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THE SYSTEMATICS OF SUBAERIAL ALGAE

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1. Introduction

Over the past millions of years the land on our planet has been the testing ground for many experiments or, more dramatically, the battleground for many invasions. A myriad of ancestral plant forms came from the sea and lakes to exploit the terrestrial environment. Those life forms were algae, simple photoautotrophic organisms that eventually prepared the land for the terrestrial flora and fauna that were to follow. They successfully conquered the land in terms of making it a useable new habitat for themselves and developed new forms and processes to adapt. Those plant “invaders” or “conquerors” are represented today by algae living among us populating soils and other terrestrial habitats.

Most of the photosynthetic organisms that occur nowadays in aquatic habitats belong to this heterogeneous category generally called algae. These organisms are phylogenetically unrelated, or only distantly related, and differ enormously in terms of gross morphology, ultrastructure, biochemical traits and many other important features. Several lineages of algae successfully colonized terrestrial environments. Although from the ecological point of view the most important conquest of land was that of the green algae of the streptophyten lineage (those that gave rise to land plants), several other groups did succeed in becoming terrestrial. Representatives of these lineages are presently commonly found in terrestrial environments and unlike land plants, have maintained a very similar morphology to that of their aquatic relatives. The Charophyta and the Chlorophyta *sensu stricto* are the two groups of eukaryotic algae that along with the prokaryotic Cyanobacteria (blue-green algae) have been most successful in colonizing terrestrial environments.

Subaerial algae are terrestrial algae that live on stable exposed surfaces above the soil (Nienow, 1996), they are perhaps the most obvious, and yet most overlooked, group of algae. They produce rich growths (in the form of green, red, brown or black streaks) on a wide range of surfaces, including natural rocks, urban walls, woodwork, metal, bark and leaves of trees and hair of animals. Subaerial algae are particularly abundant and widespread in areas with humid climates sometimes causing significant economic problems. This problem is serious in tropical areas (such as Singapore), where legislation forces owners of

houses to keep their homes algae free! In countries with ancient and rich cultural heritage (i.e. Spain, Italy and Greece), the effects of algal deterioration on monuments has been studied in detail and great efforts have been made to limit their development. Cyanobacteria are well-known agents of biodeterioration of monuments in tropical regions (Gaylarde and Gaylarde, 2000), but remain underexplored and relatively unknown in terms of modern systematic assessments (Crispin and Gaylarde, 2004). Often overlooked in these habitats, the total diversity of these taxa is typically underestimated (Ferris et al., 1996). In this report, we summarize the current state of knowledge of the diversity and systematics of the subaerial algae, with special attention to some important types of habitats (in particular the tropical rainforest), for which the subaerial algal flora is poorly known and in urgent need of further investigation.

2. Floristics

Subaerial algal studies are available mostly from Europe with very limited coverage from other continents, although in the last few decades Antarctica has been studied in great detail (e.g. Broady, 1996). In terms of habitats, natural rock surfaces are the most extensively studied from Central Europe (e.g. Frémy, 1925; Jaag, 1945; Golubic, 1967), South America (e.g. Büdel, 1999), North America (e.g. Johansen et al., 1983), Africa (e.g. Frémy, 1930; Büdel, 1999) and Asia (e.g. Fritsch, 1907a, b). Algae growing on concrete and other artificial surfaces have gained great attention in the last decades, due to their biodeterioration effect for both temperate (e.g. Ortega-Calvo et al., 1991; Gaylarde and Gaylarde, 2000; Rindi et al., 2003; Rindi and Guiry, 2003, 2004) and tropical regions (e.g. Wee and Lee, 1980). Epiphytic algae occur on a variety of plant substrata, with tree bark inhabiting forms the best known and studied in Europe (e.g. Schlichting, 1975), Africa (e.g. Printz, 1921), Asia (e.g. Fritsch, 1907a, b; Islam, 1960; Handa and Nakano, 1988; Nakano et al., 1991), South America (e.g. Möbius, 1888; Lagerheim, 1890; Schmidle, 1901) and North America (e.g. Cox and Hightower, 1972; Wylie and Schlichting, 1973; Dillard, 1989; John, 2003). Little information exists about algae growing on animals; although sloths (Weber Van Bosse, 1887; Thompson, 1972), spiders (Cribb, 1964), lizards (Gradstein and Equihua, 1995), polar bears (Lewin and Robinson, 1979), prosimians (Sanderson, 1963) and birds (Schlichting et al., 1978) have all been found to support subaerial algae.

3. Biodiversity and Systematics

The vast majority of the photosynthetic microorganisms occurring in terrestrial habitats belong to four groups: the Cyanobacteria (Komárek, 2003a), the Chlorophyta and the Charophyta (sensu Lewis and McCourt, 2004) and the Heterokontophyta (sensu Andersen, 2004). From a numerical point of view,

the prokaryotic Cyanobacteria and the eukaryotic Chlorophyta account for the largest numbers of species currently described. The Chlorophyta consist of four main lineages. Three of these, Chlorophyceae, Trebouxiophyceae and Ulvophyceae, form well-supported monophyletic groups and are usually separated at the class level (Lewis and McCourt, 2004; see Adl, 2005, for recent classification). The fourth lineage, Prasinophytes, is basal and it has been shown to be non-monophyletic. Most species of subaerial Chlorophyta are currently ascribed to the class Trebouxiophyceae, which includes several widespread genera (e.g. *Chlorella*, *Myrmecia*, *Prasiola*, *Stichococcus* and *Trebouxia*). The Chlorophyceae are mostly freshwater algae, but the class includes also some common subaerial genera (i.e. *Bracteacoccus* and *Chlorococcum*). The Ulvophyceae is largely formed by the marine green algae (Sluiman, 1989); however, it also includes an important lineage of subaerial algae, the order Trentepohliales (Lopez-Bautista and Chapman, 2003). Recently, a second ulvophycean subaerial lineage, represented by the genus *Spongiochrysis* (order Cladophorales), has been discovered (Rindi et al., 2006). The Charophyta are members of the other major lineage of green plants (the Streptophytes) and the phylum includes the closest relatives to the algae that gave rise to the land plants. Charophyta occur mostly in freshwater habitats but the phylum also includes some subaerial taxa, including one of the most widespread genera, *Klebsormidium*. The Heterokontophyta are a large group of eukaryotic algae separated into several classes and varying greatly in gross morphology. Subaerial forms are found in two different classes, the Bacillariophyceae, or diatoms, and the Xanthophyceae or yellow-green algae. To date, the main taxonomic treatments concerning algae of terrestrial habitats are still entirely based on traditional morphological concepts (Ettl and Gärtner, 1995). Early phycologists described several subaerial algae that produce populations recognizable with the unaided eye (e.g. Agardh, 1824; Kützing, 1849; Rabenhorst, 1868). Most subaerial algae, however, are small in size and occur in nature in only small amounts; they can therefore be observed and examined accurately only when growing in unialgal cultures (John, 1988). Thus, the number of described taxa increased considerably in the second half of the last century, with the widespread development of culturing techniques. This has particularly been the case with unicellular green algae, for which many taxa have been described entirely on the basis of cultured material (studies by Ettl, Hindák, Komárek and co-workers from Europe, and by Brown, Bold, Deason, Trainor and co-workers in the USA).

3.1. SYSTEMATICS OF SUBAERIAL CYANOBACTERIA

Although the cyanobacteria are some of the most widely distributed, ubiquitous organisms on the planet they are also historically understudied. Among the most prevalent and abundant algal lineages with subaerial members, cyanobacteria serve an important role in community succession (Gerrath et al., 2000). Growing

on such diverse habitats as rocks, soils (Jaag, 1945), tree bark (Desikachary, 1959) and dripping walls (Johansen et al., 2004), the taxonomy and biodiversity of these taxa is still mostly unknown (Komárek, 2003b). Among the oldest recorded fossils, the cyanobacteria were significantly involved in the formation of life on the planet as some of the earliest colonizers (Schopf, 1996). Unfortunately, they are also among the most poorly characterized and catalogued organisms, in part due to the prevailing belief among classic monographers (i.e. Geitler, 1932; Desikachary, 1959) that many species are cosmopolitan. However, recent studies have noted that these organisms may not be as cosmopolitan as previously assumed (e.g. Komárek, 1999) and endemic taxa are currently being described from newly explored habitats, especially subaerial ecosystems (e.g. Flechtner et al., 2002, Casamatta et al., 2005, Casamatta et al., 2006, Kastovska et al., in press). However, cyanobacterial diversity is still underreported due to difficulties in employing morphological characters to identify species and a lack of specialists exploring novel habitats. Thus, the subaerial habitats are a nearly unexplored treasure of cyanobacterial biodiversity.

The taxonomy of cyanobacteria has gone through major rearrangements in the last two decades, culminating in the recent revisions of Komárek and Anagnostidis (Anagnostidis and Komárek, 1985, 1990; Komárek and Anagnostidis, 1989, 1999, 2005). Their approach is based on a combination of morphological, ultrastructural, biochemical and (in part) genetic data and has proposed a substantial rearrangement in comparison with the traditional (i.e. Geitler, 1932) and the simplified Drouetian system (Drouet, 1981). Many new genera have been erected and the circumscription of many traditional genera (including some widespread in subaerial habitats, such as *Gloeocapsa*, *Lyngbya* and *Phormidium*) have been substantially rearranged. In the last 15 years, an increasing number of investigations have studied the phylogeny of the cyanobacteria, mainly using 16S rDNA gene sequences (Wilmotte, 1994; Otsuka et al., 1999; Wilmotte and Herdman, 2001; Suda et al., 2002; Casamatta et al., 2005; Rajaniemi et al., 2005). This molecular approach, coupled with careful ecological and morphological assessments, has enabled researchers to begin cataloguing the great biodiversity undoubtedly present in this lineage.

Preliminary observations on subaerial cyanobacterial taxa have revealed several intriguing facets. First, there are many more species of cyanobacteria (particularly the filamentous Oscillatoriales and coccoid Chroococcales lineages) than are evidenced by employing traditional taxonomic keys, and consequently there are numerous new species to be described. Second, in a number of broadly defined genera, such as *Leptolyngbya*, *Microcoleus* and *Nostoc*, the 16S rRNA and 16-23S internal transcribed spacer (ITS) sequence data demonstrate that more genera must be recognized if monophyly is to be achieved. Third, ITS regions vary widely between strains, and have been informative for making systematic decisions at both the genus and species levels. Fourth, in *Leptolyngbya* the ITS regions are not always congruent with phylogenies based on 16S rRNA sequences, and we suspect that at least some of the absence of congruence is due

to multiple operons within genomes. Fifth, when distinctive habitats of geographically/climatically isolated regions are studied closely, they always have endemic species of cyanobacteria. For example the Nostocacean lineage, composed of members that may produce nitrogen-fixing specialized akinete cells, is among the most common components of subaerial algal communities, and two new endemic genera in this group have recently been described: *Rexia* (Casamatta et al., 2006) and *Mojavia* (Kostakova et al., in review). Thus, as these habitats are explored we anticipate that more new taxa, as well as emendations of some existing genera of cyanobacteria are anticipated from the subaerial habitat (Casamatta et al., 2005; Kastovska et al., in press).

3.2. SYSTEMATICS OF SUBAERIAL CHLOROPHYTA

The taxonomy of the green algae is also in a phase of major rearrangements. The existence in the Chlorophyta of four main groups, three of which represent monophyletic lineages (Chlorophyceae, Trebouxiophyceae and Ulvophyceae), is now widely accepted. Arrangement at all other taxonomic levels, however, is still unclear. The flood of molecular data collected in the last two decades has given rise to dramatic modifications at every level of classification, and chlorophytan taxa widespread in terrestrial habitats have been among the most affected. A number of traditional orders (Chlorellales, Chlorococcales, Chlorosarcinales) originally circumscribed using vegetative morphology, are now known to contain phylogenetically unrelated taxa. Reclassification into different groups has taken place even at lower taxonomic levels, especially the genus level. Several common genera of subaerial chlorophytes, such as *Chlorella*, *Chlorococcum*, *Neochloris* and *Trebouxia*, have been shown to include species that in fact belong to different classes (Huss et al., 1999; Friedl and O'Kelly, 2002; Krienitz et al., 2003; Lewis and McCourt, 2004). Splitting of groups described on traditional morphological basis and erection of new genera is a general trend in the current microchlorophyte taxonomy (e.g. Krienitz et al., 2004; Buchheim et al., 2005). In the Charophyta, molecular studies have led to the recognition of six main groups (Mesostigmatophyceae, Chlorokybales, Klebsormidiales, Zygnematales, Coleochaetales and Charales), but the arrangement at lower taxonomic levels has been comparatively less affected.

Some algal groups, which are currently studied in detail in our laboratories, are selected to illustrate recent developments in the systematics of subaerial green algae.

3.2.1. *Trentepohliales*

The order Trentepohliales is a subaerial order of the class Ulvophyceae (Chapman, 1984; Lopez-Bautista et al., 2002) widely distributed in humid climates, and particularly abundant and diverse in tropical regions. They are usually found growing on leaves, tree bark, stem and fruits as well as rocks and

human constructions (buildings, fences, etc.). Conflicting hypotheses have been presented on the systematic position of this order. Phragmoplast-type cytokinesis suggested an affinity with the Charophycean lineage (Streptophytes) while the components of the flagellar apparatus suggested an affinity with the Ulvophyceae in the Chlorophycean lineage (Chlorophytes). Recent phylogenetic analyses (Lopez-Bautista et al., 2002; Lopez-Bautista and Chapman, 2003) using the nuclear-encoded 18S rDNA sequences from taxa representing both the Chlorophytes and Streptophytes unequivocally indicated that the subaerial Trentepohliales are closely related to marine ulvophycean algae in the Chlorophyta lineage. The subaerial trentepohlialean flora appears to be the sister group to the siphonous and hemisiphonous marine ulvophycean algae. As presently circumscribed, the order contains one family and six genera, which are entirely separated on morphological grounds: *Trentepohlia*, *Physolinum*, *Printzina*, *Phycopeltis*, *Cephaleuros* and *Stomatochroon*. Approximately 70 species are currently included in this order but the taxonomic position of many is uncertain. Despite their relatively simple morphology (i.e. branched uniseriate filaments) trentepohlialean taxa are a taxonomically difficult group. A highly plastic morphology is correlated to environmental factors making the circumscription of species and genera not only difficult but also confusing. More recent studies (Lopez-Bautista et al., 2006a) on the systematic of trentepohlialean taxa using 18S rDNA indicate that the morphological criteria traditionally used for the circumscription of genera and species are not correlated with phylogenetic patterns. Representatives of the genus *Cephaleuros* formed a well-supported monophyletic clade, while *Trentepohlia* resulted polyphyletic and strains of *Trentepohlia*, *Phycopeltis*, *Printzina* and *Physolinum* are assorted in several different lineages. Furthermore, nuclear DNA content analyses in Trentepohliales (Lopez-Bautista et al., 2006b) are correlated with phylogenetic advancement in the Trentepohliales with basal taxa having the smallest genomes while more derived taxa have substantially larger genomes. At the species level, *Cephaleuros virescens* is a textbook example of a common taxon considered to have a worldwide distribution in tropical and subtropical regions. However, in our phylogenetic analyses *C. virescens* seems to represent a complex of morphologically similar entities, with the real *C. virescens* (type) probably restricted to tropical South and Central America (Lopez-Bautista et al., 2006a).

3.2.2. Prasiolales

The order Prasiolales is an order of marine, freshwater and terrestrial green algae widespread in temperate regions. Although terrestrial taxa do not represent the majority of the order, they include some subaerial species that are very common and widespread in temperate regions with humid climate (*Prasiola crispa*, *P. calophylla*, *P. furfuracea* and *Rosenvingiella radicans*). The phylogenetic position of this group has long been uncertain and molecular evidence supporting their inclusion in the Trebouxiophyceae has become available only quite recently (Friedl and O'Kelly, 2002; Karsten et al., 2005). As presently circumscribed, the order

contains four accepted genera: *Prasiococcus*, *Prasiola*, *Prasiolopsis* and *Rosenvingiella*. *Prasiola* and *Rosenvingiella* are the two largest genera and their relationships have long been uncertain; for a long time it has been believed that species of *Rosenvingiella* were developmental forms of *Prasiola*. Utilizing a combination of field studies, culture experiments, and chloroplast-encoded *rbcL* sequences the relationships at the species and genus level have been recently clarified (Rindi et al., 2004). The same study model was applied to elucidate the taxonomic position of *R. radicans*, one of the most common subaerial algae in northwestern Europe. The taxonomic identity of this species has been uncertain for more than two centuries; this has traditionally been one of the most problematic aspects of the taxonomy of this group. In the past this alga has been mostly considered a filamentous form of *P. crispa*; in the last few decades, it has been frequently regarded as a terrestrial form of the marine species *Rosenvingiella polyrhiza*. Culture studies and phylogenetic analyses of the *rbcL* data consistently indicated that this alga is in fact an independent species, and the new name *Rosenvingiella radicans* was proposed for it. The combination of culture studies and molecular data showed that in this group at least three different species have an identical morphology (*R. radicans*, the filamentous form of *P. crispa* and an alga of uncertain identity indicated as *Prasiola* sp. Manchester; Rindi et al., 2004).

3.2.3. *Spongiochrysis Hawaiiensis*

During recent fieldwork in Hawaii several samples were collected from subaerial habitats. The microscopic examination of a bright golden-yellow coating occurring on the bark of many trees on several beaches along the windward coast of O'ahu revealed that they were produced by a unicellular green alga with a very unusual pattern of cell division. Production of new cells took place by a budding-like mechanism, which has been reported so far only for two genera of Trebouxiophyceae, *Marvania* (Hindák, 1976) and *Stichococcus* (a single species, *Stichococcus ampulliformis*; Handa et al., 2003). Complete 18S rDNA sequences for two populations of this alga resulted into a surprising discovery (Rindi et al., 2006). Phylogenetic analyses positioned this intriguing alga as a member of the Cladophorales/Siphonocladales clade of the Ulvophyceae. This was a discovery of enormous interest (Rindi et al., 2006) as it showed that a subaerial habit has developed in an algal group that was formerly believed to be almost entirely aquatic (the Cladophorales) and that a second subaerial lineage (beside the Trentepohliales) exists in the class Ulvophyceae. Once again, it also showed that identical morphologies and identical mechanisms of reproduction have developed independently in completely separated green algal lineages, and studies based only on morphological methods are insufficient to understand the diversity of many subaerial microchlorophytes.

3.2.4. *Klebsormidium*

Klebsormidium is one of the most common genera of terrestrial Charophyta. It consists of about 20 species of green algae occurring on soil, subaerial surfaces

and semi-aquatic habitats all around the world. The systematics of this genus has been entirely based on traditional morphology (Ettl and Gärtner, 1995; Lokhorst, 1996; John, 2002). Although molecular data are available, these have been obtained as part of investigations aimed at high-level phylogenetic relationships; the species-level relationships in *Klebsormidium* have not been examined with molecular tools. We have obtained and isolated into unialgal cultures numerous strains of this genus from subaerial habitats in a wide range of locations from Europe. Although the morphology of the field material was virtually identical and attributable to *Klebsormidium flaccidum*, preliminary experiments in culture have shown a very large range of morphological variation (Rindi, unpublished data). Whereas most strains produce only tridimensional filaments that remain completely submerged, some populations produce also a superficial layer of parallel filaments that cover completely the surface of the medium (as reported typical for the *K. flaccidum* by Lokhorst, 1996). In other strains, after a few weeks in culture the filaments get fragmented into many short fragments, giving the cultures the appearance of a green "soup." Overall, our preliminary experiments indicated that even in this group a great deal of genetic diversity is hidden behind a very similar morphology. It is evident that *Klebsormidium* is one of the genera for which comparative studies based on morphology and molecular data are most needed.

4. Tropical Rainforests

Previous investigations by earlier naturalists in tropical rainforests (Fritsch, 1922; Frémy, 1930; Gardner, 1932) were not specifically focused on the subaerial habitats and did not attempt to provide an inventory of algal diversity in such habitats. Until recently, no studies have focused specifically on these habitats and the information available is based entirely on a classical morphological approach. No investigations have thus far attempted to characterize the subaerial algal flora of these forests and to examine in detail their biodiversity using state-of-the-art methods. This is unfortunate from a practical point of view since tropical rainforests can be considered highly specialized chemical factories, with many molecules proven to be highly effective drugs or very valuable compounds (Del Campo et al., 2000, Kotake-Nara et al., 2001, Hyunsuk et al., 2005, Wu et al., 2005). Gaps in the biology and diversity of subaerial algae are even more substantial for microalgae from tropical rainforests. To present a synthesis of the biodiversity status for subaerial algae of tropical forests is difficult or even impossible (Andersen, 1992).

Rainforests are highly humid and wet, thus particularly suitable for subaerial algae. It has been largely demonstrated that rainforests, especially tropical, are among the most diverse ecosystems on the planet, and are repositories of a large number of endemic taxa (Therezien, 1985; Williams et al., 2003, Burnham and Johnson, 2004; Funk and Berry, 2005); the necessity of their conservation is

largely accepted and justified. Several taxa of Trentepohliales that have been described in the last decade were originally discovered in tropical forests (Thompson and Wujek, 1992, 1997; Neustupa, 2003, 2005); and *S. hawaiiensis*, the second known terrestrial lineage in the Ulvophyceae, was recently discovered in an environment that is essentially rainforest-like (Rindi et al., 2006). Rainforests have also been shown to be centres of diversity for many animal, plants and algae (i.e. Trentepohliales), and it is perfectly reasonable to expect that they also host a much higher diversity of subaerial algae than currently appreciated. Unfortunately, tropical rainforests are among the most endangered ecosystems in the world and are rapidly disappearing due to deforestation, climatic changes and other human activities (Bulte and Van Kooten, 2000, Williams et al., 2003, Fearnside and Laurance, 2004, Laurance et al., 2004). The risk that many tropical algal lineages will become extinct before they are discovered is largely acknowledged.

5. Morphological Convergence

It is now generally accepted that gross morphology and reproductive features do not reflect phylogenetic patterns in most groups of green algae, both in the chlorophyten lineage (Krienitz et al., 2003; Fawley et al., 2004; Henley et al., 2004; Krienitz et al., 2004; O'Kelly et al., 2004) and in the charophyten lineage (McCourt et al., 2000; Gontcharov et al., 2003). Furthermore, in several different lineages of subaerial algae, the structure of the thallus has converged towards a relatively limited number of morphological types. Consequently, a great deal of genetic diversity is often hidden behind identical or very similar morphologies. Although this is a phenomenon common to many plant and animal groups, for terrestrial green algae this makes their taxonomy particularly problematic, due to the limited number of characters useful for a reliable morphological identification. With almost no exception, subaerial green algae have a simple thallus and a reduced size. Three main types of thallus morphology (Fig. 1) are found: (i) unicellular; (ii) sarcinoid (regular packets formed by a small number of cells); (iii) uniseriate filamentous. In terms of number of species, the unicellular morphology is clearly the most widespread (Fig. 1A); this is typical of many common genera shown to be polyphyletic (*Bracteacoccus*, *Chlorella*, *Chlorococcum*, *Muriella*, *Myrmecia*, *Stichococcus*, *Tetracystis* and *Trebouxia*). The sarcinoid morphology (Fig. 1B) occurs in a more limited number of genera (e.g. *Apatococcus*, *Chlorokybus*, *Chlorosarcina*, *Desmococcus* and *Prasiococcus*) but it is characteristic of some of the most successful taxa, that is *Desmococcus olivaceus* is often reported as the most common green alga in the world (Laundon, 1985; Ettl and Gärtner, 1995). Uniseriate filaments are found in a relatively limited number of species (Fig. 1C), mainly belonging to two different groups: *Rosenvingiella* and *Prasiola* in the Trebouxiophyceae (Rindi et al., 2004) and *Klebsormidium* in the Charophyta (Karol et al., 2001; Turmel et al., 2002). *Klebsormidium*, however, is

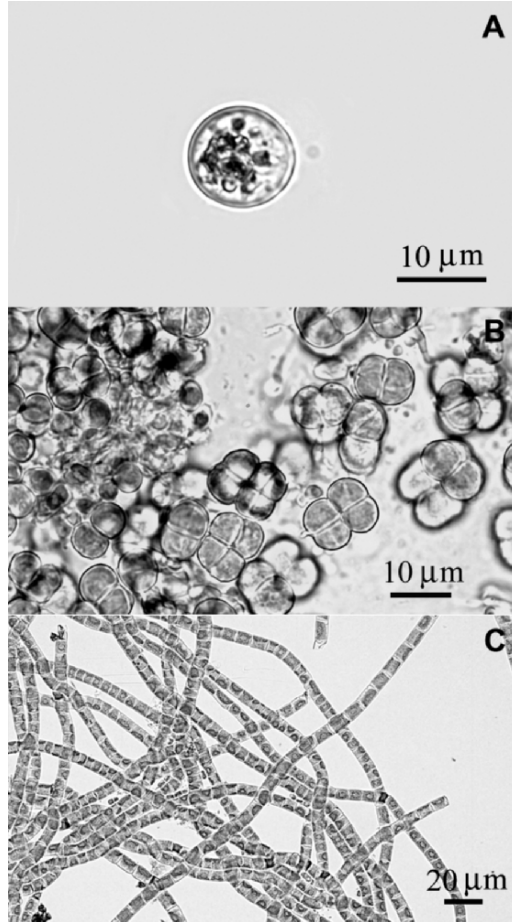


Figure 1. (A) *Spongiochrysis hawaiiensis*; (B) *Desmococcus olivaceus*; (C) *Klebsormidium flaccidum*.

one of the most successful and widespread genera on a global scale and occurs in a wide range of habitats.

Although the causes for this morphological convergence are not well understood, it is clear that a simplification of the thallus from aquatic to subaerial habitats has generally been favoured. Other adaptations include, but are not restricted to, the capacity to utilize water in the form of vapour (Lange et al., 1990, Ong et al., 1992), the production of mucilaginous envelopes retaining moisture (Nienow, 1996), the production of resistance stages such as akinetes, the production of pigments acting as a protection from solarization (Whitton and Potts, 1982, Siefermann-Harms, 1987), the production of anti-freezing compounds (Raymond and Fritsen, 2000) and the production of mycosporine-like

amino acids as protection from UV radiation (Lange et al., 1990; Karsten et al., 2005). Since most terrestrial algae cannot survive in extremely dry conditions, it is therefore reasonable to assume that the possibility of a wide dispersal, allowing colonization of habitats with favourable conditions, plays a fundamental role in the survival of these organisms. Most studies in which algae have been isolated from air samples have shown a preponderance of small unicellular forms (Brown et al., 1964; Rosas et al., 1987; Kristiansen, 1996). It is considered that a spheroid unicell up to 12 μm in diameter, as found, for example in species of *Chlorella* and *Stichococcus*, is the ideal airborne alga (Roy-Ocotla and Carrera, 1993).

6. Conclusions

Although economically and ecologically important, subaerial algae have been largely understudied compared to marine and freshwater algae, and many basic aspects of their biology are still poorly understood. For historical reasons, most studies on diversity, taxonomy and ecology of subaerial algae have been carried out in Europe. Very few investigations, almost entirely limited to Europe, have examined comprehensively the subaerial algal flora of a certain geographical area. Studies on the taxonomy of subaerial algae are available for several groups. However, the large majority of these morphology-based investigations were conducted between the early 1800 and 1960. Work carried out in recent decades has been much more limited and has usually focused on a few, specific groups often involving biodeterioration. Amazingly, the few studies of subaerial algae in North America have yielded a wealth of putatively new taxa to science. Despite this body of information, in general the knowledge of subaerial algae is fragmentary, and even an estimate of their biodiversity is impossible at the present time. In the last 20–25 years algal systematics has changed dramatically due to the development of PCR and DNA sequencing techniques. The molecular data that are currently available for subaerial algae have been produced as part of more general studies, focused primarily on algal phylogeny at the class or order level. However, the taxonomic coverage of the molecular data currently available is still uneven; whereas large datasets exist for several algal groups, for other species or genera, even those that are very common, nothing or very little is available. For example to date no sequences have been deposited in GenBank for *D. olivaceus* and *Apatococcus lobatus*, which are the two most common subaerial green algae reported in the world (Laundon, 1985). Given these reasons, it is clear that for many subaerial algae a correct taxonomic circumscription and an understanding of their diversity would be achieved only through a combined approach, in which morphological datasets based on both field collections and cultured materials are combined with extensive datasets of molecular information. As the diversity of many groups of terrestrial algae is still very poorly understood, the availability of new collections, inventories of their biodiversity and molecular characterization is particularly urgently needed.

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