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Chapter 3

**AN OVERVIEW OF THE BIODIVERSITY AND
BIOGEOGRAPHY OF TERRESTRIAL GREEN
ALGAE**

***Fabio Rindi¹, Haj A. Allali², Daryl W. Lam²
and Juan M. López-Bautista²***

¹Martin Ryan Institute, National University of Ireland, Galway.

²Department of Biological Sciences, The University of Alabama,
Tuscaloosa, AL35487-0345.

ABSTRACT

Microscopic green algae are among the most widespread microorganisms occurring in terrestrial environments. For more than two centuries, generalizations on the diversity and biogeography of these organisms have been based entirely on morphological species concepts. However, ultrastructural and molecular data produced in the last 30 years have revealed a scenario in substantial contrast with morphological classifications. It has become clear that these organisms have been affected by an extreme morphological convergence, which has restricted their morphology to a narrow range, not indicative of their great genetic diversity. Their habit is very simple and uniform, usually referable to a few types (unicellular, uniseriate filamentous, sarcinoid colony) and offers very few characters useful for taxonomic and systematic purposes. These factors make the identification of terrestrial green algae and a correct interpretation of their biogeography very difficult. “Flagship” taxa

with easily recognizable habit are the ones for which the best generalizations are possible. Examples of such taxa include the order Trentepohliales (for the highest diversity occurs in humid tropical regions of central-south America and south-eastern Asia) and members of the order Prasiolales (which are typically associated with polar and cold-temperate regions). In consideration of the recent developments, it is clear that many basic concepts about the biogeography of terrestrial green algae will have to be reconsidered critically. A deep understanding of this topic will require considerable work on many aspects of the biology of these organisms (systematics, distribution, dispersal, physiology), in which species circumscriptions based on molecular data will be a mandatory requirement.

INTRODUCTION

The bulk of organisms performing oxygenic photosynthesis in terrestrial environments represents a very heterogeneous and evolutionarily diverse assemblage. Although vascular plants are the most conspicuous and morphologically complex among these organisms, this group includes also a great number of microscopic algae. Species of microalgae occur virtually in every type of terrestrial habitat, including the most extreme, such as walls of urban buildings (Rindi, 2007a), biotic crusts in hot deserts (Lewis & Flechtner, 2002; Flechtner, 2007), Antarctic snow (Broady, 1996) and air at 2,000 m height (Sharma *et al.*, 2007). They are small in size (mostly 5-50 μm) and characterized by a simple morphology, often unicellular; for this reason, most species are not observable as individual specimens and become visually detectable only when producing large populations, typically in the form of black, green, red or brown patches (Figure 1).

Terrestrial microalgae belong primarily to three different evolutionary lineages: the blue-green algae (or Cyanobacteria), the green algae (Chlorophyta and Streptophyta) and the diatoms (Bacillariophyceae, Ochrophyta). From a numerical point of view, the green algae and the blue-green algae include the majority of the species described. It is generally reported that blue-green algae represent the main component of the terrestrial microalgal vegetation in tropical regions, whereas green algae represent the dominant element in temperate regions (Fritsch, 1907; John, 1988). In general, however, patterns of geographical distribution in terrestrial algae are poorly understood, mainly because the diversity of these organisms is itself poorly

understood. Here, we discuss this topic for terrestrial green algae, reviewing the information available and pointing at directions for future work.



Figure 1. Examples of assemblages of terrestrial algae. Figure 1A: building covered by black stripes formed by cyanobacteria (Cayenne, French Guiana). Figure 1B: population of the cyanobacterium *Nostoc commune* growing on soil, mixed with plants. Figure 1C: the green alga *Klebsormidium flaccidum* (Klebsormidiophyceae) growing at the base of a urban wall (Pisa, Italy). Figure 1D: a population of the green alga *Rosenvingiella radicans* (Trebouxiophyceae) forming a green belt at the base of a wall (Galway, Ireland). Figure 1E: *Trentepohlia rigidula* (Ulvophyceae) forming red patches on the bark of a tree (Barro Colorado Island, Panama). Figure 1F: specimens of *Phycopeltis arundinacea* (Ulvophyceae) producing orange dishes on the surface of a leaf of ivy (Ashford Castle, Ireland).

TERRESTRIAL GREEN ALGAE: DIVERSITY AND SYSTEMATICS

Green algae are photosynthetic eukaryotes bearing double membrane-bound plastids containing chlorophyll *a* and *b*, accessory pigments found in embryophytes (beta carotene and xanthophylls) and a unique stellate structure linking nine pairs of microtubules in the flagellar base (Lewis & McCourt, 2004). They are one of the most diverse groups of eukaryotes and include morphological forms ranging from flagellated unicells, coccoids, branched or unbranched filaments to multinucleated macrophytes and taxa with parenchymatic tissues (Pröschold & Leliaert, 2007). Dating based on molecular data suggests that the most recent common ancestor of all green algae may have existed 1100-1200 million years ago (Yoon *et al.*, 2004). In general, however, reconstruction of the evolutionary history of these organisms is a very speculative matter, because of the limited fossil record. Phylogenetic calibrations have been possible only for a few groups in which the presence of a calcified cell wall has produced a good fossil record, such as the marine orders Bryopsidales and Dasycladales (Verbruggen *et al.*, 2009).

From a systematic point of view, the green algae have been traditionally a difficult group. In the past the classification of these organisms has undergone several major rearrangements, due mostly to the fact that different criteria, based on different types of evidence (morphological, ultrastructural, molecular), have been adopted at different stages (Lewis & McCourt, 2004; Pröschold & Leliaert, 2007). Important advancements have been made in the last 30 years, in which new types of data have complemented the bulk of morphological information produced in the two previous centuries. The development of electron microscopy in the 70s of the last century revealed many important ultrastructural characters, which have since proved to be key features for the classification of the green algae. Mattox & Stewart (1984) proposed a new classification in which the ultrastructure of the basal body in flagellated cells and the cytokinesis during the mitosis were considered the two most important features. In the last 20 years, the advent of molecular systematics has represented a revolution for the classification of many algal groups, and green algae have been among the most affected. DNA sequence data have generally confirmed conclusions based on ultrastructure (Lewis *et al.*, 1992; Friedl & Zeltner, 1994; Friedl, 1995) and have shown that in the green algae morphological characters are often not good indicators of

phylogenetic relationships. It is now established that the green algae belong to a well-supported monophyletic group, the Viridiplantae, in which the land plants are also included (Figure 2).

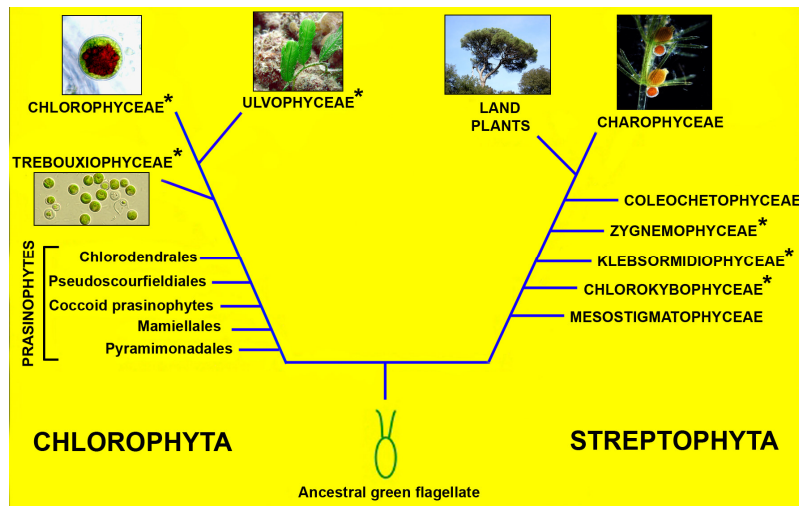


Figure 2. Schematic diagram showing the phylogenetic relationships among the major lineages of green algae based on DNA sequence data, based primarily on Lewis & McCourt (2004). Lineages of green algae including terrestrial members are marked with an asterisk.

The Viridiplantae are subdivided in two major lineages, the Chlorophyta and the Streptophyta (Bremer, 1985). The Chlorophyta include green algae in which the cells normally divide with production of a phycoplast during the cytokinesis. This lineage consists of three groups that form well-supported clades and are recognized at the level of class (Chlorophyceae, Trebouxiophyceae and Ulvophyceae), and a non-monophyletic group called Prasinophytes. The Prasinophytes represent an unnatural agglomeration of unicellular organisms whose classification is still in need of rearrangement, viewed as the form of cell most similar to the ancestral green alga (believed to be a flagellate aquatic unicell, Lewis & McCourt, 2004). The Streptophyta include the land plants and groups of green algae that produce a phragmoplast in the cytokinesis. These consist of several groups (Charophyceae, Chlorokybophyceae, Coleochaetophyceae, Klebsormidiophyceae, Mesostigmatophyceae and Zygnemophyceae) which form well-supported clades, but whose relative relationships are not yet well-resolved.

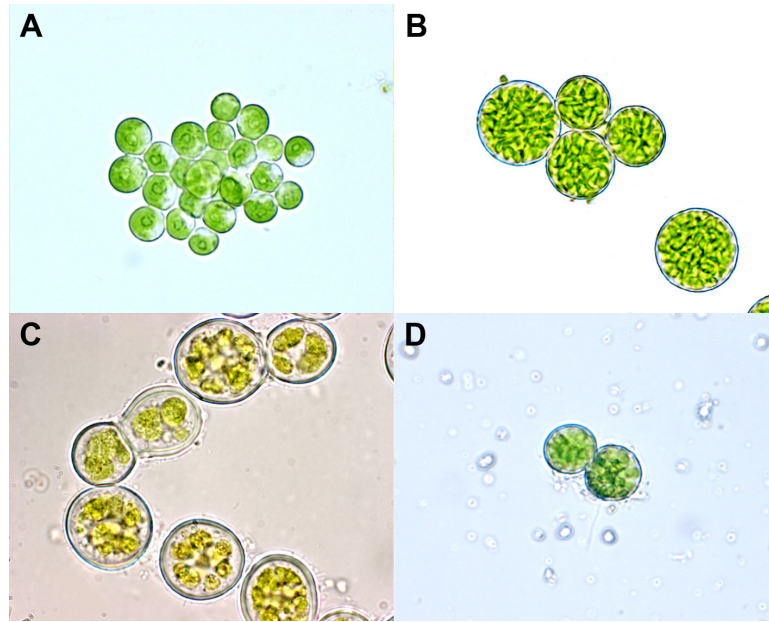


Figure 3. Examples of terrestrial green algae with unicellular morphology. Figure 3A: *Chlorella* cfr. *vulgaris* (cells 7-8 μm in diameter). Figure 3B: *Dictyochloropsis* sp. (cells 10-20 μm in diameter). Figure 3C: *Spongiochrysis hawaiiensis* (cells 10-15 μm in diameter). Figure 3D: *Trebouxia* sp. (cells 9-10 μm in diameter).

About 800 species of green microalgae are known to occur in terrestrial environments. Soil is the type of habitat from which most of them have been reported (Metting, 1981); however, the range of habitats occupied by these organisms is extremely wide and includes natural rocks (Golubic, 1967), biotic crusts in deserts (Flechtner, 2007; Lewis, 2007), concrete walls (Rindi & Guiry, 2002), woodwork (John, 1988), iron rails (Schlichting, 1975), tree bark (Barkman, 1958), leaves and fruits (López-Bautista *et al.*, 2002) and hair of animals (Lewin & Robinson, 1979). Their morphology is very simple and typically referable to three different habits: 1) single cells (Figure 3; examples: *Chlorella*, *Chlorococcum*, *Stichococcus*, *Trebouxia*); 2) “sarcinoid” habit, i.e. packet-like colonies formed by a limited number of cells (Figure 4; examples: *Apatococcus*, *Desmococcus*, *Chlorosarcina*, *Chlorokybus*); 3) uniseriate filaments, either branched or not (Figure 5; examples: *Klebsormidium*, *Printzina*, *Rosenvingiella*, *Trentepohlia*). The study of terrestrial green algae has a long history, which dates back to the beginning of systematics. Some

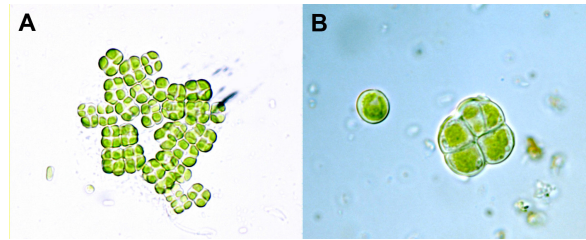


Figure 4. Examples of terrestrial green algae with sarcinoid morphology. Figure 4A: *Chlorosarcinopsis* sp. (cells 5-7 μm wide). Figure 4B: *Desmococcus olivaceus* (cells μm 4-7 wide).

species are among the earliest-known organisms, having been described by Linnaeus (1753, 1759) or other early authors (e.g., Agardh, 1824; Kützing, 1843, 1849; Nägeli, 1849). The systematics and taxonomy of these organisms have been investigated for two centuries and a half; nevertheless, the most important advancements have been made in the last 20 years, when molecular data have become available. It is now clear that the terrestrial green algae are a polyphyletic assemblage originated through many independent colonisations of the land by different lineages of aquatic algae, both marine and freshwater (Lewis & McCourt, 2004; Lewis, 2007; Cardon *et al.*, 2008). The capability to adapt to terrestrial conditions is taxonomically widespread, as indicated by the fact that terrestrial members occur in at least six different groups (Chlorophyceae, Trebouxiophyceae, Ulvophyceae, Chlorokybophyceae, Klebsormidiophyceae and Zygnemophyceae; Figure 2); most of the species currently known belong to the class Trebouxiophyceae (Lewis & McCourt, 2004). The molecular data have also revealed that the genetic diversity of terrestrial green algae is much higher than suggested by their simple morphology. Different species, sometimes belonging to unrelated evolutionary lineages, have converged into an almost identical morphology, and several taxa described on morphological basis have been shown to be polyphyletic complexes of cryptic species. A typical example of this situation is the widespread genus *Chlorella*, which has been shown to be an artificial agglomeration of algae belonging to two different classes, the Trebouxiophyceae and the Chlorophyceae (Huss *et al.*, 1999); this genus is being gradually dismantled and subdivided into several separate genera (Krienitz *et al.*, 2004; Zhang *et al.*, 2008).

Other common genera which have been revealed as polyphyletic or paraphyletic include *Chlorococcum* (Buchheim *et al.*, 2002), *Klebsormidium*

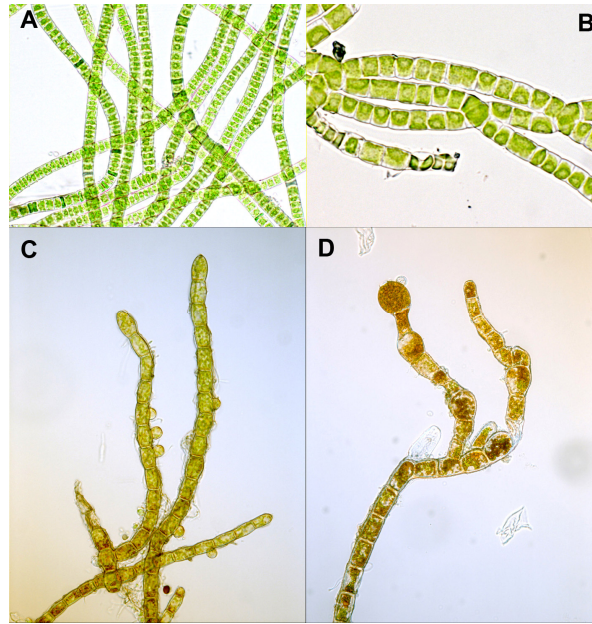


Figure 5. Examples of terrestrial green algae with filamentous morphology. Figure 5A: *Rosenvingiella radicans* (cells 8-12 μm wide). Figure 5B: *Klebsormidium flaccidum* (cells 6-8 μm wide). Figure 5C: *Trentepohlia* sp. (cells 10-14 μm wide). Figure 5D: *Printzina bosseae* (cells 12-15 μm wide).

(Mikhailyuk *et al.*, 2008), *Koliella* (Katana *et al.*, 2001), *Planophila* (Friedl & O'Kelly, 2002), *Printzina* (Rindi *et al.*, 2009) and *Trentepohlia* (Rindi *et al.*, 2009). It is now generally acknowledged that such morphological convergence is a typical trait of the evolution of terrestrial green algae, which represents a substantial complication for the systematics of these organisms. A direct consequence of this phenomenon is that the taxonomy and the phylogenetic relationships of many taxa will require a careful reassessment based on a polyphasic approach (Pröschold & Leliaert, 2007), in which molecular data will play a fundamental part.

Biogeography of Terrestrial Green Algae

The biogeography of microscopic organisms has traditionally been a complex matter, and in recent years it has become subject of great controversy. Two different schools of thought have been established. A view embraced primarily

by researchers with ecological background assumes that free-living microorganisms have a cosmopolitan distribution and that eukaryotes smaller than 1 mm in size (such as most terrestrial microalgae) are distributed worldwide, wherever their habitat requirements are satisfied (Finlay, 2002; Fenchel & Finlay, 2003; Finlay & Fenchel, 2004). The rationale behind this view is that, due to their small size and large population sizes, these organisms will produce large amounts of new propagules (cysts, eggs, spores) capable of dispersal on very long distances, which will make the probability of local extinction low. Conversely, a view founded on taxonomic grounds believes that many microorganisms are not cosmopolitan; they have a more or less restricted distribution and the wrong impression of ubiquity is due to undersampling, misidentifications and reliance on morphological species concepts (Foissner, 2006, 2008). In recent years this theory has received the support of molecular evidence obtained from several groups of microscopic eukaryotes (Šlapeta *et al.*, 2005, 2006; Luo *et al.*, 2006; Evans *et al.*, 2008a, 2008b). For terrestrial green algae, the knowledge required to confirm or disprove either of these two scenarios is not yet available. The problems mentioned earlier in relation to systematics and taxonomy imply that many basic ideas about the biogeography of terrestrial microalgae will have to be reconsidered after a detailed reassessment of the taxonomy of many taxa. The information available in the literature about the geographical distribution of terrestrial green algae is generally vague and so far has been based entirely on morphological species concepts. Numerous floristic studies are available, especially for soil algae (Metting, 1981, and references therein) and algal assemblages growing on artificial substrata (Rindi, 2007a, and references therein). However, great caution should be used when trying to draw generalizations based on these studies, because taxonomic incongruities and differences in the nomenclature used make it difficult to compare the results of different investigations. In general, there is a certain number of species that, as defined on morphological basis, appear to be cosmopolitan or very widely distributed. Typical examples are *Apatococcus lobatus*, *Chlorella vulgaris*, *Desmococcus olivaceus*, *Klebsormidium flaccidum*, *Stichococcus bacillaris* and *Trentepohlia aurea*. These species have been reported from almost every region in which terrestrial green algae have been studied, and in taxonomic accounts they are defined as cosmopolitan, or widely distributed (Printz, 1939; Ettl & Gärtner, 1995; John, 1988, 2002); *Desmococcus olivaceus* has been defined the “commonest green alga in the world” (Laundon, 1985). Conversely, many other species are known in nature only from the type locality or from a restricted number of locations (*e.g.*, Thompson & Wujek,

1992; Broady & Ingerfield, 1993; Thompson & Wujek, 1997; Neustupa & Šejnohová, 2003; Neustupa, 2005; Novis, 2006; Rindi *et al.*, 2006).

Unfortunately, the small size and simple morphology of these organisms make their identification (and therefore the characterization of their distribution) very problematic. With the exception of relatively few species that produce visible populations, most terrestrial green algae are not observable with the unaided eye and their presence is only revealed by growth in culture (John, 1988; Broady, 1996). The case of species which are only known from the original culture and were never observed in nature is not infrequent. At the same time, the scarcity of features useful for identification and the homoplasious morphology of many lineages make the identification of these algae a difficult task, for which the expertise of specialized taxonomists is usually mandatory. In general, the most reliable conclusions can be drawn for “flagship” taxa with a characteristic morphology, which makes them easily recognizable in the field.

The order Trentepohliales (class Ulvophyceae) represents the best example of such a taxon. This order includes subaerial algae capable of growing on numerous substrata, such as natural rocks, concrete walls, plastic nets, tree bark, leaves, stems and fruits (Chapman, 1984; Thompson & Wujek, 1997; López-Bautista *et al.*, 2002). These algae produce large amounts of carotenoids (such as β -carotene and haematochrome) that give them a bright orange, yellow or red color, making them easily recognizable. Although identification at the species level may be very difficult, the recognition of members of this order and their attribution to one of the five genera currently accepted (*Cephaleuros*, *Phycopeltis*, *Printzina*, *Stomatochroon*, *Trentepohlia*) are generally straightforward. It is well documented that the Trentepohliales are most diverse and abundant in humid tropical regions, where they are the most common terrestrial green algae. In the tropics they are well known for their profuse development (Wee & Lee, 1980; John, 1988; Rindi & López-Bautista, 2008; Rindi *et al.*, 2008a) that may become cause of major practical nuisances, such as disfiguration of buildings (Wee & Lee, 1980) and infection of plants of commercial interest (Chapman & Waters, 2001). Because of such association with warm and humid climates, Aptroot & Van Herck (2007) suggested that the recent geographical expansion in western Europe of species of lichens with southern affinities may be due to the effect of global warming on their *Trentepohlia* phycobionts. Floristic studies based on morphology have reported the highest richness of Trentepohliales for Queensland, Australia (31 taxa), the area of Bogor in Indonesia (30 taxa), India (27 taxa), French Guiana (29 taxa) and Panama (24 taxa) (Rindi & López-Bautista, 2008, and references

therein; Rindi *et al.*, 2008a). Molecular data have become available for the Trentepohliales only recently (López-Bautista & Chapman, 2003; López-Bautista *et al.*, 2006; Rindi *et al.*, 2009) and have revealed that the genetic diversity of this group is even higher than suggested by morphology. For example, *Cephaleuros virescens*, *Printzina lagenifera* and *Trentepohlia arborum* are considered widespread species with pantropical distribution (Printz, 1939; Cribb, 1970; Ettl & Gärtner, 1995; Thompson & Wujek, 1997). Morphologically they are well-defined and generally easy to identify. The phylogenies presented by López-Bautista *et al.* (2006) and Rindi *et al.* (2009), however, suggest that the morphologies typical of these species have evolved separately in several lineages. Therefore, these entities should be regarded as complexes of cryptic species rather than individual species of their own. Actual cryptic species are likely to have more restricted distributions, and further collections and molecular data will be necessary for a correct characterization of their systematics and biogeography. A similar situation was found for *Trentepohlia umbrina*, another trentepohlialean species reported as geographically widespread (Printz, 1939). Although showing an identical morphology, specimens from subtropical areas sequenced by Rindi *et al.* (2009) are separated with strong support and appear to represent a different species from European strains, which represent the genuine *Trentepohlia umbrina* (originally described by Kützing (1843), from tree bark in southern Germany). This suggests the possibility that the distribution of this species is relegated to temperate regions and that tropical strains will have to be accommodated into one or more separate species; even in this case, however, further molecular data are required. In recent studies, it has been shown that other species of *Trentepohlia* and *Printzina* have a wider geographical distribution than previously thought. For example, *Printzina bosseae* and *Trentepohlia dusenii*, which were previously known only from the old world (*P. bosseae* from tropical Asia and some regions of Oceania; *T. dusenii* from Cameroon, India and Queensland), were recently discovered in French Guiana by Rindi & López-Bautista (2008). Similarly *Trentepohlia minima* and *Trentepohlia treubiana*, previously known from several regions of Australasia, were recently recorded for Panama by Rindi *et al.* (2008a). It is likely that detailed surveys conducted in other tropical regions will reveal a wider geographical distribution for many other species of Trentepohliales.

The order Prasiolales belongs to the Trebouxiophyceae and represents one of the most versatile groups of green algae, including species distributed in marine, terrestrial and freshwater habitats (Rindi *et al.*, 2007). The distribution of these algae is associated with polar regions and cold-temperate regions with

humid climate; the only members of this order recorded in geographical areas with warmer climates are freshwater species of *Prasiola* occurring in cold mountain streams (Naw & Hara, 2002; Rodríguez & Jiménez, 2005). *Prasiola crispa* is a particularly well-known case, because its characteristic thallus formed by dark-green, curled blades, is easily recognizable. This species occurs in polar and cold temperate regions of both hemispheres; it is the most common terrestrial alga in Antarctica, where it forms large populations at sites where penguin rookeries deposit large amounts of guano (Broady, 1996; Lud *et al.*, 2001). In the past Antarctic specimens have been placed into a separate subspecies (*Prasiola crispa* subsp. *antarctica* (Kützing) Knebel; Knebel, 1935), and molecular data have confirmed their distinctness from populations of the northern hemisphere; *rbcL* sequences suggest separation at the species level (Rindi, unpublished data). Marine species of *Prasiola* occur in the supralittoral and upper intertidal zone on rocky shores, producing large green patches in spots fertilized by seabird guano (Rindi, 2007b). Although also present in the southern hemisphere, marine *Prasiola* have their centre of diversity in the North Atlantic and North Pacific, where at least 6 species occur (*Prasiola borealis*, *P. delicata*, *P. furfuracea*, *P. linearis*, *P. meridionalis* and *P. stipitata*). In molecular phylogenies, these species form a well-supported monophyletic group (apart for *Prasiola borealis*, which occurs in a separate clade; Rindi *et al.*, 2007). The substitution rate of the *rbcL* gene in this group is unexpectedly low and does not match the considerable variation in vegetative morphology and life history. This suggests that marine *Prasiola* might have derived from a geologically recent trans-Arctic evolutionary radiation, a type of event that is well documented for several species of marine macroalgae (Lindstrom, 1987, 2001). Further molecular datasets based on different markers should help to clarify interspecific relationships and reveal geographical patterns in this group.

Klebsormidium is a genus of filamentous green algae occurring in many different terrestrial habitats, in particular soil, natural rocks and bases of concrete walls (Ettl & Gärtner, 1995; Lokhorst, 1996; John, 2002). Although it has been more frequently recorded in temperate and polar regions than in the tropics, its distribution is essentially cosmopolitan. *Klebsormidium flaccidum* is the type species of the genus and one of the most widely distributed terrestrial green algae (Printz, 1964; Ettl & Gärtner, 1995; John, 2002). Recent molecular data, however, have shown that taxonomic accounts of *Klebsormidium* based on morphology do not reflect its phylogeny, and the taxonomic identity of *K. flaccidum* requires clarification (Sluiman *et al.*, 2008; Mikhailiyuk *et al.*, 2008; Rindi *et al.*, 2008b). Mikhailiyuk *et al.* (2008) showed

that strains of *Interfilum*, a freshwater genus with very different morphology, are nested within *Klebsormidium* and render it paraphyletic. Strains of *Klebsormidium flaccidum* sequenced by Rindi *et al.* (2008) did not form a monophyletic group and were scattered among several clades in the phylogeny of the genus, revealing how complicated the delimitation of species in *Klebsormidium* is. Overall, the bulk of molecular information currently available for this genus points at the existence of a great genetic diversity hidden behind a simple and uniform morphology. Once the circumscription of species in *Klebsormidium* is reassessed on the basis of robust molecular phylogenies, we feel that the distribution of many species will turn to be more restricted than presently believed, both in terms of habitat and geography.

CONCLUSION

The cases illustrated above show how molecular data are reshaping species delimitations in terrestrial green algae and, indirectly, basic concepts about their biogeography. Until individual species are unambiguously defined and the taxonomy of the main groups is reassessed, it will be impossible to draw strong conclusions about the biogeography of terrestrial green algae. It is clear that for terrestrial and freshwater microalgae species concepts based only on morphological grounds cannot stand anymore. Species should be defined using a polyphasic approach combining as many different types of data as possible (morphological, molecular, ultrastructural, biochemical, physiological, ecological). The key importance of molecular data is now obvious, and the production of robust phylogenies based on multiple molecular markers will be essential to clarify systematics and taxonomy of many groups. The vast majority of the data available is currently represented by 18S rRNA gene sequences. The great popularity of this marker is due to its usefulness for inference at class and/or order level, which represents an important advantage for green microalgae. Since the morphology of these organisms is highly homoplasious and offers very few characters useful for identification, the 18S rRNA sequence will give an immediate indication of the phylogenetic placement of any green microalga for which an identification based on morphology is impossible or only tentative. However, the substitution rate of this gene is usually not suitable to clarify relationships at genus and species level; for this purpose, the use of other, more variable molecular markers is necessary. The most frequently used are ITS rRNA (Beck *et al.*, 1998; Müller *et al.*, 2005; Luo *et al.*, 2006; Yahr *et al.*, 2006;

Sluiman *et al.*, 2008; Mikhailyuk *et al.*, 2008), the *rbcL* gene (Novis, 2006; Rindi *et al.*, 2007, 2008b, 2009), the 26S rRNA gene (Friedl & Rokitta, 1997) and the type 1 introns of the actin gene (Kroken & Taylor, 2000; Nelsen & Gargas, 2006, 2008). However, the taxon sampling and number of sequences available for these markers are still limited and mostly circumscribed to specific taxa. It is clear that to increase the amount of sequences (and expand substantially the taxon sampling) represents an absolute priority. Other types of molecular data for terrestrial green algae are scanty and restricted to Amplified Fragment Length Polymorphisms (AFLP); Müller *et al.* (2005) showed their usefulness in unravelling subspecific diversity in *Chlorella vulgaris*.

The availability of a large bulk of distributional data, based on accurate identifications, represents the other critical requirement for a clarification of the biogeography of terrestrial green algae. Due to the problems about species concepts and taxonomic identity outlined above, distributional records available in the literature need to be considered with great caution and re-evaluated case by case. Samples of terrestrial green algae are available in many herbaria or other public collections and represent a very valuable resource in this regard; but these records should also be subjected to a critical taxonomic re-examination. In general, the number of systematists working on terrestrial algae is much more limited than for other groups of algae and plants, and these organisms are comparatively undersampled. Therefore new surveys and investigations of natural history will be very important in the future and it is highly desirable that this type of work will receive high support from funding agencies. These surveys should ideally focus on geographical areas and habitats that have been underexplored, where it is expectable to find new species. This is particularly true for the tropics, which, for historical reasons, have received less coverage and less scrutiny by skilled algal taxonomists. Investigations in tropical regions continue to lead to the discovery of new species (Neustupa, 2003; Neustupa & Šejnohová, 2003; Neustupa, 2005; Neustupa *et al.*, 2007; Rindi *et al.*, 2006; Rindi & López-Bautista, 2007; Eliáš *et al.*, 2008; Zhang *et al.*, 2008; Neustupa *et al.*, 2009) and the diversity of subaerial algae in these regions is probably immense, especially in rainforest environments. The high humidity and the great habitat diversity typical of rainforests are ideal to support a great diversity of terrestrial algae. The limited information available supports this idea (Neustupa, 2005; Rindi *et al.*, 2006; Neustupa & Škaloud, 2008), and it is important that these environments are investigated in detail before human impacts cause irreparable damages. The records produced in future surveys should ideally be based on morphological

and molecular data and made verifiable by conservation of voucher specimens. However, with the accumulation of sequence data and the improved characterization of algal biodiversity, new molecular data based on environmental sampling and cloning will become increasingly important in the future. This approach has shown a great potential in revealing the genetic diversity of several microalgal assemblages (Fawley *et al.*, 2004; Kirkwood *et al.*, 2008; Sherwood *et al.*, 2008). In subaerial algal communities it has not yet been widely used, and it will certainly be an important tool for their study in the future; the possibility to unravel the presence of species that cannot be grown in culture represents its most important strength.

Investigations concerning other aspects of the biology of terrestrial algae can also provide valuable information to understand their biogeography. Range and mechanisms of dispersal are particularly important, as they contribute directly to determine the geographical distribution of species. Studies on this topic have been carried out in several regions, mainly by collection air samples, concentration of algal cells and examination in culture (Brown, 1971; Rosas *et al.*, 1989; Roy-Ocotla & Carrera, 1993; Marshall & Chalmers, 1997; Tormo *et al.*, 2001). The evidence available suggests that the diversity and abundance of airborne algal particles show climatic, topographical, geographical, diurnal and seasonal variation; tropical regions exhibit generally higher diversity and abundance than other climatic regions (Sharma *et al.*, 2007). It is generally recognized that single cells 10-12 μm wide (such as species of *Stichococcus*) are ideal airborne algae, which can be carried in the atmosphere for thousands of km (Roy-Ocotla & Carrera, 1993). However, many studies on airborne algae do not provide identifications at species level; when provided, they are based on morphological concepts, with the same limitations already mentioned for distributional studies. Data on the physiology of species of terrestrial green algae (desiccation tolerance, survival ranges, optimal temperature, optimal range of irradiance for photosynthesis) are generally limited. Mechanisms of protection and adaptation to high UV radiation are the only aspect that has received considerable attention (Lud *et al.*, 2001; Karsten, 2005; Hughes, 2006; Karsten, 2007a, 2007b and references therein), and detailed studies are available only for a few types of habitat, such as biotic crusts of deserts (Gray *et al.*, 2007) and algal communities growing on artificial surfaces (Ong *et al.*, 1992; Häubner *et al.*, 2006; Karsten *et al.*, 2007b). This is unfortunate, because physiological data (especially temperature ranges and optima) may provide very useful information to interpret distributional data and predict the geographical distribution of a species.

The information summarized here highlights how much work on all aspects of the biology of terrestrial green algae is necessary in order to achieve a deep understanding of their biogeography. Once the taxonomy of the most common species is sorted and reliable distributional information is available, the distribution records combined with physiological information will allow to design ecological niche models incorporating the effects of climatic parameters, which would be very useful to predict shifts in distribution due to climatic changes; at present, such models are inexistent for terrestrial algae. As a general conclusion, the biogeography of terrestrial green algae is a poorly-explored area, which holds a great potential for a bulk of exciting research and which deserves much greater attention than received so far.

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