

## ACROCHAETIALES (RHODOPHYTA) : TAXONOMY AND EVOLUTION

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**ABSTRACT.** — An emended diagnosis of the order Acrochaetiales is provided. The history of the classification of the order is reviewed in the context of arguments against its recognition. Support for Acrochaetiales is provided based on cladistic analyses, and the proposed evolutionary relationships of this taxon with other florideophyte orders are discussed.

**RÉSUMÉ.** — Une modification de la diagnose de l'ordre des Acrochaetiales est proposée. L'historique de la classification de cet ordre est revu en considérant les arguments qui sont opposés à sa reconnaissance. Le fondement des Acrochaetiales s'appuie sur les analyses cladistiques; les relations phylogénétiques de ce taxon avec les autres ordres de florideophytes sont discutées. (traduit par la rédaction).

**KEY WORDS :** Acrochaetiaceae, Acrochaetiales, algal taxonomy, *Audouinella*, phylogeny of red algae, Rhodophyta.

### INTRODUCTION

CHEMIN (1937) originally suggested that the order Acrochaetiales (Nemaliales) be elevated to ordinal rank (as «Acrochoetiales»), but he provided no description or formal characterization of the order, merely stating, «Sous ce terme nouveau, je rangerai les genres *Acrochaetium* (*Chantransia*), *Colaconema* et *Rhodochorton*. . . La simplicité de leur forme et de leur structure, la variété de leur mode de reproduction, de leur mode de vie, du développement des spores, me les fait considérer comme des formes primitives». At that time, the Nemaliales were characterized as lacking a «typical» auxiliary cell and being haplo-biontic (KYLIN, 1932). According to article 32.1c of the International Code of Botanical Nomenclature (ICBN) (VOSS et al., 1983), Chemin's comment does not constitute a valid description of the order.

FELDMANN (1953) also proposed the Acrochaetiales and provided a characterization, which, albeit brief, satisfies the requirements of the ICBN for valid

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publication. He stated «L'extrême simplicité de l'appareil femelle des *Acrochaetiales* justifie la création pour cette famille d'un ordre spécial, celui des *Acrochaetiales* caractérisé par l'absence de rameau carpogonial qui l'oppose à toutes les autres *Floridées*». Although this characterization might be construed as incidental mention (and therefore invalid under Article 34.1), FELDMANN (1954) clearly considered the order to be formally created since he used the name without further comment. In a subsequent paper, FELDMANN (1962) again discussed the order and elaborated on his previous comments. He stated «The lack of a carpogonial branch and the extreme simplicity of the vegetative frond seem to me sufficient reasons to put these algae in a separate order, the *Acrochaetiales*». It is of interest that in neither of these papers was the original suggestion of Chemin cited, even though Feldmann was likely to have been aware of the earlier publication. Although the description by Feldmann (1953) is sufficient for nomenclatural purposes, it does not provide an adequate description of the order for taxonomic purposes.

DREW (1954), followed by DIXON (1961), ABBOTT (1962) and PAPENFUSS (1966), did not accept the order and all of these workers argued for maintaining the *Acrochaetiaceae* in *Nemaliales*. More recently, GARBARY (1978) argued for recognition of the *Acrochaetiales* based on its phylogenetic position, and this conclusion was supported by the cladistic analyses of GABRIELSON et al. (1985) and GABRIELSON and GARBARY (1987).

In this paper we provide an emended description of the order, explain why the order has not been accepted by most phycologists, and discuss proposed evolutionary relationships with other orders of red algae based on our cladistic analyses.

***Acrochaetiales* Feldmann emend. Garbary et Gabrielson**

Branched or unbranched filamentous Rhodophyta with 2-layered pit plug caps and a pit plug membrane; auxiliary cells absent; carpogonium terminal or lateral and borne on an undifferentiated vegetative filament.

Type genus : *Acrochaetium* Nägeli in NÄGELI et CRAMER (1858 : 532)  
= *Audouinella* Bory de St. Vincent (1823 : 340).

## DISCUSSION

### 1. Controversy over ordinal recognition

DREW (1954) was the first to comment on FELDMANN's (1953) proposal of ordinal status for the *Acrochaetiaceae*. In her classic paper on development of carposporophytes, she recognized two groups of families in *Nemaliales* (as *Nemalionales*) : those with «comparatively or extremely simple carposporophytes» including the *Acrochaetiaceae* (as *Chantransiaceae*), *Batrachospermaceae* and some taxa of *Bonnemaisoniaceae* and *Helminthocladiaceae*, and those with «more elaborate or even highly specialized carposporophytes» including the *Naccariaceae*, *Galaxauraceae* (as *Chaetangiaceae*) and *Bonnemaisoniaceae*.

She regarded the former as a more or less homogeneous assemblage and, apparently on this basis, rejected Feldmann's proposal. In the main part of «Die Gattungen der Rhodophyceen» (KYLIN, 1956, p. 82) the Acrochaetiaceae (as Chantransiaceae) is treated as a family in Nemaliales (as «Nemalionales») with no reference to Feldmann's paper. Only in the «Nachtrag» (prepared by Elsa Kylin following the death of her husband in December, 1949) is reference made to Feldmann's proposal, but it is not supported apparently because, «In der Familie Chantransiaceae sensu Kylin gibt es sowohl Formen mit Endständigen Karpogonen als mit Karpogonastchen...».

As DIXON (1964) pointed out, FELDMANN (1953) «... was beginning to become critical of the accepted usage of the term «carpogonial branch...». Feldmann recognized three types of mature carpogonial branches which he considered to represent stages in the evolution of the structure : 1) the carpogonium is borne directly on a vegetative cell, 2) the carpogonium is borne on a special branch, which is itself borne on a vegetative cell and 3) the carpogonium is borne on a carpogonial branch that is borne on a «rameau adventif spécialisé : le gonophore».

All subsequent arguments for rejecting Feldmann's proposal of ordinal status for the Acrochaetiales have revolved around the definition of a carpogonial branch. For example, both DIXON (1961) and ABBOTT (1962) emphasized that there are other taxa in Nemaliales *sensu lato* that have «sessile carpogonia» or that lack «true carpogonial branches». Dixon argued in favour of maintaining the Gelidiaceae as a family in Nemaliales (as Nemalionales), noting that «sessile carpogonia of a type similar to those of *Acrochaetium* occur also in *Gelidium*...» and he used this comparison to reject ordinal status for the Acrochaetiales. Abbott pointed out that in some taxa of Helminthocladiaceae only the carpogonium participates in gonimoblast formation (e. g. *Liagoropsis*), whereas in other taxa the entire carpogonial branch is involved in cystocarp formation (e. g. *Trichogloea*). In referring to species of *Acrochaetium* in which only the carpogonium is involved in gonimoblast formation, Abbott called the subtending cells «stalks». She states, «In some, therefore, the carpogonium, placed terminally on a special branch, may be thought to be just as sessile as if it were produced directly on a vegetative filament...». This creates a very restricted definition for a carpogonial branch, based on whether the cells subtending the carpogonium are involved in carposporophyte formation and is very different from Feldmann's definition cited above. Abbott labeled a carpogonium «sessile» if it was borne on one vegetative cell, or a «carpogonium on a one-celled stalk» when it was borne on more than one cell. Despite the use of this elaborate terminology, Abbott appears to consider all carpogonial branches as homologous, stating «Neither usage is meant to imply that these female reproductive structures are different from the more elaborate ones in, for example, the Dumontiaceae, or the more fixed ones in the Rhodomelaceae».

FELDMANN (1962) emended his ordinal description for Acrochaetiales, adding to the reproductive characterization a vegetative one, «... the extreme simplicity of the vegetative frond...» PAPENFUSS (1966) challenged both of

Feldmann's ordinal features, citing, as had DIXON (1961) and ABBOTT (1962), numerous examples of sessile carpogonia in the nemaliallean families Helminthocladiaceae and Batrachospermaceae, and in the Gelidiales. In addition, he noted that certain genera of Ceramiaceae (Ceramiales) as well as the *Chantransia*-stages of certain nemaliallean families (currently classified in Batrachospermales) had a thallus structure similar to Acrochaetiaceae. These similarities, however, do not necessarily indicate a close evolutionary relationship among these taxa, there being numerous vegetative, reproductive, life history and ultrastructural features that segregate them. Furthermore, all of the characters that circumscribe a taxon must be considered together, not in isolation. Most English-speaking phycologists followed Dixon, Abbott and Papenfuss and did not recognize the Acrochaetiales, whereas, for the most part, continental European phycologists adopted Feldmann's proposal.

GARBARY (1978) presented several evolutionary hypotheses (as cladograms) about the phylogenetic relationships of the Acrochaetiaceae and concluded that only if it could be demonstrated that the taxon was reduced from a nemaliallean ancestor could it be classified as a family in Nemaliales. Because there was no evidence to support such a phylogenetic position for the Acrochaetiaceae and because of, in Garbary's view, the pivotal position of the taxon as being closest to the ancestral progenitor (s) of the Florideophycidae, he argued in favour of ordinal recognition for the Acrochaetiaceae. However, in most recent syntheses of red algal taxonomy (e. g. KRAFT, 1981; WEST and HOMMERSAND, 1981; DIXON, 1982) his position has not been followed.

## 2. Infraordinal taxonomy

The Acrochaetiales are usually regarded as comprising a single family, the Acrochaetiaceae. FELDMANN (1962), however, recognized two families, the Acrochaetiaceae and Audouinellaceae. Aside from life history features (haplobiontic versus probably diplobiontic), which were poorly-defined and have not held up with subsequent investigation, criteria for familial segregation were based on chloroplast number and morphology, and presence or absence of pyrenoids. The Acrochaetiaceae was characterized as having cells with primarily single chloroplasts and pyrenoids, whereas the Audouinellaceae had more than one chloroplast per cell and were devoid of pyrenoids. These chloroplast features (in addition to others) are considered by some authors to define genera (e. g. PAPENFUSS, 1945), whereas other authors only consider them useful at the specific level (e. g. DREW, 1928). In our concept of the order we recognize only a single family, the Acrochaetiaceae.

There is an ongoing controversy regarding generic classification in the family. Different classifications recognize from one to eight genera, and numerous different schemes for generic segregation have been proposed in the last twenty years. Much of the literature on this subject was reviewed by GARBARY (1979) and WOELKERLING (1983) and is not treated here. We believe that a number of genera will eventually be segregated in this complex, but until these are ade-

quately characterized we follow the single-genus concept of DREW (1928), DIXON and IRVINE (1977) and GARBARY (1979).

### 3. Taxonomic relationships

With the recent dismantling of the Nemaliales sensu DIXON (1982) – an order universally recognized by post-Kylinian red algal phycologists as being heterogeneous – all arguments (discussed above) for maintaining Acrochaetiaceae as a family in that order have become irrelevant. Dixon considered the order to comprise 13 families : Acrochaetiaceae, Batrachospermaceae, Bonnemaisoniaceae, Dermonemataceae, Helminthocladiaceae, Galaxauraceae (as «Chaetangiaceae»), Gelidiaceae, Gelidiellaceae, Lemnaceae, Naccariaceae, Nemaliaceae, Thoreaceae and Wurdemanniacae (usually classified in Gigartinales); currently only four remain : Dermonemataceae, Galaxauraceae, Helminthocladiaceae and Nemaliaceae. Most of the suggestions for ordinal segregation for these families had been made prior to DIXON (1982) (e. g. KYLIN, 1923; CHEMIN, 1937; FELDMANN and FELDMANN, 1942; LEE, 1980, «Lemneales»), however, the recent impetus for splitting-up Nemaliales was the demonstration by PUESCHEL and COLE (1982) that the order was heterogeneous with regard to the number of cap layers overlying pit plugs. The universal acceptance of this character for delineating orders, or what appear to be related groups of orders, was that it supported other vegetative, reproductive and life history characters that earlier had been considered useful at segregating taxa at ordinal rank. Thus recognition of Gelidiales originally proposed by KYLIN (1923), was supported by their possession of pit plugs with single-layered caps, another feature not found in any other nemalialean family. Likewise, the Bonnemaisoniales (including Bonnemaisoniaceae and Naccariaceae), originally proposed by FELDMANN and FELDMANN (1942), was supported by their lacking pit plug caps, again a feature not found in any other Nemaliales. In addition, the freshwater families Batrachospermaceae, Lemnaceae and Thoreaceae were segregated to a new order, Batrachospermales, based on their having an enlarged outer plug cap layer (PUESCHEL and COLE, 1982). The remaining families, including the Acrochaetiaceae, all possess 2-layered plug caps.

In all of the trees resulting from our cladistic analyses (GABRIELSON et al., 1985; GABRIELSON and GARBARY, 1987), Acrochaetiales appear as an independent lineage at the base of the florideophyte assemblage of orders. In the first analysis there were no autapomorphies that uniquely defined Acrochaetiales, yet numerous synapomorphies (e. g. presence of tetrasporangia and a filamentous gonimoblast and 2-layered pit plug caps) separate the order from Bangiales, and one, lack of syntagmatic construction, separates it from all other florideophytes. In the later analysis in which the character states were more accurately represented in the individual orders, the presence of both B- and R-phycoerythrin was shown to be a unique feature of Acrochaetiales (see GLAZER et al., 1982).

In the Adams consensus trees produced from the two cladistic analyses (Figs. 1 and 2) a major polytomy occurred at one node and includes, in the first analysis, the orders Palmariales, Corallinales, Gelidiales, Hildenbrandiales and a lineage supporting the remaining florideophytes. In the second analysis the corresponding node included the orders Corallinales, Batrachospermales, Nemaliales, and one lineage supporting the orders Palmariales, Gelidiales and Hildenbrandiales, and another the florideophytes that lack pit plug caps (i. e. Bonnemaisoniales, Ceramiales, Gigartinales and Rhodymeniales). The presence of a polytomy indicates that relationships among taxa at that node are unresolved and thus, all taxa and lineages that share that node might possibly be the sister taxon of the ancestor that gave rise to the Acrochaetiales at node E (Figs. 1, 2). Over the years, and by various workers, Acrochaetiales have been considered to be related to taxa in Batrachospermales, Gelidiales, Nemaliales and Palmariales, and each of these proposed relationships is discussed below, as is the likelihood of a relationship with Corallinales or Hildenbrandiales.

#### A - Relationships with Gelidiaceae

The one-celled carpogonial branch of Gelidiaceae (including Gelidiellaceae – see MAGGS and GUIRY, 1987) is the primary reproductive feature interpreted as being shared with Acrochaetiales (DIXON, 1961; PAPENFUSS, 1966). However, Gelidiales, with their *Gelidium*-type spore germination, syntagmatic construction with two periaxial cells per axial cell, 1-layered pit plug caps, moniliform files of nutritive auxiliary cells, compound cystocarps and transversely divided cystocarps (GABRIELSON and GARBARY, 1986), evidently are not the sister taxon of Acrochaetiales. Furthermore, HOMMERSAND and FREDERICQ (1987) consider the Gelidiales to be characterized by intercalary carpogonia, rather than sessile ones. Although intercalary carpogonia have been reported in Acrochaetiales, e.g. WEST (1969) and LEE and KUROGI (1978), they are found intermixed with terminal ones and thus cannot be considered a general feature of the morphology of Acrochaetiales. WEST's (1969) observation most likely represented a cultural abnormality and it is of interest that he did not observe postfertilization development in such intercalary carpogonia.

In our most recent cladistic analysis (GABRIELSON and GARBARY, 1987), Gelidiales and Hildenbrandiales are hypothesized to share a common ancestry based on similar patterns of spore germination and 1-layered pit plug caps. Based on the features cited above, it is highly improbable that there is a close phylogenetic relationship between Acrochaetiales and either of these taxa.

#### B - Relationships with Batrachospermales

There are a number of similarities between Acrochaetiaceae and Batrachospermales based primarily on the filamentous *Chantransia*-stages produced by the latter. These stages are only superficially similar, however, and are part of a radically different life history pattern in Batrachospermales in which somatic meiosis occurs and there are no tetrasporangia in the life history (see SHEATH, 1984 for review). Tetrasporangia are present in all known sexual (and some ase-

xual) life histories in Acrochaetiales. In addition, pit plugs in the two groups are different with all Batrachospermales having an expanded outer plug layer (PUESCHEL and COLE, 1982) and syntagmatic morphology.

### C - Relationships with Nemaliales

Many Acrochaetiales, with their monosporangia, stellate chloroplasts and large pyrenoids, are similar to filamentous (tetrasporophytic) stages of Nemaliales. There is also a strong resemblance in the morphology of sexual reproductive organs and postfertilization development and the number of pit plug cap layers between these taxa. We regard these features as being retained primitive characteristics (i. e. homoplasious) that do not indicate a monophyletic group including both orders. FELDMANN (1961) and Abbott (pers. comm.) have speculated that the Acrochaetiaceae evolved through reduction from taxa currently placed in Nemaliales. Abbott uses this argument to retain Acrochaetiaceae in Nemaliales. This might be the case for some taxa of Acrochaetiales, but until it has been specifically demonstrated using features other than reproductive morphology (e. g. comparative ultrastructure or biochemistry), it should be regarded as an interesting hypothesis, not as a basis for including Acrochaetiaceae in Nemaliales.

### D - Relationships with Palmariales

The possibility of a relationship between Acrochaetiales and Palmariales has been broached several times. CABIOCH and GUIRY (1977) suggested that *Halosacciocolax* be included in Acrochaetiaceae, however, this possibility was discounted by GARBARY (1978) because of the degree of morphological elaboration exhibited by the genus. Recently, HAWKES and SCAGEL (1986) retained *Halosacciocolax* in Palmariales. GLAZER et al. (1982) suggested that *Rhodophysema* be transferred to Acrochaetiales based on similarities in vegetative morphology and the presence of 2-layered pit plug caps and B-phycoerythrin, features *Rhodophysema* shares with *Audouinella concrescens* (Drew) Dixon and *A. membranacea* (Magnus) Papenfuss. DECEW and WEST (1982), however, interpreted the life history of *Rhodophysema* as being homologous with *Palmaria* and placed the former genus in the Palmariales. HAWKES and SCAGEL (1986) concurred with this placement. Until more definitive studies are carried out, we feel that *Rhodophysema* should remain in Palmariales and that the transfer of certain species of *Audouinella* to Palmariales and/or the synonymy of Acrochaetiales and Palmariales should all be avoided.

The basic pattern of development in the Palmariales is the disc and there is no hint of a filamentous ontogeny (with the possible exception of the parasitic *Halosacciocolax*). This contrasts with Acrochaetiales where filamentous development predominates (WOELKERLING, 1983) except in certain species (e. g. *A. concrescens*) or in the tetrasporophytic stages of some species with stellate chloroplasts (e. g. *A. secundata* (Lyngbye) Dixon) where discs are formed. Of primary importance is whether or not these similarities are homologous. Certain life histories in Acrochaetiales are similar to those in Palmariales in that carpo-

sporophytes are absent (e. g. *A. subimmersa* (Setchell et Gardner) Garbary et Rueness (LEE and KUROGI, 1978, as *Rhodochorton*) and *A. purpurea* and *A. floridula* (Dillwyn) Woelkerling (STEGENGA, 1978, as *Rhodochorton*). GUIRY (1987) provides a discussion of these life histories and concludes that they are similar. We concur that these are basically *Palmaria*-type life histories, however, it is questionable whether or not this feature defines a monophyletic group in *Audouinella*, let alone represents a synapomorphy of some *Audouinella* species with *Rhodophysema*. The mechanisms that MAGNE (1982) invoked for the origin of the *Palmaria*-type life history can be operating in all florideophytes and a particular life history pattern may have arisen several times in different groups (see GABRIELSON and GARBARY, 1987 for further comments).

### CONCLUSIONS

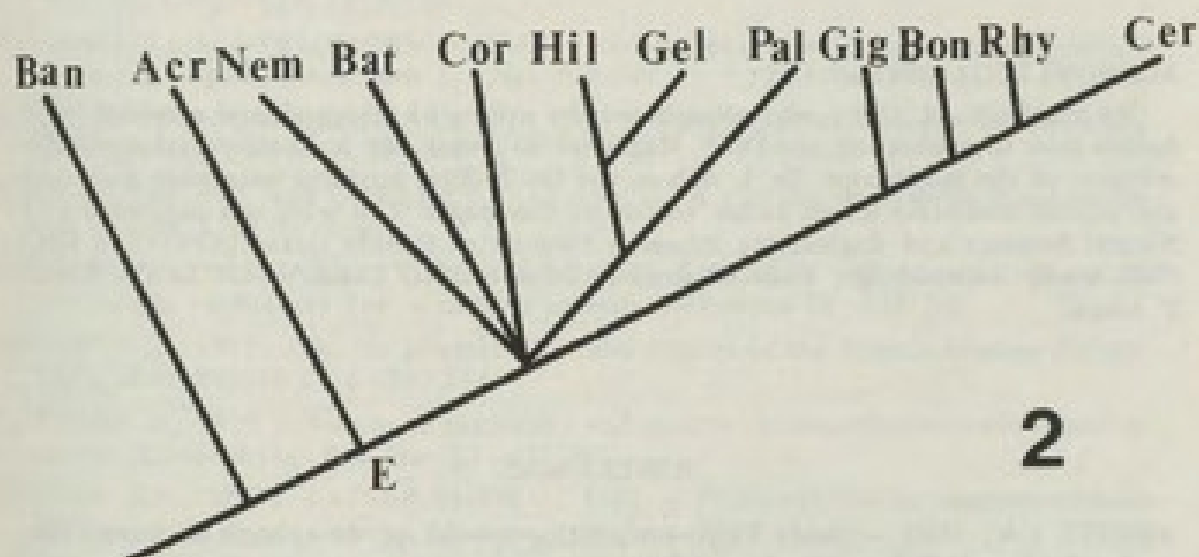
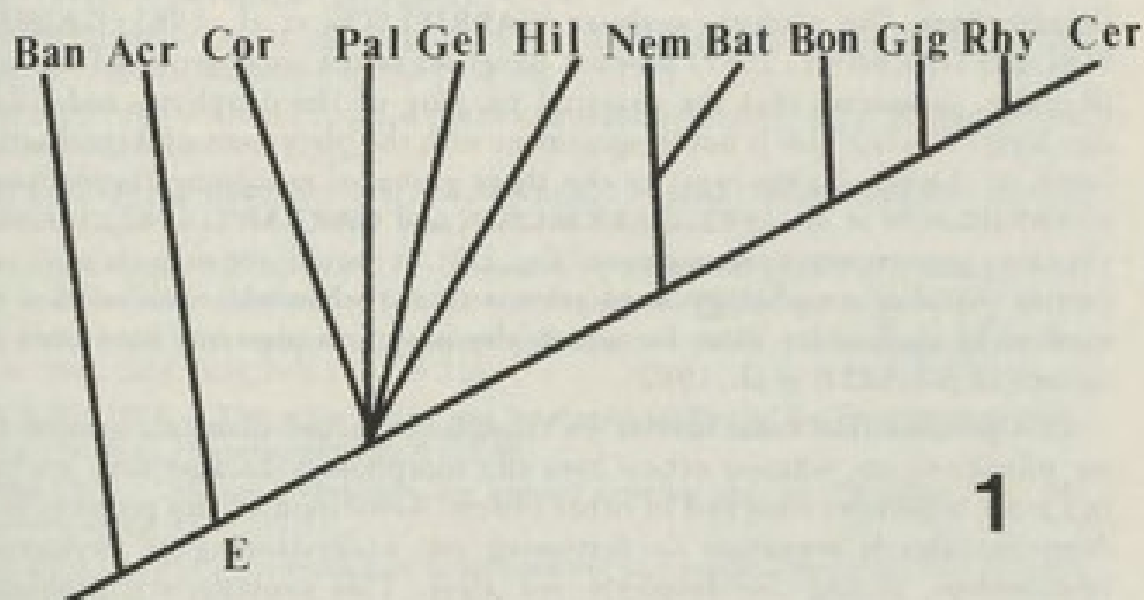
Our cladistic analyses (GABRIELSON et al., 1985; GABRIELSON and GARBARY, 1987) would support the hypothesis that the ancestral progenitor of florideophytes was filamentous in all life history phases. If such an organism was extant, it would be classified in Acrochaetiales. CHADEFAUD (1960) was of similar opinion with his placement of Acrochaetiales as the first group of Eo-floridées. This filamentous morphology has been retained in all phases of the life history only in extant Acrochaetiales. Many groups of florideophytes have also apparently retained this feature in the tetrasporophytic generation of their life history, i.e. Nemaliales, Batrachospermales and some Gigartinales. The similarity in vegetative structure between Acrochaetiales and some filamentous Ceramiaceae (e.g. *Ptilothamnion*, *Spermothamnion*) that was noted by PAPENFUSS (1966) is clearly a convergence, because the closest relatives of these genera are all syntagmatic. Thus, the presence of a free-living filamentous stage in the life history does not imply relationship with Acrochaetiales since this is a homoplasious feature.

This is not to say that taxonomic confusion between Acrochaetiales and other florideophytes is absent. Such problems, however, are at the species level and it may be that a number of species identified as Acrochaetiales belong to other groups. Two such examples are : 1) the suggestion that *Acrochaetium hauckii* Schiffner is part of the life history of *Kallymenia microphylla* J. Agardh (CODOMIER, 1973) (however, see alternative interpretation in GUIRY and MAGGS, 1984), and 2) the finding that *Acrochaetium polyidis* (Rosenvinge) Børgesen is part of the life history of *Helminthora divaricata* (C. Agardh) J. Agardh (MAGNE and ABDEL-RAHMAN, 1983).

It is possible that Acrochaetiales as they are presently constituted are polyphyletic. Some characters that suggest a polyphyletic origin are the diversity of chloroplast morphologies (see WOELKERLING, 1983 for summary) and phycobilin pigments (GLAZER et al., 1982) and the wide range of life history patterns (WOELKERLING, 1983; GUIRY, 1987). At present it is difficult enough to try and correlate chloroplast morphologies with vegetative structure.



reproduction and life history and phycobilin types within the family, let alone to try and indicate relationships of some taxa with other orders. Of particular interest in this regard, however, is the group of *Audouinella* species that only produce tetrasporangia in their life history (WEST, 1970, 1979), or that have a life history similar to *Rhodophysema* (see above discussion). As those taxa,



Figures 1-2. — Cladograms showing Adam's consensus trees of orders of Florideophycidae and Bangiales showing position of Acrochaetiales. NOTE : these figures are redrawn from GABRIELSON et al. (1985) (Fig. 1) and GABRIELSON and GARBARY (1987) (Fig. 2); see those papers for details of cladistic methods and characters. Abbreviations : Ban - Bangiales; Acr - Acrochaetiales; Pal - Palmariales; Hil - Hildenbrandiales; Gel - Gelidiales; Cor - Corallinales; Nem - Nemaliales; Bat - Batrachospermales; Gig - Gigartinales; Bon - Bonnemaisoniales; Rhy - Rhodymeniales; Cer - Ceramiales.

which are clearly derived from other red algal orders are recognized and correctly classified, the Acrochaetiales will become better circumscribed. Further studies of pit plug morphology and mitosis along the lines of PUESCHEL and COLE (1982) and SCOTT (1986), but directed specifically at Acrochaetiales and potential relatives may be the most direct route to resolving these issues.

A major question that remains is the nature of the pit plug in the ancestral florideophyte. Our cladistic analyses (GABRIELSON et al., 1985; GABRIELSON and GARBARY, 1987) propose Bangiales as the sister group of Florideophycidae, suggesting that the ancestral pit plug of florideophytes had a single cap layer. Whereas this is not in agreement with the placement of Acrochaetiales (with its 2-layered plug caps) as the sister group of remaining florideophytes (GABRIELSON et al., 1985; GABRIELSON and GARBARY, 1987), it remains the most parsimonious arrangement (Fig. 1-2). It would not surprise us if variation in pit plug morphology were present in Acrochaetiales. Critical taxa that need to be studied are those for which phycoerythrin pigments have been characterized (GLAZER et al., 1982).

It is possible that some species are «simple» branched filaments because they are primitively so, whereas others have this morphology because they are reduced from organisms classified in other orders. Resolution of this problem in the Acrochaetiales is important to furthering our understanding of phylogenetic relationships among florideophyte red algae. This evolutionary problem is analogous to (and almost as important as) the evolution of unicells in bangiophyte red algae.

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