INTRODUCTION

The Editors

Freshwater algae have been a subject of interest for naturalists and professional scientists in the British Isles for more than two centuries. As can be seen from the long reference list, many made observations over long periods and their records range from notes in natural history periodicals to long ecological accounts in learned journals. Nowadays an increasing number of people are required to name algae accurately, particularly those involved in managing and monitoring the water environment. All this suggests the need for readily available modern books, that are straightforward to use, on how to identify freshwater algae in the British Isles, Europe and worldwide. However, such books do not exist, and the present Flora sets out to fulfil this need for freshwater and terrestrial algae other than diatoms.

Before explaining the scope of the Flora, it is worth giving a little background. Following the 'Earth Summit' held in Rio de Janeiro in June 1992, various international and national strategies were prepared for the conservation and sustainable use of biological diversity. The oceanic planktonic algae have received some attention because of their importance in global processes, but freshwater algae were mostly included simply as estimates of numbers. The UK Biodiversity Steering Group Report (Biodiversity, 1995a) estimated there to be 20 000 algal species in the UK, about 650 of which are seaweeds. However, a checklist of the freshwater and terrestrial algae of Great Britain and the Republic of Ireland (Whitton *et al.*, 1998a) reported only about 5000 species. Other sources of information and new discoveries are in the second edition of *A Coded List of Freshwater Algae of the British Isles* (Whitton *et al.*, 2003). However, many more detailed field surveys are needed to provide a more reliable estimate of species diversity. Of those species that are known, it is possible to comment reliably on the overall status of only a hundred or so in the phyla covered here. In addition to the commonest species, a few others are sufficiently distinctive to make a sound assessment of their general distribution. The red alga *Thorea hispida*, the water-net *Hydrodictyon reticulatum* and some charophytes (stoneworts) are examples.

The situation is of course dynamic with losses and gains due to natural changes or human activity. This has been recognized for the charophytes, of which 12 species were included in the second volume of the UK Government's *Biodiversity: the UK Steering Group Report* (Biodiversity, 1995b) as 'priority species' in need of conservation action. They are the only algal group in the British Isles for which a Red Data book has been written (Stewart and Church, 1992), although more than 300 desmids have been proposed as candidate Red List species in a report for Plantlife listing the most important areas for this group in the UK (John and Williamson, 2007). The charophytes are the only other freshwater group of algae for which important areas have been recognized (see Stewart, 2004) and at least seven 'Biodiversity Action Plans' (BAPs) have been prepared for them. Other algae are known to have disappeared from specific sites and are vulnerable following the widespread loss or degradation of freshwater habitats. Unfortunately, these have mostly been neglected by those concerned with conservation in the British Isles, presumably because of their small size. This lack of interest contrasts with parts of continental Europe where freshwater algae have received more attention. 'Red Data Lists' of algae exist for, among others, the Czech Republic, Germany, Poland and Slovakia. The list for Germany is especially comprehensive, with over a thousand algal species mentioned as threatened (Ludwig and Schnittler, 1996).

New records for the British Isles of previously unrecorded species are sometimes suspected to be new introductions, although it is often difficult to be sure, except possibly in charophytes (see p. 742). What is clear is that some potentially nuisance species have become much more abundant during the past century, including some bloom-forming blue-green algae and the macroalgae *Cladophora glomerata*, *Ulva* (= *Enteromorpha*) *flexuosa*, *Hydrodictyon reticulatum* and *Vaucheria sessilis* (Whitton, 1974; John *et al.*, 2001). These species all show great morphological variation, suggesting that they may be undergoing rapid evolutionary changes. Such changes add to the need for a reliable Flora to record what is now present.

The last fairly comprehensive account was West and Fritsch's *A Treatise on British Freshwater Algae*, published in 1927 by the same publisher as the present Flora. Much of this material had already been published by G.S. West in 1904 and was never revised. He died 10 years before the appearance of the new book. More recent identification guides for the British

Isles deal with the commoner species (Pentecost, 1984a; Bellinger, 1992; Bellinger and Sigee, 2010), specific habitats (Belcher and Swale, 1976, 1979) and specific groups (Lind and Brook, 1980; Barber and Haworth, 1981; Kelly, 2000). None is comprehensive enough to identify the majority of the species in most mixed field samples. Often those with little experience of algae fail to appreciate the limitations of such guides, and may ignore small but significant differences between their material and the text descriptions and illustrations. Sometimes these differences are highly significant and dismissing them inevitably leads to misidentification. Identification requires access to far more books, journals and microfiches than possessed by most institutes and universities, let alone individuals. The situation has improved considerably since publication of the first edition due to the availability on the worldwide web of taxonomic information including image databases (e.g. AlgaeVision: http://www.nhm.ac.uk/research-curation/research/projects/algaevision/index.html; Protist Information Server: http://protist.i.hosei.jp/index.html), downloadable files and scanned journals and books that are often no longer in copyright and long out of print (see Biodiversity Heritage Library website).

SCOPE OF FLORA

The Flora deals with the British Isles, comprising Great Britain (England, Scotland, Wales), Ireland (Northern Ireland, the Irish Republic), the Isle of Man and the Channel Islands. The United Kingdom is Great Britain and Northern Ireland. All major groups of freshwater and terrestrial algae are included (Table 1), apart from diatoms for which there is only a short introduction (p. 348). Species of slightly brackish environments are included, but the salinity limits differ slightly between groups. As in most Floras for other parts of the world, all marine blue-green algae are included, because some species occur in both freshwater and marine environments. Symbiotic algae, such as lichen phycobionts, are only briefly mentioned. Several lichen phycobionts are mentioned in *The Lichens of Britain and Ireland* (Smith *et al.*, 2009), but it is unclear whether the algal genera are based on studies of British lichens or of extra-British material. As in the first edition, colourless dinoflagellates (Dinophyta) are included if they belong to genera which are predominantly photosynthetic, but not otherwise. However, in this edition there is a full account of colourless euglenophytes and this has been prepared in response to comments made by Dr John Lund in the foreword to the first edition.

Almost 450 of the nearly 900 desmid species now known from the British Isles are described and illustrated – many more than in the first edition. This is mainly for reasons of space, but also because a long delayed monograph covering several important genera has just been published (Brook and Williamson, 2010). The desmids are in fact the only algal group where there is an older monograph for the British Isles. William and George West published a five-volume series between 1904 and 1923, with the last completed

Table 1. *Numbers of taxa of freshwater and terrestrial algae known from the British Isles; not included are colourless species and the 69 strictly marine Cyanobacteria (although described in the Flora) and colourless species. The taxa in parentheses are included in the total recorded from the British Isles, but are not described and illustrated in the text (mostly desmids and chrysophytes). Doubtful includes species and subspecific taxa. Numbers of subspecific taxa are only very approximate since many are mentioned although discounted as not worthy of recognition.*

PHYLUM	Taxa described in Flora		
	Species	Subspecific taxa	Doubtful
Cyanobacteria (blue-green algae)	364	5	10
Rhodophyta (red algae)	22	1	1
Euglenophyta (euglenoids)	166	27	
Cryptophyta (cryptomonads)	19	1	
Dinophyta (dinoflagellates)	54	3 (13)	10
Raphidophyta	2		
Haptophyta	5		
Chrysophyta (golden-brown algae)	122 (38)	11 (5)	11
Xanthophyta (yellow-green algae)	76	1	6
Eustigmatophyta	4		
Phaeophyta (brown algae)	2		1
Prasinophyta (primitive green algae)	15		1
Chlorophyta (green algae)	1114 (474)	196 (430)	50
Glaucophyta	3		
TOTAL IN FLORA	1968 (512)	245 (448)	89

Total number of British freshwater algae (excluding diatoms): 2480 species (3173 taxa).

by Dr Nellie Carter: 690 species and 450 varieties of desmid were described and meticulously illustrated. As a consequence, more is known of the distribution and abundance of desmids than any other algal group, making it easier to select the commoner and more distinctive species. Those recorded from the British Isles, but not described and illustrated in the Flora, are listed under each genus. A list of all species known up to the time of publication is given in *A Coded List of Freshwater Algae of the British Isles* (Whitton *et al.*, 1998b, 2003). Additions to taxa other than diatoms are included in the attached DVD (see below).

Taxonomy

Because 24 contributors have prepared the main entries for the different taxonomic groups, it is inevitable that there are differences in depth of cover. However, the editors have tried to ensure that the level of treatment is as similar as possible and there is consistency in the form of the entries.

The arrangement of the phyla follows the *Coded List of Freshwater Algae of the British Isles* (Whitton *et al.*, 1998b, 2003). Orders are arranged alphabetically under a higher taxonomic category (usually phylum), genera are alphabetical under the order (or family in the Zygnematales), and species are alphabetical within the genus. Each species entry includes its current accepted name, authority, date of publication and basionym (if required). The synonyms listed are usually ones used widely in the literature on British freshwater algae or in major taxonomic treatments. The author of each taxonomic name is given in full with initials or other conventions used following the recommendations given by Brummitt and Powell (1992). A list of standardized abbreviations and other conventions associated with the citation of authors of taxa is provided (p. 777).

The descriptions are mostly brief, diagnostic, and emphasize characters essential for identification. As few technical terms are included as possible, but some are essential. Specialist terms for a particular taxonomic group are sometimes discussed more fully in the introduction to that group (e.g. Charales, Oedogoniales), but otherwise are defined in the Glossary (p. 770). Little consideration is given to ultrastructural detail, since most users of this volume will not have access to scanning or transmission electron microscopy. Most taxonomic entries are accompanied by comments on world distribution and, where available, information on ecology. However, comments on world distribution should be treated with caution, since information on the freshwater algae of many regions is sparse, dubious or non-existent. Detailed distribution within the British Isles is mentioned where sufficient information is available, as is the case for many desmids. In some cases localities are mentioned including vice-counties. There are 111 vice-counties in Great Britain and 40 in Ireland, with the Isle of Man and the Channel Islands representing a further two (see end-papers). Clearly the amount of ecological information provided depends on the current state of knowledge. No doubt some species are much more widespread than is usually considered to be the case, because their characteristic habitat is seldom sampled or not sampled at the optimum time of year. Many records, such as those for some of the filamentous members of the Zygnematales, date back to the early nineteenth century and were unaccompanied by ecological information. Additional information is provided for environmentally important algae, such as those which can cause a nuisance or are important for monitoring water quality and long-term changes in the environment.

Inevitably material will be discovered that does not correspond to any of the taxa described and illustrated, possibly representing an entirely new record for the British Isles. Hence, there will be a need to consult literature from other parts of the world. Mention is made of culture-based taxonomic systems and in a few identification keys a character becomes evident only after material has been grown in the laboratory. Culturing can be quite simple (see Methods, p. 17–18), and is essential for organisms whose diagnostic features become apparent only under nutrient limitation or other stressful conditions. This applies to some blue-green algae, many filamentous chlorophytes and the xanthophyte *Vaucheria*. It is expected that most material will be identified from freshly collected field samples examined under bright-field illumination, although if available, differential interference microscopy can be helpful.

All species and infraspecific taxa recognized here are given a unique identifying eight-digit code number designed to assist researchers wanting to collect and store information on computer file. The full list of codes used was published as *A Coded List of Freshwater Algae of the British Isles* (Whitton *et al.*, 1998b); an updated version is available at a Centre for Hydrology and Ecology website (Whitton *et al.*, 2003), although with less of the accompanying information. The code used is hierarchical with the first two digits representing the phylum or one or more major subgroups within a phylum, the next two digits the genus, the next three digits the species, and the last digit a variety or other infraspecific taxon. Doubtful taxa are only given a code number in the Flora if they were listed in the 2003 version of the *Coded List* or had either been overlooked in the first edition or discovered following its publication. However, code numbers have been introduced in the text for new records and to reflect nomenclatural changes; these are also included in the downloadable version of the *Coded List* in the accompanying DVD.

Keys

The aim of the keys is to aid the accurate identification of any sample containing freshwater or terrestrial algae collected in the British Isles. The keys are based in large part on taxonomically important characters clearly visible with the light microscope; only where there is no alternative have we resorted to reproductive, ecological or more obscure characters. They are usually dichotomous with each character presented as two descriptive choices; the choice to follow is the one that most closely agrees with the specimen. Some characters are not absolute (e.g. free-living or attached, solitary or colonial), making it necessary on occasion to back-track and follow an alternative proposition. There are genera for which a character applies only to a subset of its species or a particular environmental condition. In such cases the genus is keyed out in more than one place and the generic name is followed by 'in part'. On occasion characters used in the key relate only to material sampled from the British Isles. Finally, the keys are not constructed in such a way that phylogenetically related taxa necessarily key out together. The keys are 'artificial' rather than 'natural' and are designed to make it as easy as possible to identify samples to the level of species.

Keys are at their least satisfactory when used to identify taxa where quantitative characters show continuous variation, with each character a graded series of overlapping expressions. In such cases it is often more useful to use a table for comparing character combinations than a traditional key, and this has been adopted where appropriate. Blue-green algae (Cyanobacteria) present a particular problem, because so many of the characters are overlapping. Some of the keys in previous Floras are riddled with problems and have seldom been used in practice. Keys are given here only where they seem especially helpful. However, there is available separately an electronic, multi-access identification key for all the blue-green algae recorded in the British Isles (Whitton *et al.*, 2002). A much expanded version is being prepared as a response to new software for the production of multivariate keys. This makes it easier for people to use the key to obtain names using different taxonomic approaches to blue-green algae/cyanobacteria.

Organisms that may cause confusion

Before using a key, be sure that the specimen really is an alga and, if it is, that it is free-living rather than part of a symbiotic association. Some small, morphologically simple organisms are almost impossible to separate from bacteria if they are stained with iodine, but others sometimes cause confusion even if they are colourless. The colourless bacterium *Achromatium*, which is frequent in calcareous silts where hydrogen sulphide is present, gets attention simply because it is so large. Colourless bacteria $<2\,\mu m$ wide and gliding filaments $<1\,\mu m$ are sometimes hard to distinguish from very pale blue-green algae of similar dimensions. In such cases it is essential to have access to a fluorescence microscope to check whether or not chlorophyll *a* is present; if it is absent, then the organism is not a blue-green alga or eukaryotic alga. Coloured bacteria may be even more difficult to distinguish from blue-green algae by visual inspection, but again the difference is easy to resolve using fluorescence. This applies especially to green and purple photosynthetic bacteria, which live in oxygen-free (green bacteria) or nearly free (purple bacteria) environments with hydrogen sulphide. Possible confusion between plates of the purple sulphur bacterium *Thiopedia* and the blue-green alga *Merismopedia* are discussed under the latter genus (p. 67). It is likely that some records of planktonic *Merismopedia* were in fact *Thiopedia*. Superficially the two can look very similar, although they are far apart phylogenetically. A number of blue-green algae and a few eukaryotic algae can live in similar microhabitats to some of the purple sulphur bacteria, especially *Chromatium*.

The green alga *Chlorella* occurs symbiotically with a number of common freshwater organisms, including amoebae, sponges and ciliated protozoans such as *Paramecium* and *Ophrydium*. The latter protozoan is quite common in some parts of the British Isles (as *O. versatile* Müller), where it sometimes develops in huge quantities in ponds and lakes as irregular, spherical, oval or sausage-like, grey-green gelatinous masses that might easily be mistaken for an alga (see Eaton and Carr, 1980). Many protozoa feed on small-celled algae, so there may be doubt in a particular case as to whether intracellular algae are true endosymbionts or are merely those which have been eaten recently. However, if the sample is still alive, it is usually quite easy to decide with green algae inside ciliates or amoebae. Typically, all the cells of intracellular symbionts look bright green and healthy, whereas cells which have been eaten usually include some which are yellowish or starting to look disorganized. However, the situation may be harder to distinguish with some dinoflagellates and chrysophytes, because some photosynthetic species are also capable of ingesting other cells under some conditions (phagotrophic); this applies, for instance, to some *Ochromonas*. In addition there are also colourless dinoflagellates and chrysophytes which behave phagotrophically. If doubt persists, it is worth rechecking samples a day later when the difference between live and partially digested is likely to be clear, although even this is not always the situation, because some phagotrophic organisms appear to delay digestion of the ingested cells.

Lichen algae are mentioned only briefly in the Flora and in most cases it is easy to decide whether or not a lichen has been included in a sample. Simple lichens, known as protolichens, may show little structure macroscopically, but can be recognized under the microscope by the presence of many fungal hyphae. However, fragments of the more typical lichen *Verrucaria* often look like free-living green algae when sampled by scraping rocks in rivers. These are common in the middle stretches of many fast-flowing rivers, but may be partially smothered by other encrusting algae such as *Hildenbrandia* and so it may not be obvious that lichen is being removed in a sample. In this case the fungal component often looks more like parenchymatous tissue than obvious filaments.

The algal genus (or genera) known to be present in particular lichens is (or are) listed by Smith *et al.* (2009). However, the original study on its occurrence may not have been done on material from the British Isles, so caution should be used in assuming that the presence of a particular lichen indicates the presence of symbiotic material of a particular blue-green or eukarytic algal genus. It is often hard to relate the structure seen in material taken from a lichen with that of the free-living algae, especially in the case of the morphologically more complex blue-green algae.

Another potential source of confusion is the juvenile filaments of mosses and liverworts. These are sometimes abundant together with leafy shoots of the same species, such as on damp soils or the leading edge of rocks in rivers. In this case the bryophyte filaments (hyphae and protonema) are easy to distinguish, because the cross walls are mostly oblique and the outer walls often have a dull brown colour. However, in highly acidic streams (below pH 3) or streams and mine spoils with very high levels of heavy metals such as zinc or copper, several mosses may exist only as juvenile filaments. In this case the cross walls are usually transverse like a typical green alga and sometimes the walls are not coloured brown. The most obvious distinguishing factor is that the chloroplasts are characteristic of mosses – numerous and disc-shaped, much like a higher plant. Published records from other countries of the green alga *Cladophora* in highly acidic streams have always proved to be juvenile filaments of bryophytes.

For additional information on organisms that might be mistaken for algae, see the pictorial account by C.F. Carter entitled *Organisms Likely to be Confused with Algae* on the DVD accompanying this Flora.

Illustrations

Most species are illustrated by line drawings that emphasize important details needed for identification. However, the Rhodophyta (red algae) are illustrated by halftone photographs of their general habit and microscopic detail. The DVD-ROM photo catalogue consists mostly of colour photographs of algal habitats, macroscopic growths and photomicrographs of living material taken under bright field illumination and/or differential interference contrast microscopy. Some scanning electron microscope photographs of dinoflagellates and euglenophytes are included to assist the interpretation of line drawings.

About two-thirds of the line drawings are new, with most of the remainder taken from various literature sources and modified to a greater or lesser degree. If the original figure had thin lines or other unsatisfactory features, it has been redrawn or sometimes only a portion of it used. Inevitably, redrawing has sometimes resulted in changes in the relative thickness of lines or in the effects of shading. We have omitted from old figures any labelling, and in some cases have added or removed shading. If an original figure has been modified or redrawn, then the person responsible is acknowledged in the section dealing with the sources of the illustrations (p. 783).

A problem in preparing the Flora has been to decide whether figures taken from the earlier literature are still under copyright. Furthermore, some authors state that their figure is ‘after’ an earlier author. In some such cases the figure has been little if at all changed from that of the earlier author, while in others it was changed considerably when redrawn. Sometimes earlier authors do not mention that their figure has been taken from another source, yet it is clear that this is the case. We have tried to acknowledge all the sources of illustrative material and other assistance, but apologize to anyone omitted inadvertently. Ideally every species should have been drawn or photographed afresh from British Isles material, but to achieve this would have delayed publication by many years. Where an illustration is based on material from other countries, we have selected material which resembles what we believe to occur in the British Isles, although inevitably a few anomalies will have been introduced.

DISTRIBUTION AND ECOLOGY

The Editors

Introduction

Algae are almost ubiquitous in waters capable of supporting photosynthetic life and no body of water in the British Isles has been reported to have conditions extreme enough to prevent algal growth. Providing some moisture is present, at least intermittently, then algae can also grow in a wide range of terrestrial habitats. Not surprisingly, such algae are much more conspicuous in the wetter parts of the region. A few algae, such as the algal components of lichens and several widespread microorganisms, are symbionts. Some algae are large enough to be treated as macrophytes (see Glossary, p. 768). The charophyte *Chara hispida* (Plate 2E), for instance, often exceeds 1 m in length. On the other hand, the great majority of species are microscopic and visible to the naked eye only when their numbers are large enough to discolour the water or form obvious surface growths. The type of habitat and size of the organisms determine what sort of method is best for collecting samples.

The algae living in the water column of lakes and larger rivers – the phytoplankton – have been studied for a long time. This is partly because of their ecological importance, but also because the larger species are easy to sample with a net and are also often attractive organisms to observe. However, the smaller species are more of a problem to sample (see Methods). Descriptive accounts of lake phytoplankton have divided the organisms into size classes, although the limits and terms for these classes have not always been the same. The *net plankton* are the largest planktonic algae to be retained in fine mesh nets (<60 μm across). The *picoplankton* are less than 2 μm in any dimension, while the *nannoplankton* occupy the next largest size range. Freshwater algal researchers have usually adopted 20 μm as the upper limit, but the literature sometimes adopts much higher values, typically 60 or 80 μm. Some species of phytoplankton are present in the water column throughout the year, although they may vary markedly in abundance according to the season. Other species exist for part of the year on bottom sediments or are associated with plant growths in shallower parts of the water body. Some planktonic algae are confined to the marginal shallows, where they are normally associated with submerged higher plant vegetation (metaplankton). The flora associated with *Myriophyllum spicatum* is often especially rich.

When phytoplankton multiply to such an extent that they discolour the water they form what are known as waterblooms, especially when the cells rise to the surface, as with gas-vacuolate blue-green algae and lipid-rich organisms such as *Botryococcus*. The term waterbloom is now often used more widely to describe scums and mats of algae floating on or just beneath the water surface, although the two rather different uses of the term can be a source of confusion.

Benthic algae are those attached to all kinds of substratum, ranging from sheets of rock to fine silt and other living organisms. The charophytes or stoneworts are the largest benthic freshwater algae, growing over silt or fine sand and are anchored by rhizoids arising at intervals from creeping branches. In the past these algae have been collected and treated along with flowering plants, which is probably part of the reason why they have been given the most attention by conservationists. Other larger algae, such as the filamentous *Spirogyra* (Plate 1D) and *Oedogonium*, are often visible in the marginal shallows of lakes and ponds as free-floating masses or entangled around submerged aquatic plants or other underwater objects. Most fine-leaved aquatic plants provide suitable surfaces for filamentous algae.

The small algae attached to or associated with submerged surfaces are referred to as epilithic, epipelic, epipsammic, epiphytic or epizoic, according to whether they are growing on rocks, silt, sand, plants or animals, respectively. Many epilithic algae are capable of growing on a wide range of hard surfaces, as has been demonstrated when artificial substrates, such as glass and plastic, are examined after having been left submerged for some days or weeks. Epipelic organisms often form a distinctive community on silt and fine sand; many of these species show gliding motility, although some of them also produce mucilage and the whole community may form a mucilaginous layer. Especially in rivers, epipelic communities of diatoms and blue-green algae in late spring and early summer may rise from the bottom during the day and float at the surface. Epipsammic communities are less common in freshwater than in marine environments, but larger sand particles sometimes dominate the bottom of particular stretches of river and here may be found algae which are attached to individual particles rather than moving freely between smaller particles, as in epipelic communities.

The diverse assemblages of microscopic algae associated with surfaces are not necessarily all firmly attached, but may form a surrounding community which includes some attached organisms, others loosely associated with the surface, perhaps in a mucilaginous film, while others are small motile flagellates or phytoplankton floating in the water. Aufwuchs or periphyton are terms used frequently for this assemblage. At one time the term aufwuchs was applied only to plant surfaces, but now both terms are applied to any type of surface. Filamentous algae frequently associated with the periphyton include creeping or crustose forms (e.g. *Aphanochaete, Protoderma*) and those having an erect and/or a prostrate system of branches (e.g. *Stigeoclonium, Chaetophora, Draparnaldia*). On limestone rocks some are partly endolithic (e.g. *Gongrosira debaryana, Gomontia perforans*) or almost entirely so, such as some forms of narrow sheathed blue-green algae. Occasionally benthic forms are swept from the bottom by current or wave action to become temporary members of the plankton; in the case of lakes and ponds these are referred to as tychoplankton.

Algae occur in many terrestrial habitats and are broadly divided into those associated commonly with soil and algae on soil-free surfaces (subaerial algae). These subaerial algae not only grow on a very wide range of inanimate surfaces, but are associated also with other plants, especially the leaves (epiphyllic) or trunks (corticolous) of trees (Plate 1A).

Distribution in the British Isles

The varied geology and geomorphology of the British Isles along with its Atlantic climate gives rise to a very diverse range of algal habitats. The inland waters of Great Britain cover about 1.04% (2404 km^2) of its total land area (Smith and Lyle, 1979). These comprise over 5500 lakes and reservoirs (<25 km^2), with by far the largest number in Scotland (3788). In the north and west of the British Isles, the climate is cooler, rainier and more oceanic and the geology dominated by hard Palaeozoic rocks. This contrasts to 'lowland' Britain where the climate is warmer and drier and the geology more varied.

Some early generalizations concerning algal distribution patterns in the British Isles remain true today (West and West, 1909a; West and Fritsch, 1927). For example, desmids are more diverse in mountainous than lowland areas, and are more diverse in the relatively base-poor waters on older Palaeozoic rocks or rocks of igneous origin than on calcareous rock formations. West and Fritsch (1927) concluded that filamentous zygnematalean algae (*Zygnema, Mougeotia*) are also well represented in mountainous areas where the water is reasonably soft and of an 'acid' pH, whereas 'an abundance of the commoner unicellular forms are found in low-lying quiet waters'. The group of green algae belonging to the Chlorococcales *sensu lato* are most abundant and diverse in the nutrient-enriched ponds and lakes characteristic of lowland areas of England, southern Scotland and parts of eastern Ireland.

During much of the nineteenth and twentieth centuries, industrialization and the spread of urban areas brought about changes to the landscape which have had a major influence on water quality. The effect of intensive agriculture has been even greater than the influence of industry in many areas during the second half of the twentieth century. The input of sewage effluent, agricultural fertilizers and farm wastes has resulted in the artificial nutrient enrichment of waters (Neal *et al.*, 2010), a process known as eutrophication. During the second half of the twentieth century the influence of atmospheric contamination in rainfall became increasingly apparent, with the initial emphasis on acidic deposits and then later on combined nitrogen (mainly ammonium-N). In addition, the effects of climatic warming on peatlands have influenced the drainage streams. As a consequence of these various factors, there is evidence that waters draining mountainous and other upland areas have often changed in chemistry, including their nutrient composition (Ellwood and Whitton, 2007; Ellwood *et al.*, 2008). However, it is usually unclear just how the various environmental factors have influenced the nutrient composition of the drainage from any particular catchment, although it is likely that in most cases this has increased. Further downstream, where human influence and hence eutrophication and modifications to flow regime become increasingly important, there have been many changes in the composition, diversity and abundance of algal species.

Several terms are used so loosely in the older literature and sometimes even recent literature that it is difficult to be sure of the type of environment. We have tried to resolve this as far as possible and ensure that the wording in this edition is unambiguous. The main problems are:

1. Use of the words 'acidic' and 'acidity'. Acidic environments have often meant low pH, but in other cases are highly acidic environments strongly buffered against pH change. For most algae these are very different environments, with a much more restricted flora in the latter due to problems of control of internal pH (Gross, 2000), although sometimes nutrient concentrations are high, permitting conspicuous growths. 'Low pH' is sometimes used here even if there is no information about acidity, although in almost all such cases the environment is probably not highly acidic.
2. Use of the term 'nutrient-rich' when probably all that is meant is base-rich, rather than with high concentrations of combined nitrogen and/or phosphate, although in some cases the water may combine all of these. It is particularly difficult to decide

what is meant for records of cyanobacteria in some Floras. A related problem is whether nutrient-rich refers to combined nitrogen and phosphate or merely phosphate concentrations, although there has been an increasing tendency to focus only on the latter in water management studies, such as those related to the Water Framework Directive. The same applies to the terms eutrophic and eutrophication.

3. The term 'dystrophic' was widely used in the older limnological literature for lakes and sometimes also rivers with water coloured at least slightly brown due to humic materials. Some authors have assumed that such waters are low pH ('acidic') without taking measurements, but there are plenty of cases where this is not true. Streams, rivers and lakes which combine high calcium, pH well above neutral and sufficient humic materials to colour the water pale brown, at least at some times of year, are among the most algal species-rich in the British Isles and have provided a number of the new records for blue-green algae in this volume.

The excessive growth of algae caused by nutrient enrichment results in the blockage of inland waterways, significantly affects the cost of treating drinking water, reduces the amenity and conservation value of water, and leads to the death of fish and other organisms. Changes in amounts and types of algae have been monitored over the long term in several of the larger lakes (e.g. Loch Leven in Scotland, Windermere in the English Lake District, Lough Neagh in Ireland), as well as the relatively small and shallow lakes of the Cheshire Meres and the Norfolk Broads. Many smaller water bodies, such as farm ponds, have disappeared or become degraded through in-filling or general lowering of the water table, drainage/land reclamation and nutrient enrichment and contamination by pollutants. To some extent these losses have been compensated for by the creation of new gravel pits, ornamental ponds, canals, fish ponds and reservoirs. Although the majority of algae are found in aquatic habitats, some of those most commonly encountered are on paving stones, walls, gutters, roofs, glasshouses, tree trunks and wooden or concrete posts. Such subaerial algae are usually overlooked until they are present in sufficient quantity to form mats or crusts. In common with other cryptogamic groups, these algae are more diverse and evident in the wetter western parts of the British Isles.

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HISTORY OF FRESHWATER ALGAL STUDIES IN THE BRITISH ISLES

The Editors

Natural historians first started to look at algae carefully about two centuries ago, but no doubt many before then had noticed green slimes or algal blooms in their local pond. One of the earliest records for freshwater algae in the British Isles comes from Scotland. The twelfth century abbey of Soulseat, near Stranraer in Dumfries and Galloway, was described as 'monasterium viridis stagnii', or 'the Monastery of the Green Stank', as translated in a Victorian visitor's guide. Malodorous blooms, almost certainly caused by blue-green algae, frequently affected the Abbey, situated on a peninsula in a small lake; these blooms still persist to this day. As pointed out by Griffiths (1939b), the development of waterblooms could be a warning of impending tragedy. Two early chroniclers of a lake turning red at Finchampstead, Berkshire, forewarned of the untimely death of William Rufus in 1100.

There were a few scattered observations on freshwater algae during the eighteenth century, but mostly these were made on samples of common organisms used as demonstrations for the microscope. A 1777 record by Stephen Robson for *Chara hispida* (Plate 2E) in Hell Kettles, two well-known ponds in County Durham, is of interest, because this stonewort, which is about the largest alga in the British freshwater flora, still thrives in the same pond. Such old records are important, because they help us to assess the extent to which changes have taken place, but it was a century later before there were many records with sufficient detail to make such comparisons. This brief history of freshwater algal studies in the British Isles looks mostly at the older accounts, because these are the ones which readers are least likely to come across. A few of the more recent are mentioned, but for each one there are many more for which there is no space. Most research in recent decades by phycologists in the British Isles has been floristic or ecological and there are few critical taxonomic studies on freshwater algae other than diatoms and some green algae. Hopefully, someone will one day write a full account of research on British freshwater algae during the past half century, especially the wide range of ecological studies.

The first attempt to bring together existing knowledge was the publication of Dillwyn's *British Confervae* between 1802 and 1809, which included freshwater as well as marine algae. A few records relating to freshwater algae in Scotland appeared in Greville's *Flora Edinensis* (Greville, 1824) and many more in a series of volumes on the *Scottish Cryptogamic Flora* published between 1823 and 1828. Greville also prepared a contribution on diatoms for the second volume of Sir William Hooker's *British Flora* (Hooker, 1833). Twelve years later Hassall (1845) published the first forerunner of the present volume, *A History of the British Freshwater Algae*.

Prior to the appearance of Hassall's book, John Ralfs, a surgeon turned mycologist and phycologist, had published seven papers in the *Transactions of the Botanical Society of Edinburgh* and the *Annals and Magazine of Natural History* on one particular group of freshwater algae, the desmids. His name was to be indelibly linked with this species-rich group of green algae with the publication in 1848 of the *British Desmidiae*. In the introduction to this volume, now accepted as the starting point for the naming of desmids, he writes, 'Until a recent period, the study of minute objects which form the subject of this work had been more neglected than almost any other branch of Natural History', and went on to express the hope that he 'might be able to present to the British Naturalist such a description of our species as seemed necessary towards making the knowledge of them at home keep pace with its advance on the Continent'. He further comments, 'I soon discovered not only that we possessed many species hitherto undescribed, but that various points in their economy, not devoid of interest, remained still unexplained or doubtful'.

Within the next few years another group of algae, the diatoms, attracted the attention of microscopists and these are still the favourites of many professional and amateur microscopists. Smith's *Synopsis of the British Diatomaceae* appeared between 1853 and 1856. The great improvements in design and availability of microscopes in the last two decades of the nineteenth century led to a considerable increase in interest in freshwater algae in many parts of Europe, including the British Isles. Here, the Irish botanist, William Archer, was by far the most prolific, producing some 230 short notes and papers from 1858 to 1885. Most were published in the *Proceedings of the Dublin Microscopical Club* or the *Annals and Magazine of Natural History*. Most of his recordings and observations were made in the

Wicklow and Dublin areas, although just a few excursions were made to counties Galway and Wicklow. His accounts included descriptions of algae new to science as well as of their sexual reproduction and often complex walls. Almost all of his new records are listed in the section titled '*Hand-list of the algae of counties Dublin and Wicklow*' in a '*Guide to the County of Dublin*' (Macalister and M'Nab, 1878). For a full list of Archer's publications, see Prescott (1984) and Nordstedt (1896).

During the second half of the nineteenth century, further papers on British desmids were written by the microscopist M.C. Cooke: there was even a description of a new *Cosmarium* from Trafalgar Square (Cooke, 1880). From 1882 to 1884, this prolific author issued his *British Fresh-Water Algae*, and published in 1886 as a supplement to the latter, *British Desmids*. Sadly, as West and Fritsch were to comment (West and Fritsch, 1927, p. 1), neither his work nor Wolle's *Freshwater Algae of the United States* (published in 1887), contributed much to further knowledge of the algae. Indeed they believed some of Cooke's illustrations were positively misleading and stated (op. cit., p. 2) that 'It may be doubted if 25 per cent of the British freshwater algae could be identified with certainty from Cooke's book'!

William West and his son, George S. West, were the leading figures in freshwater botany in Britain over some 40 years, starting in the late 1870s. Together they made immense contributions to the taxonomy and distribution of the British freshwater algae. They travelled by rail, carriage, pony and steamer to many parts of the British Isles, making extensive collections not only in the more accessible parts of England, but also in the then remote regions of Scotland, Ireland and North Wales. As the Wests became increasingly acknowledged as leading world experts on freshwater algae, their opinions were sought on material from many countries – Spain, Portugal, Denmark, USA, the West Indies, Africa, the Far East, Australia and even Antarctica. Some 140 papers, monographs and books were published between 1888 and 1918. For the British Isles there were descriptions of more than 500 taxa, of which 210 were new to science. The great achievement of the Wests was to prepare a series of monographs in which all known British desmids were described and illustrated. This is the five-volume *Monograph of the British Desmidiaceae* (West and West, 1904a, 1905, 1908, 1911 and 1923). Nellie Carter, one of G.S. West's students, completed the final volume following G.S. West's death in the 'flu epidemic of 1919 at just 43 years of age. Nellie Carter told one of the editors (DMJ) that, had he lived, G.S. West almost certainly intended writing a British Freshwater Algal Flora in a format similar to that of the desmid monograph. He was proposing to describe all the genera and species of freshwater algae known to occur in the British Isles. More about the Wests, father and son, can be found in the article by John, Huxley and Williamson in the DVD.

Researchers who made substantial contributions in the following decades included Carter herself, F.E. Fritsch, B.M. Griffiths, W.H. Pearsall, M.F. Rich and M. Rosenberg. Fritsch is best known internationally for his comprehensive two-volume *The Structure and Reproduction of the Algae*, but for the British Isles *A Treatise of the British Freshwater Algae* was as important. The first edition was published by G.S. West in 1904 and Fritsch became a co-author of a substantially revised second edition in 1927. Fritsch was Professor of Botany at Queen Mary College, London, and had a great influence not only through his own research, but also the training and encouragement he gave to many students. One of his most lasting contributions is the collection of published illustrations of freshwater algae, now housed at the Freshwater Biological Association at Windermere as 'The Fritsch Collection of Illustrations of Freshwater Algae'. This became of major assistance to those working on algal taxonomy worldwide (Lund, 1961e) and the Collection became available in 1964 in the form of a microfiche with regular supplements prepared by J.W.G. Lund and colleagues. The microfiche edition was published by Interdocumentation Company AG, Switzerland (IDC). It is now hoped to make at least part of the Collection freely available on the worldwide web. Fritsch also provided the first detailed accounts for the British Isles of algal communities in several types of environment, particularly fast-flowing streams and phytoplankton in rivers.

Early accounts of lake phytoplankton are especially valuable if they are detailed enough to permit comparisons between old and recent surveys. Some of those by the Wests, Griffiths and Pearsall are useful for this purpose, although considerable care is needed in comparing different sets of records because of uncertainty about sampling methods, name changes and misidentification (Whitton, 1974). Some of the early phytoplankton studies included comparisons from a range of lakes and led to biological classifications of lake types. The survey by the Wests (W. and G.S. West, 1909a) was an early example, although the best known surveys were those of Pearsall (1924, 1930, 1932) in the English Lake District, which increasingly combined environmental data with phytoplankton studies. A modern synthesis of this information has been given by Talling and Heaney (1988).

Fritsch and Pearsall succeeded in raising funds for the establishment in 1931 of a laboratory to study all aspects of the freshwaters of the British Isles. The birth of the Freshwater Biological Association on the shores of (Lake) Windermere in Cumbria, housed at first in the mock-Tudor Wray Castle, later in the converted Ferry House Hotel, led to detailed, long-term surveys of the phytoplankton of the English Lake District. For instance, J.W.G. Lund and colleagues combined regular measurements starting in the late 1940s of algal cell densities in Windermere and other lakes with experimental studies on the diatoms *Asterionella formosa* and *Melosira italica*. By the 1970s these had not only provided considerable insight into the ecology of these widely distributed