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Taxonomy of Rhodophyta with particular reference to Mediterranean species

Abstract

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Most taxonomists have moved to systematics in our days, but this does not apply for the Mediterranean workers who still are confronted with the inheritance of a large number of poorly known taxa and a complex flora that includes elements of several different origins. The first task will keep its byzantine status as long as no serious attempt is made to catalogue the literature published in some ten languages and start the typification of the hundreds of valid names described since the Linnean period. The second task, to identify and circumscribe the taxa, necessitates a broad comparative approach that local workers have only recently realised. The taxonomy of red algae, having its roots in the Mediterranean and being mainly based on features of the gonimoblast development and the presence/absence of an auxiliary cell, as originally founded by Schmitz and Oltmanns and later refined by Kylin and his students, remains a challenge. While molecular systematics straggle to guide us in the complex world of these over a billion years old organisms, our understanding of taxon relationships will remain based on structural diversity for many years to come. Such data range from thallus morphology and reproduction to ultrastructure of cell components. We need to enrich and update this enormous bank of information continuously, applying modern technologies but also keeping the Linnean classification system that has proven efficient and on which taxonomy relies upon.

Introduction

The fossil record indicates that the red algae are the oldest multicellular plants dating since the Proterozoic (1.25-0.75 BYA; Butterfield & al. 1990). The molecular studies show that they are the most diverse eucaryotes (see Freshwater & al. 1994), and hence the Swede Harald Kylin (1879-1949) must be recognized as one of the greatest taxonomists of all times. Forty-five years ago, Kylin (1956) monographed the red algae describing some 680 genera and including some 3700 species. Presently, these numbers have slightly increased to 828 genera and about 4500 species, and the question is where the high diversity of red algae remains still hidden.

Several answers seem plausible. Firstly, it is clear that we have underestimated the uniqueness of many structures by describing a large number of similar characteristics as homologies. For example, auxiliary cells are known in the *Ceramiales*, *Corallinales* and several other orders but it is now apparent that these cells, although seem to function in a similar way, are not homologous but have developed independently several times. Secondly, it is also apparent that a large number of taxa have gone extinct, as for example it is documented in the *Corallinales* where the fossil record shows an impressive number of extinct genera and one family (see Woelkerling 1988). Therefore, many species of the present-day rhodophytes could simply be relics, while other (like members of the Ceramiales) may have undergone explosive radiations in the past 20 MY. A third explanation that counts for the primitive *Bangiophyceae* is that molecular diversity is not always expressed structurally, as it is apparently the case in the genera *Porphyra* C. Agardh and *Bangia* Lyngbye.

Taxonomy of *Rhodophyta*

Features of the pre- and post-fertilization development [originally studied by the French Bornet and Thuret and later used in the classification system proposed by the Germans Schmitz & Hauptfleish (1896) and Oltmanns (1904)] remain widely accepted in the description of classes, orders and families. These features include the type of carpogonium with regard to its position and structure (modified vegetative cells *vs.* terminal cells of branches and provided with trichogynes), whether an auxiliary cell exists (or not), and the way by which the zygote is transferred (or not) to one (i.e. procarpic condition) or several auxiliary cells that form carposporophytes.

For example, in the *Corallinales*, there is a report that the zygote is transferred externally to an auxiliary cell that is placed below the poly-carpogonial system and later fuses with neighboring somatic cells before the production of carposporangia (Lebednik 1977). In the *Ceramiales*, the auxiliary cell (or cells) develop after the fertilization, but there are also reports where auxiliary cells are lacking in some species or genera. In the *Gigartinales sensu lato*, the situation is more variable but in the majority of families we have non-procarpic fertilizations where the zygote is successively transferred to a series of auxiliary cells.

With the advent of the electron microscope a new period started as the ultrastructure of cells could be investigated. The study of pit-plugs (Pueschel & Cole 1982), has proven to be particularly significant as at least 6 different types were discovered. A cell membrane covering the proteins of the plug was found to be characteristic for the class *Florideophyceae* (segregating it from the *Bangiophyceae*), while within the *Florideophyceae*, outer cap layers were found in a group of 6 orders distinguishing them from a group that lacks inner cap layers. Significant was also the finding of congruence between these ultrastructural characteristics of pit-plugs and a gene phylogeny based on the 18 S rDNA (Choi & al. 2000).

The Mediterranean Species

The taxonomy of red algae in general has no major impact on the taxonomy of Mediterranean species, because we do not have Mediterranean endemics beyond the level of tribe (see Halosieae Cormaci & Furnari 1994). On the other hand, several Mediterranean species are types of genera and families, and therefore their identity critically affects the status of the relevant taxa.

According to my count some 200 genera and about 550 species of red algae are currently recorded in the check-lists of the Mediterranean flora. These numbers are slightly higher than those in the NE Atlantic (where 181 genera and 509 species are recorded; Guiry pers. comm.), but lower than those in the Central Atlantic (where 225 genera and 655 species are recorded; Wynne 1998). Yet, it must be noted that several other Mediterranean taxa described since the time of Linnei and Agardh remain untypified and taxonomically unclarified and to what extent these poorly studied species are endemics or synonyms is unknown.

The majority of species of the present-day flora are common for the Mediterranean-Atlantic region, and their biology is mostly known from studies of Atlantic material. While workers focus their studies on the introduced species, less attention is paid on the Mediterranean endemics whose number is estimated to be between 20 and 40 % of the flora. Three scenarios are plausible for these endemics:

1) they represent species with unknown wider distributions outside the Mediterranean Sea,
2) there are true endemics that evolved after the Messinian period and these should be called neoendemics, and
3) there are relics from the Tethyan (or Palaeotethyan) period and these should be named palaeoendemics.

Some examples that illustrate cases of these three groups will be given.

Balliella cladoderma (Zanardini) Athanasiadis

This is a deep water species considered to be endemic, but it was recently recorded also from the Azores (Athanasiadis 1996a: 42). One of its distinctive features is the dark staining, typical roundish cells (known as gland cells), that are distally connected to periaxial cells abaxially and/or adaxially. Ontogenetic studies in the red algae are extremely poor, and this also applied to the origin of these gland cells, until recent observations revealed that these cells are not produced in situ (i.e. from periaxial cells) but are cut off from axial cells and subsequently are laterally transferred following the part of cell wall that forms the daughter (periaxial) cell. Because in the majority of the *Ceramiales* mature carpogonial branches have the same (abaxial) position on periaxial cells, the development of carpogonial branches was investigated in *B. cladoderma* and an identical ontogenetic pattern was demonstrated (Athanasiadis 1996a, fig. 8A). Axial procarps were also found sporadically in some other genera (Athanasiadis 1996a, fig. 15G, 88G), while it should be mentioned that *Warrenia* Harvey is the only genus in the *Ceramiales* where carpogonial branches develop and remain permanently on axial cells. The significance of axial *vs.* periaxial cells in the evolution of red algae in general remains to be investigated.

Nemastoma dichotomum J. Agardh

This is a sublittoral endemic species, that is the generitype and the type of the family

Nemastomataceae. Yet, the species delimitation in *Nemastoma* J. Agardh remains unresolved. Three other species are described from the Mediterranean, a fourth species is known from the Canary Isles, while there are also records of the genus from Ireland and Sweden (Athanasiadis 1988, 1996b). The family *Nemastomataceae* has been traditionally used as one of the classical non-procarpic examples in the *Gigartinales*, where a connecting filament leads the zygote to several auxiliary cells successively. This was based on early studies of *Nemastoma* from the western Mediterranean and the Atlantic, and not from its type locality in the N. Adriatic Sea. In a study of Aegean and Adriatic material (including the type specimens), it was found that no connecting filaments exist, and that auxiliary cells and carpogonial branches are borne on specialised rhizoidal filaments (Athanasiadis 1988). Moreover in mature carposporophytes, no fusion (or other type of zygote transfer) between carpogonia and auxiliary cells were observed, so that the occurrence of parthenogenesis was postulated in these Aegean and Adriatic populations. Whether there are more differences between eastern and western Mediterranean plants referred to *N. dichotomum* remains to be investigated, like the life history of the genus where tetrasporophytes remain unrecorded (apart from a spurious report by Reinsch in 1875).

Tenarea tortuosa (Esper) Bory

In the Mediterranean, the littoral zone is characterised by the presence of several endemics and, given the adverse conditions that algae in general experience in that zone, such entities should rather be regarded as neoendemics (see Athanasiadis 1996b: 239). One of these endemics is the monotypic genus *Tenarea* Bory that is restricted to the southern Aegean and eastern Ionian Seas. The generic status of *Tenarea* has been questioned, because *T. tortuosa* is anatomically identical to the genus *Titanoderma* Nägeli differing only by a strictly back-to-back growth of its thallus. Some authors have interpreted this structure as an integral multilayered unit with isobilateral organization, although the two parts are not connected by secondary pit plugs, which is characteristic for any integral thallus in the subfamily *Lithophylloideae* (where *Tenarea* undoubtly belongs). If *Tenarea* is generically distinct from *Titanoderma,* that has a worldwide distribution and is known from fossils dated since 38 MY ago, *Tenarea* must be a Tethyan relic (Athanasiadis 1995). The alternative hypothesis is that *Titanoderma* is paraphyletic and that *Tenarea* is an advanced member of *Titanoderma.* The situation is more complex in view of two other Mediterranean endemics of the genus *Goniolithon* Foslie (which have been placed in *Titanoderma* by some authors), while molecular studies have indicated a close relationship between *Titanoderma* and the geniculate genus *Amphiroa* Lamouroux (Bailey 1999). The generic status of *Tenarea* and its origin, remain unresolved pending a thorough phylogenetic investigation of the entire subfamily *Lithophylloideae.*

Mesophyllum macedonis Athanasiadis

Mesophyllum macedonis Athanasiadis (1999) was recently described as a new Mediterranean endemic from the North Aegean Sea. The comparative study indicated that the new species was most similar to far remote taxa from the Caribbean and the Pacific than to Mediterranean and NE Atlantic congeners. Hence, the hypothesis that *M. macedo-*

nis could be a Tethyan relic was supported as the most parsimonious scenario, explaining the disjunct and spot-distribution of this new species. Presently, a revision of the genus *Mesophyllum* and related genera is under investigation (see Adey & al. 2001) in order to establish cladistically taxon-relationships and to point out the putative sister-taxa of *M. macedonis*. Obviously this work is far more complex, as it has to consider species of *Mesophyllum* on a worldwide basis, but it is the only way we have to establish taxon-relationships and confirm biogeographic hypotheses of Tethyan relics.

Other putative Tethyan relics

Other species that should be included in the list of putative palaeoendemics are the Aegean *Beckerella mediterranea* Huvé that has its congeners in the Indo-Pacific, while other putative Tethyan relics are *Peyssonnelia immersa* Maggs & Irvine (known only from the North Aegean and the southern British Isles; see Athanasiadis 1987), *Mesophyllum macroblastum* (Foslie) Adey (known only from the western Mediterranean and southern Australia), and *Lithophyllum racemus* (Lamarck) Foslie. The latter species is a common coralline forming rhodoliths in the NE. Atlantic and the Mediterranean Sea, and it represents the first living alga that has been formally synonymised with fossil taxa described from deposits in Europe dated since the Burdigalian (16-22 MYA; Basso & al. 1996).

Conclusions

Knowledge of the Mediterranean flora is significant not because this region is a goldmine, like the Indo-Pacific where we still discover new genera, families and orders, but because it is the place that has undergone profound geological and climatic changes since it was created in the Palaeozoic. The present flora has many elements in common with the neighboring Atlantic, and has also received several alien species in the past 100 years, but most significantly it includes palaeoendemic and neoendemic species, and clarifying the origin of these elements can help us understand the evolution of red algae in general.

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