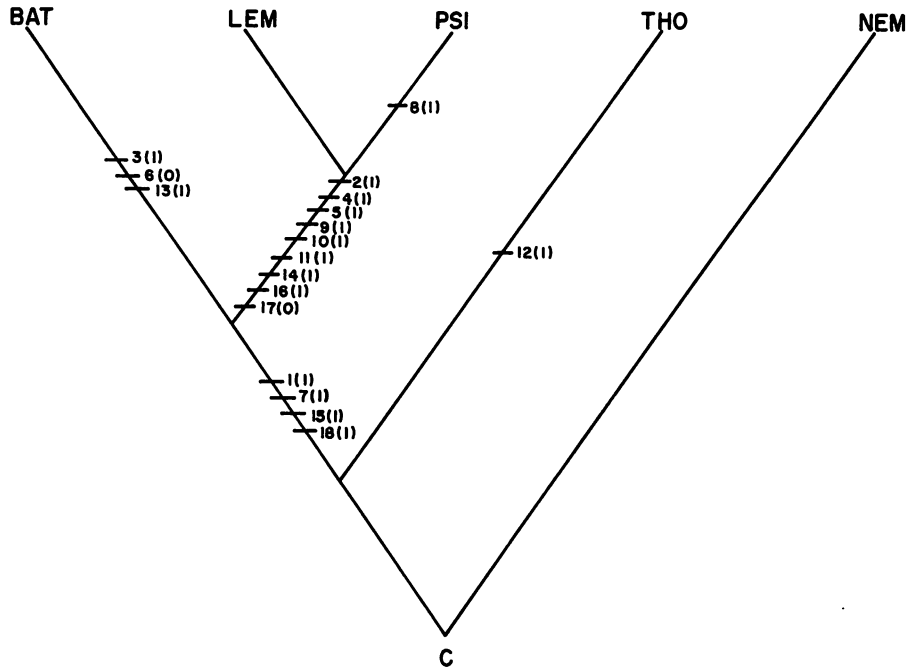


Fig. 1. Three equally parsimonious cladograms (A, B and C) using Lundberg rooting based on assumed plesiomorphic states of characters 1, 4, 5, 8, 11-13. CI=1.0. BAT=*Batrachospermum*; LEM=*Lemanea*; NEM=*Nemalionopsis*; PSI=*Psilosiphon*; THO=*Thorea*. Unbounded numbers refer to characters and numbers in parentheses refer to character states as listed in Table 2.

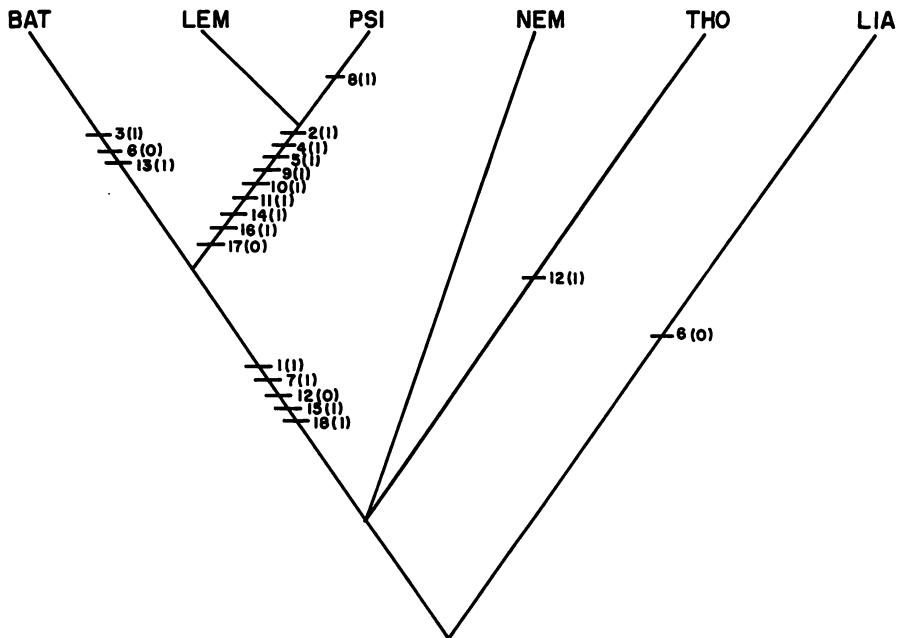


Fig. 2. Consensus tree using Liagoraceae as an outgroup. CI=0.9. BAT=*Batrachospermum*; LEM=*Lemanea*; LIA=*Liagoraceae*; NEM=*Nemalionopsis*; PSI=*Psilosiphon*; THO=*Thorea*. Unbounded numbers refer to characters and numbers in parentheses refer to character states as listed in Table 2. The tree above the Liagoraceae node is the same as the consensus tree derived from the cladograms in Fig. 1.

nation of characters in a Florideophycean group of algae make *Batrachospermales* a well-defined entity almost certainly derived from a common ancestor.

However, there is little published information to help in the choice of a sister group for the *Batrachospermales*. Until recently (Pueschel and Cole 1982), the families *Batrachospermaceae*, *Lemaneaceae* and *Thoreaceae* were placed in the *Nemaliales*, but Gabrielson and Garbary (1987 p. 134) conclude that from their cladistic analysis of Rhodophycean orders, 'there is no clear evidence that *Batrachospermales* and *Nemaliales* shared a common ancestry...'. In spite of this, in their search for an ancestral red alga, Gabrielson *et al.* (1985) reproduced a series of cladograms grouping *Nemaliales* and *Batrachospermales* together as a monophyletic group. Closer inspection, however, reveals that the two characters responsible for the shared branch are unlikely to be reliable.

Firstly, the coding of *Batrachospermales* as having only unipolar spore germination is incorrect (in both Gabrielson and Garbary 1987 and Gabrielson *et al.* 1985), as carpospore germination in *Lemanea* are reportedly bipolar (Atkinson 1890; Mullahy 1952). In this respect *Batrachospermales* is not the same as *Nemaliales* which apparently always has unipolar germination of spores. The second character, the presence of an empty spore mode of germination, is described by Gabrielson and Garbary (1987 p. 134) as a highly homoplastic character and not one upon which to base a sound phylogenetic tree. It must also be stressed that Gabrielson *et al.* (1985) conclude that the relationships between all Florideophycidean orders are unresolved in that analysis.

The *Corallinales* share only a single pit plug character (the presence of a dome-like outer cap layer) with *Batrachospermales* and in all other respects are highly divergent (Gabrielson and Garbary 1987). There is also no evidence to suggest that the pit plug structure found in the two orders are homologous, and the apparent absence of a 'cap membrane' in the *Corallinales* (Pueschel 1987) indi-

cates a fundamental difference. The existing cladistic analyses, therefore, do little to provide a suitable outgroup for *Batrachospermales*. We chose *Liagoraceae* as an outgroup since it is more likely to be a monophyletic group than the whole of the *Nemaliales* (Kraft 1989), and it has more vegetative and reproductive features in common with the *Batrachospermales* than any other Floridiophycidean group. However, because there is no evidence to suggest that the *Liagoraceae* are a sister group of *Batrachospermales*, out scoring of plesiomorphic characters may have resulted in a tree that is not globally parsimonious.

An alternative view is that *Batrachospermalean* algae evolved in isolation from an *Acrochaetialean*-like progenitor as suggested by Mori (1975) for *Batrachospermum*, all similarities between the upright cladome of *Batrachospermalean* and that of other Floridiophycidean algae have arisen by parallelism. The unique life history mode and requirement for freshwater of *Batrachospermalean* algae support such a view, implying that outgroup analysis would only result in a globally parsimonious tree if the *Acrochaetiales* were used as the sister-group. Kumano (1979) considers that on the basis of phycoerythrin absorption spectra (type IV = β -phycoerythrin), *Batrachospermales* are more closely related to the *Acrochaetiales* than the *Nemaliales*.

Due to the simple vegetative structure of *Acrochaetialean* algae, however, there are insufficient common and shared characters which can be scored for both the *Acrochaetiales* and the *Batrachospermales*. It is for this reason, and those mentioned above, that we chose the *Liagoraceae* in spite of some misgivings about the homology of characters between it and *Batrachospermales*. As alternative means of rooting our cladogram we, like Kraft (1989), used hypothesised plesiomorphic states in certain characters using informal outgroup comparisons (see characters scored).

Phylogenetic Relationships

The relationships explicated here are not novel; on the contrary, they reiterate what phycologists have long presumed (e.g. Kylin 1956, Bourrelly 1985). Our hypothesized phylogeny does not contradict the existing familial structure of Thoreaceae (*Thorea* and *Nemalionopsis*), Batrachospermaceae (*Batrachospermum*) and Lemaneaceae (*Lemanea* and *Psilosiphon*), and it strongly supports the circumscription of the latter two families which together form a monophyletic group. Lemaneaceae and Batrachospermaceae are therefore hypothesized as sister groups, a result which will facilitate the study of relationships within those two families. There is a critical lack of information concerning reproductive morphology in all but *Batrachospermum* and *Lemanea*, and the confirmation, refutation or refinement of our proposed phylogeny will depend on further investigations upon members of the smaller Batrachospermalean genera.

The families and genera recognized in this paper can be identified solely on the basis of vegetative characters, as outlined in the following key.

Key to the families and genera of Batrachospermales

- 1 Gametophyte uniaxial 2
- 1 Gametophyte multiaxial (Thoreaceae) 4
 - 2 Thallus apex not pseudoparenchymatous; outer cortical cells not forming cohesive outer rind (Batrachospermaceae) *Batrachospermum*
 - 2 Thallus apex pseudoparenchymatous; outer cortical cells forming cohesive outer rind separated from the axial filament (Lemaneaceae) 3
- 3 Thallus without any regular macroscopic nodes and internodes; outer rows of cortical cells nearly uniform in size and shape *Psilosiphon*
- 3 Thallus with regular macroscopic nodes; outer rows of cortical cells differentiated from large swollen inner cells to smaller superficial cells *Lemanea*
 - 4 Thallus with long hair-like filaments arising from periphery *Thorea*

- 4 Thallus without long hairs protruding from periphery *Nemalionopsis*

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T. J. Entwisle* and O. Necchi Jr.** : 淡水産紅藻カワモヅク目の系統解析

カワモヅク目は単系的な藻群で良く整理され、最近ではカワモヅク科:カワモヅク(著者らの定義による)、レマネア科:*Lemanea*, *Psilosiphon*, チスジノリ科:オキチモヅク, チスジノリの3科5属で構成される体系が受け入れられている。我々の行なったこれら5属の分岐分類学的な解析はこの体系を支持するが、この結果を立証するためにはさらに*Psilosiphon*, オキチモヅクおよびチスジノリの有性生殖器官の形態に関する情報と紅藻植物門のどの目と類縁を持つか(姉妹分類群は何か?)の理解が必要である。ここではカワモヅク目の科と属に対し、栄養成長に関わる形質に基づいたkeyを与えた。(*National Herbarium of Victoria, Birdwood Ave, South Yarra, Victoria 3141, Australia. **Instituto de Biociências, Letras e Ciências Exatas, Universidade Estadual Paulista, Departamento de Botânica, Caixa, Postal 136, 15001—São José do Rio Preto, SP, Brasil)