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Taxonomy of *Phaeophyceae* with particular reference to Mediterranean species

Abstract

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At present the taxonomy of *Phaeophyceae* is based not only on morphological characters, but also in ultrastructural and biochemical characters and in molecular data. Although molecular techniques have allowed us to clarify the taxonomy of brown algae, many problems remain unresolved. The main changes that the taxonomy of *Phaeophyceae* has undergone in recent years, particularly concerning Mediterranean taxa, and the problems that remain without solution are presented.

Introduction

The class *Phaeophyceae* contains about 265 genera and 1500-2000 species (Hoek & al. 1995). In the Mediterranean Sea this class are represented by 86 genera and 265 species (Ribera & al. 1992). They are almost all marine; only a few species live in estuaries and freshwater habitats. Most of the brown algae grow in the eulittoral and the upper sublittoral zones and are dominant members of the marine flora in many parts of the world, specially in cold and temperate waters.

The main characteristics of the brown algae are: yellow-brown plastids due to carotenoid pigments, in particular fucoxanthine, in addition to chlorophylls a and c; plastids with 3-thylakoid lamellae and chloroplast endoplasmic reticulum confluent with nuclear envelope; laminaran as food storage; alginic acid, fucoidine and cellulose in the cell walls; mitochondria with tubular cristae; physodes containing phlorotannins; two heterokont lateral flagella only present in reproductive cells.

The taxonomy of *Phaeophyceae* has been based classically on morphological characters: construction of the macroscopic plant (haplostichous or filamentous thallus/polystichous or parenchymatous thallus), type of growth (diffuse growth/meristematic growth), life history (isomorphic/heteromorphic/diplontic) and sexual reproduction (iso-or-anisogamous/oogamous). In recent years the taxonomy of *Phaeophyceae* is based also on ultrastructural characters: motile cells, pyrenoid (as you could see later, phylogenetically very

informative) and biochemical characters: pheromones, lipids, polyols and steroid and terpenoid secondary metabolites and finally on molecular data.

Molecular techniques are new tools which could implement the insufficient morphological data and lead to the construction of phylogenies in *Phaeophyceae*. The most common molecular marker used is the ribosomal DNA. The most used regions are the small subunit (SSU), the large subunit (LSU) and also the combined SSU + LSU. The sequence of the large subunit (*rbcL*) of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and Rubisco spacer have also been used.

Although, in recent years the molecular techniques have allowed to clarify the taxonomy of brown algae, a lot of problem remain unresolved not only at ordinal level, but also at level of families, genus and species. The main changes that the taxonomy of *Phaeophyceae* has undergone in recent years, particularly concerning Mediterranean species, and the main problems that remain without solution are the following:

1. - The redefinition of the order *Ectocarpales*
2. - Taxonomic complexity within the order *Ectocarpales*
3. - Validity of the order *Ralfsiales*
4. - Taxonomic position of the family *Cystoseiraceae*
5. - Taxonomic position of the family *Phyllariaceae*

1. - The redefinition of the order *Ectocarpales* (Rousseau & Reviere 1999a) to include taxa possessing an exerted, pedunculated pyrenoid (*Ectocarpales*, *Chordariales*, *Dictyosiphonales* and *Scytosiphonales*).

Classification of the *Phaeophyceae* into orders began with Oltmanns (1922) who considered seven orders and Kylin (1933) who considered eleven orders. These systems are based on the characters of thallus constructions and mode of growth and in the type of gamy and life history. Since then other attempts to classify the brown algae have resulted in a great variety of different schemes. According to Reviere & Rousseau (1999) the main problem has been whether to recognize narrower or wider circumscription for the *Ectocarpales*.

The narrower concept of *Ectocarpales* is based on Kylin (1933) that recognized as different orders *Ectocarpales* (haplostichous thallus, isomorphic life history) *Chordariales* (haplostichous thallus, heteromorphic life history) and *Dictyosiphonales* and *Punctariales* (both with polystichous thallus and heteromorphic life history). This concept was followed more or less by Wynne & Kraft (1981), Bold & Wynne (1978, 1985), Wynne (1982), Womersley (1987) and Clayton (1990).

The wider concept of *Ectocarpales* is based on Fritsch (1945) that questioned the value of the character haplostichous versus polystichous and it was supported by the numerical study of the brown algae of Russell & Fletcher (1975). This order included all the families placed by Kylin in *Ectocarpales*, *Chordariales*, *Punctariales* and *Dictyosiphonales*. This concept had been used by Oltmanns (1922) that included also *Desmarestiales* and *Sporochnales* and it was followed by Parke & Dixon (1976), Clayton (1981), Tan & Druehl (1994) (as "ectocarpoids") and Burkhardt & Peters (1998) and Peters & Burkhardt (1998) (as "simple brown algae").

Tan & Druehl (1993) using gene sequences analysis of the SSU of rDNA showed that

a group corresponding to brown algae with stalked pyrenoids was clearly separated from all order *Phaeophyceae*. Tan (1995) arrived at the same conclusion.

Rousseau & Reviere (1999a) using partial SSU + LSU combined rDNA sequence data confirmed the observation of Tan & Druehl (1993) and they redefined the order *Ectocarpales* as order of *Phaeophyceae* in which cells have one or several plastids, each with one or several stalked and exserted pyrenoids; sexuality when known, isogamous or anisogamous, never oogamous; life-cycle haplodiplontic. These authors considered included in this order the *Ectocarpales sensu stricto*, the *Chordariales*, the *Dictyosiphonales* and the *Scytosiphonales*.

Siemer & al. (1998) obtained the same conclusion (*Scytosiphonales* was not included in the study) on the basis of chloroplast-encoded Rubisco large Subunit (*rbcL*) and Rubisco spacer sequences. These authors demonstrated that there is indeed a close phylogenetic relationship among the orders *Ectocarpales*, *Chordariales* and *Dictyosiphonales*. These authors pointed out that the different morphology (filamentous, pseudoparenchymatous or parenchymatous) though useful in identification, is troublesome with respect to phylogenetic interpretation. Similar observations were made, as you could see later, in a study of *Sporochneales*, *Desmarestiales* and *Laminariales* (Tan & Druehl 1996).

Kogame & al. (1999) carried out a study of the order *Scytosiphonales* using DNA sequences of *rbcL*, partial *rbcS* and partial LSU rDNA and supported the emended circumscriptions of the *Ectocarpales* of Rousseau & Reviere (1999a) because the small sequence divergence in the order *Scytosiphonales* favors its reduction to familial rank.

2. - The incongruity at family level within the order *Ectocarpales sensu lato* between the current morphological classifications and the molecular phylogeny and the incomplete knowledge of the *Ectocarpales* life history, particularly within the *Scytosiphonaceae*, *Dictyosiphonaceae* and *Punctariaceae*, since the prostrate sporophyte of some species is unknown. In many cases the gametophyte had been situated in a family and the sporophyte in a different one. Further discoveries will cause the removal of some genera and species from one family to another and species from one genus to another.

Within the order *Ectocarpales sensu lato* Siemer & al. (1998) pointed out that the *rbcL* and Rubisco space sequences have provided evidence that the current morphological classifications and the molecular phylogeny are incongruent also at family level. For example the clade *Delamarea/Hecatonema/Punctaria* is highly supported in all their trees; these taxa are traditionally placed in the *Delamaraceae*, *Ectocarpaceae* and *Punctariaceae*. However, Siemer & al. (1998) concluded that before a revised classification can be provided, a significantly increased taxon sampling is needed.

Kogame & al. (1999) showed that the molecular phylogeny of some species was not in agreement with the normal classification of the *Scytosiphonales*. *Chnoospora implexa* (*Chnoosporaceae*) was in a clade with *Hydroclathrus clathratus*, *Rosenvingea intricata* and *Colpomenia sinuosa* (*Scytosiphonaceae*). These authors questioned seriously the monophyly of the genera *Colpomenia*, *Scytosiphon* and *Petalonia*. Species of these genera did not form clades and were scattered in their overall consensus tree. The delineations of these genera have been ambiguous (based on the external morphology and structure of erect thalli). However, there are morphological characters of the prostrate sporophytes, such as thallus structure and presence or absence of plurilocular zoidangia, that were con-

gruent with the molecular phylogeny. According to these characters Kogame & al. (1999) distinguished four groups:

- (Group 1) *Scytosiphon gracilis* and *Petalonia zosterifolia* (*Scytosiphonaceae*) which have prostrate thalli identical to the minute alga *Compsonema saxicolum* (*Myrionemataceae*).
- (Group 2) *Petalonia fascia*, *P. binghamiae* and *Scytosiphon tenellus* which have discoid prostrate *Stragularia*-like thalli (*Ralfsiaceae*).
- (Group 3) *Chnoospora implexa*, *Hydroclathrus clathratus*, *Roseningea intricata* and *Colpomenia sinuosa* with prostrate thalli that produce plurilocular zoidangia.
- (Group 4) Two species of *Colpomenia*, four species of *Scytosiphon* and three species of *Petalonia* generally have not been reported to possess plurilocular zoidangia on prostrate thalli.

Kogame & al. (1999) concluded that these features are likely to be more important taxonomic criteria at the genus or family level in the *Scytosiphonales* than is the morphology of the erect gametophytes. These authors pointed out that the knowledge of the prostrate thallus morphology is still insufficient, and molecular phylogenetic study of additional species is needed.

3.- Is *Ralfsiales* a good order or should it be included in *Ectocarpales*?

Nakamura (1972) established the order *Ralfsiales* (*nomen nudum*, because he did not provide a Latin diagnosis) for filamentous taxa with discal type of germination pattern, a single parietal plate-like plastid, lacking a pyrenoid and an apparent isomorphic haplodiplophasic life cycle (*Ectocarpus*-type). The only difference with *Ectocarpales* is the absence of pyrenoid.

This order was accepted by Bold & Wynne (1978) and Tanaka & Chihara (1980, 1982). Others authors did not recognise this order: John & Lawson (1974), Russell & Fletcher (1975), Parke & Dixon (1976), South (1976) and Nelson (1982) who recommended discontinuance of the *Ralfsiales* because of "inconsistencies in its delimitation".

Trough a study of partial SSU of rDNA sequences, Tan & Druehl (1994) showed that *Ralfsiales* and *Ectocarpales* were separate orders. They suggested that *Ralfsia fungiformis* and *Analipus japonicus*, belonged to the clade of brown algae lacking a pyrenoid and were members of the advanced orders.

Rousseau & al. (2001) showed that *Nemoderma tingitanum* (*Ralfsiales*) had no clear affinity to any other group of *Phaeopyceae*.

In conclusion we can recognize the order *Ralfsiales* as a different order from *Ectocarpales*, but is still to be clarified which taxa must be included in this order. For example *Stragularia* and *Ralfsia*, two genera classically considered very close and even synonymous are situated now in *Ectocarpales* and in *Ralfsiales* respectively.

4.- Should the *Cystoseiraceae* be included in *Sargassaceae*? Should *Cystoseira* be divided into several genera?

Within the *Fucales* Saunders & Kraft (1995), on the basis of molecular data (partial SSU rRNA sequences), questioned the maintenance of *Cystoseiraceae* and *Sargassaceae*

as separate families. The main morphological difference between these two families is the position of vesicles and receptacles, which are axillary in *Sargassaceae* but axial in *Cystoseiraceae* (Jensen 1974) and the process of production of the oosphere in the oogonium. In *Sargassaceae* seven of the eight nuclei formed in the oogonium degenerate after fusion of gametes and in *Cystoseiraceae* the seven nuclei are extruded before fusion of the gametes.

However, we can find some species with characters of the two families, for example Horiguchi & Yoshida (1998) showed that in *Myagropsis*, receptacles are in an axial position as in the *Cystoseiraceae* but the oosphere was produced according to the process known in the *Sargassaceae*. These authors concluded that the use of the branching mode to separate the *Cystoseiraceae* from the *Sargassaceae* is artificial.

Rousseau & Reviere (1999b) combining the information obtained from partial SSU and LSU rDNA sequences pointed out that *Sargassaceae* and *Cystoseiraceae* formed an extremely well supported clade. In this clade, the sargassacean representatives studied (*Sargassum*, *Turbinaria* and *Antophycus*) formed a monophyletic group, whereas the cystoseiracean representatives (*Cystoseira*, *Bifurcaria*, *Carpoglossum*, *Caulocystis*, *Halidrys* and *Cystophora*) appeared paraphyletic.

According to Rousseau & Reviere (1999b) the large group *Sargassaceae-Cystoseiraceae* corresponds to only one family and it should be named *Sargassaceae* Kützing (1843) *emend.* De Toni (1895). The diagnostic characters for this family are the following: a single apical cell, a three-sided apical cell in cross-section, one egg per oogonium (*Bifurcariopsis* with four eggs should be considered as *incertidae sedis*), spermatozooids with an anterior cilium longer than the posterior one, and forming a 90° angle to it.

According to Rousseau & al. (1997) the genus *Cystoseira* appear to be polyphyletic but further investigations are needed before splitting it into several genus. For the resolution of this problem, the use of terpenoids, as taxonomic markers (Valls & al. 1993; Amico 1995; Valls & Piovetti 1995) can be a good complement to the molecular data.

5.- Where should the *Phyllariaceae* be situated? *Alariaceae*, *Lamiariaceae* and *Lessoniaceae* should only be included in *Laminariales*?

The order *Laminariales* includes six families situated in two groups: The PCP group that includes *Phyllariaceae*, *Chordaceae* and *Pseudochordaceae* and the ALL group that includes *Alariaceae*, *Lamiariaceae* and *Lessoniaceae*. The differences between the two groups are: meiospores with an eyespot in the first group and without in the second, the lack of translocation elements in PCP and its presence in ALL and finally the two family sets have different sexual pheromones (Druehl & al. 1997).

Tan & Druehl (1996) studying the SSU of rDNA suggested that *Sporochnales*, *Desmarestiales* and *Laminariales* formed a complex separated from *Ectocarpales*, *Scytosiphonales* and *Fucales*, although that *Laminariales* is parenchymatous and *Sporochnales* and *Desmarestiales* pseudoparenchymatous. They suggested also that *Laminariales* was paraphyletic.

Druehl & al. (1997) showed that within *Laminariales* the ALL complex (*Alariaceae*, *Lamiariaceae* and *Lessoniaceae*) make a very consistent clade as already suggested by Saunders & Druehl (1993).

Reviere & Rousseau (1999) pointed out that the ALL group should be considered as the

Laminariales sensu stricto. Although Druehl & al. (1997) did not suggest merging these three families, but this would appear logical on a molecular basis and on a traditional basis. The *Phyllariaceae* will likely become a separate order, however, sequences of *Saccorhiza* and *Phyllariopsis* are needed before any nomenclatural decision be taken. *Chorda* and *Halosiphon* are likely to be placed in monotypic orders too.

Sasaki & al. (2001) studied the phylogenetic relationships of several members of *Laminariales* and *Tilopteridales* comparing Rubisco gene and rDNA (SSU and LSU) sequence data. These authors pointed out, the presence of a large monophyletic group that included the *Sporochnales*, *Desmarestiales*, *Tilopteridales*, *Halosiphonaceae* and *Phyllariaceae* and proposed four different options for taxonomic treatment of these entities: (1) inclusion of all these taxa in *Laminariales*; (2) recognition of two orders - *Laminariales* (including the ALL group, *Chordaceae*, *Pseudochordaceae* and *Akkesiphycaceae*) and *Tilopteridales* (including *Tilopteridales sensu stricto*, *Halosiphonaceae*, *Phyllariaceae*, *Desmarestiales* and *Sporochnales*); (3) recognition of three orders - *Laminariales* (including the ALL group, *Chordaceae*, *Pseudochordaceae* and *Akkesiphycaceae*), *Tilopteridales* (including *Tilopteridales sensu stricto*, *Halosiphonaceae* and *Phyllariaceae*), and *Desmarestiales* (including *Desmarestiales* and *Sporochnales*); (4) a four-orders system, similar to (3) but with retention of the *Sporochnales* as distinct from the *Desmarestiales*. Among the four possibilities and until new studies were carried out, these authors favoured the four-orders system.

In conclusion we can consider that the *Phyllariaceae* are included in the order *Tilopteridales*, and the order *Laminariales* consists of the ALL group and the families *Chordaceae*, *Pseudochordaceae* and *Akkesiphycaceae*, but more studies are needed.

After the revision of the current situation of the class *Phaeophyceae* we can point out that molecular techniques have allowed us to clarify some taxonomical problems, as is the case of the redefinition of the order *Ectocarpales* or the inclusion of *Cystoseiraceae* in *Sargassaceae*. But, at the same time, this revision shows that more studies are needed, and not only from a molecular point of view, but mainly from a biochemical, ultrastructural and morphological one. Concerning biochemical characters, the knowledge of polyols, lipids and secondary metabolites distribution within the brown algae could help to resolve taxonomical problems. Concerning ultrastructure, the correlation between pyrenoid type and phylogeny is evident, but also the ultrastructure of the motile cells, specially that of the flagellar apparatus, is potentially of high phylogenetic value. Finally, although morphological characters of the vegetative and reproductive structures have been the first to be studied, many lacunas exist still in their knowledge, as for example in the case of the life cycles of numerous species. We wish to emphasize that morphological characters should continue being the base of the taxonomy and biochemical and molecular data should complete the information obtained from morphological data.

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