

#### FLORA OF GREAT BRITAIN AND IRELAND

This definitive flora provides detailed accounts of the native species, naturalised species, frequent garden escapes and casuals found in the British Isles, including some newly described ones. Full keys and descriptions enable the user to name all plants occurring in the wild and some ornamental trees and shrubs. For the first time, accounts of all the large apomictic genera are included. Each species entry begins with the accepted Latin name, synonyms and English name. A detailed description follows, with the flowering period and chromosome number. Separate descriptions are provided for infraspecific taxa and many hybrids. The status, ecology and distribution (including worldwide distribution) of the taxa are also given. Black and white line drawings illustrate an extensive glossary and illuminate the diagnostic features in several genera. This final volume of five includes historical and taxonomic introductions to the whole project and covers the pteridophytes, gymnosperms and 44 families of angiosperms.

PETER SELL (1929–2013) joined the Herbarium in the University of Cambridge's Department of Plant Sciences in 1944, holding the post of Assistant Curator from 1972 until his retirement in 1997. From 1997 to 2013 his work there on this flora continued unabated, together with frequent visits to the University's Botanic Garden throughout the flowering and fruiting seasons. He was co-author of *A Flora of Cambridgeshire* (1964) and *A Flora of the Maltese Islands* (1977), and was involved in the whole *Flora Europaea* project, also published in five volumes (1964–80) by Cambridge University Press.

GINA MURRELL joined the Herbarium in the University of Cambridge's Department of Plant Sciences in 1966, where she held the post of Assistant Curator from 2002 until her retirement in 2011. She worked with Peter Sell over a period of 45 years, and together they collected a quarter of the British Herbarium's 200,000 specimens.

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Peter Sell , Gina Murrell  
Frontmatter  
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FLORA  
OF  
GREAT BRITAIN  
AND  
IRELAND

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VOLUME 1  
LYCOPODIACEAE – SALICACEAE

PETER SELL and GINA MURRELL  
*Herbarium, Department of Plant Sciences  
University of Cambridge*

*Illustrated by Sarah Holme, Alan Leslie and Gina Murrell*



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*To our Mentors*

EDRED JOHN HENRY CORNER  
JAMES EDGAR DANDY  
HUMPHREY GILBERT-CARTER  
HARRY GODWIN  
WILLIAM THOMAS STEARN  
STUART MAX WALTERS  
ALEXANDER STUART WATT  
CYRIL WEST

Certainly no clear line of demarcation has as yet been drawn between species and sub-species – that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage.

Charles Darwin, *On the origin of species* (1859).

The whole genus [*Calystegia*], in which some 25 species world-wide may conveniently be recognised, is taxonomically difficult, and few if any of the species are morphologically clear-cut. They mostly vary considerably over their ranges and merge geographically one into another, and division into species and subspecies is of necessity somewhat arbitrary.

Dick Brummitt & Arthur Chater, *Watsonia* **23**: 161 (2000).

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## Foreword

### VOLUME 5

It has been one of the continuing satisfactions of my academic career in Cambridge that the University Herbarium, of which I was Curator from 1948 to 1973, has provided an academic base for all my specialist interest in Angiosperm taxonomy to develop. Indeed, I count myself doubly fortunate that, twelve years after my retirement from academic life, the Herbarium, with its staff and visitors, still provides such a base where scholarship can be pursued for its own sake. With great pleasure I welcome this volume, the first of a set of five promised to us by Peter Sell and Gina Murrell. My association with Peter goes back more than half a century: though I was 'senior partner' in our happy collaboration in the post-war Herbarium, ours was a symbiotic relationship from which we both greatly benefited, and I was delighted when Gina, who had been part of the team in the 1960s and 1970s, returned to the fold as Herbarium Technician in 1991.

As explained in the Preface, this project to write an entirely new critical flora of Great Britain and Ireland comes to fruition some twenty years after an earlier scheme, in which the late Professor David Valentine took a leading part, had failed to find any financial support. Both Clive Stace, to whose *New Flora of the British Isles* (1991) Peter pays tribute in the Preface, and Peter himself, were enthusiastic supporters of the Valentine project, and were prepared to play major parts in writing the Flora. It is fitting that both these eminent British taxonomists should separately carry on the tradition that David Valentine so enthusiastically advocated.

Two aspects of this new critical flora seem to be especially important. One concerns the acceptance, long overdue, of the 'alien element' in our flora as being equally worthy of taxonomic study: in this respect Stace's *Flora* represents a real change in attitude, which is to my mind unreservedly to be welcomed. The other, interestingly linked to the first by many examples, concerns the taxonomic recognition and treatment of hybrids and infraspecific variants. British botany lacks any single reference work from which the basic information about the variation of British vascular plants can be found, yet this information is increasingly needed by ecologists, conservationists, molecular biologists and biochemists, who will, as the century closes, determine the shape of much botanical study in Universities and specialised Institutions.

The authors of this impressive work have set themselves a colossal task. They have made an excellent start, and we can only wish them a successful conclusion.

S. M. Walters  
1996

### VOLUME 4

It is for me a very real pleasure to add a further word to welcome this, the second volume of 'Sell & Murrell', as this remarkable Flora is now widely known among British botanists. Of course, this new volume, containing in particular the genus *Hieracium*, must rank as Peter's very own 'labour of love'. One of the very special links that has grown up between Peter and me over our long-standing acquaintance in the pursuit of taxonomic botany must be our steady, persistent enthusiasm for critical apomictic genera. We do not have to explain or justify to each other our passions for, in my case, *Alchemilla*, and his for *Hieracium*. I have to admit, however, that his task, with 412 named and described species of *Hieracium* in this volume, casts my puny efforts with British *Alchemilla* into the shade!

Talking to Peter and Gina about the progress of this remarkable Flora, I am encouraged by what I hear. I really believe that both Peter and I will live to see its completion, in spite of the fact that we both 'creak a little at the joints' – to use one of the common euphemisms we find ourselves using from time to time to describe our state of health!

One final observation. How fortunate Peter is to have such a remarkable fellow-author in Gina! Writing and publishing books involves much more than producing a draft text. Some of the skill is straightforward, if laborious; but some requires real understanding at the level of human relations, and both these skills are possessed in abundance by Gina. So I conclude by saying to both Peter and Gina: keep up the good work to a successful conclusion.

S. M. Walters  
13 February 2002

### VOLUME 3

Sadly, Max died on the 11 December 2005. He strongly approved of our whole attitude towards variation and introductions and fully understood the treatment of apomictic genera. In Max, Cambridge had a leader in taxonomic botany and conservation of our flora for over 50 years. See his obituary in *Watsonia* 26: 215–217 (2007).

Peter Sell  
2007

## VOLUME 2

When Peter Sell died on 10 October 2013, he had written the text of the two remaining volumes of this *Flora of Great Britain and Ireland*. Gina Murrell had already retired at the end of 2011 and moved away from Cambridge. We, four friends of Peter, therefore agreed to see Volumes 2 and 1 through the press, consulting Gina on key issues. As explained in the Acknowledgements in this volume, Gwynn Ellis had already typed the text, and he and Roy Perry had checked it and incorporated amendments in consultation with Peter. Nevertheless, further checking and correction were necessary, which we have tried to do without altering the taxonomy or, in general, the substance of the text, so that we hope that this volume is as close as is possible to what Peter would have wanted. We have usually not attempted to update the accounts with information published since they were completed. Before Roy Perry's untimely death in November 2014 we continued to receive great help from him, and we have also been very fortunate in recruiting Jane Bulleid to assist with the proofreading.

Arthur O. Chater  
R. Gwynn Ellis  
Philip H. Oswald  
Chris D. Preston  
November 2014

## VOLUME 1

Once again, the four of us have collaborated in seeing this volume through the press. When Gina Murrell retired from the Cambridge University Herbarium at the end of 2011 she had just completed the typing of Peter Sell's first draft of this volume, and, although he decided that Volume 2 should be published first, he did see and approve our edited versions of substantial parts of Volume 1 before he died. These included, importantly, the section containing new taxa and combinations, though we had to make a few adjustments to take account of new combinations in the Polygonaceae that Peter was intending to make but which were created first by John Akeroyd in *Contribujii Botanice, Chuj* 48: 15–21 (2013) in preparation for his B.S.B.I. handbook, *Docks and Knotweeds of Britain and Ireland*, published in 2014. We have also updated Peter's preface and acknowledgements, originally drafted in 2010, and expanded the glossary to relate to all five volumes of this work. Similarly, R.G.E. has compiled an index to the genera included in all five volumes in addition to the usual index to the Latin and English names of the taxa described in this volume. For this final volume P. H. O. has undertaken the onerous task of co-ordinating our work and negotiating with Cambridge University Press.

Arthur O. Chater  
R. Gwynn Ellis  
Philip H. Oswald  
Chris D. Preston  
June 2017

## Preface and acknowledgements

For 70 years I have worked in the Herbarium at Cambridge University on the British and European floras. I have collected, often with Gina's company, about 30,000 numbers consisting of some 50,000 specimens from most parts of the British Isles and made many visits to Continental Europe. Particular attention has been given to most critical genera: *Cerastium*, *Chenopodium*, *Conyza*, *Crepis*, *Dactylorhiza*, *Euphrasia*, *Fumaria*, *Hieracium*, *Limonium*, *Polygonum*, *Pilosella*, *Prunus*, *Rhinanthus*, *Rumex*, *Salicornia*, *Salix*, *Scleranthus*, *Sorbus* and *Ulmus*. In helping friends in various ways I have also considered the taxonomy of *Alchemilla*, *Ranunculus* subgenus *Batrachium*, *Potamogeton*, *Rubus* and *Taraxacum*. I have also spent much time studying ecotypic and geographical variation, in particular comparing those variants which occur on the coasts in dunes, shingle and saltmarsh with those growing as arable weeds and with those in mountains. Special attention has also been given to trees and shrubs.

It had long been my wish to publish this information in a critical flora of Great Britain and Ireland. In the 1970s a group of us tried to get a grant to carry this out, but we were unsuccessful. Clive Stace then started work on his *New Flora of the British Isles*, which was first published in 1991, with a second edition in 1997 and a third in 2010. In it he gives only short descriptions and omits most of the species in the large apomictic genera and many of the infraspecific variants whose differences are not apparent in his abbreviated diagnoses. Numerous introduced species are included by Stace in a British and Irish flora for the first time, detailed descriptions and specimens of many of which have previously been difficult to find. Stace's flora is to my mind an excellent field guide, which it would be difficult to better, but it does not give the detailed descriptions that are needed to confirm the identification of a plant which is new to you. A good description in my opinion is one in which *a picture of the plant unfolds before you as you read it and includes as much of the variation as possible*.

I considered that it was possible for me to write a flora in five volumes which gave a full description of all the species in Stace's flora and to add all the apomicts and many of the infraspecific variants, but it was too large a task to attempt to include all the biological information envisaged by the group in the 1970s. It was necessary, however, to have the help of another author who lived in Cambridge, to deal with the large amount of work involved. My eye fell upon Gina Murrell, who had worked with me in the 1960s and 1970s when writing accounts for *Flora Europaea*, *Flora of Turkey* and *Flora of the Maltese Islands*. The work of one had complemented the work of the other and we were able to criticise one another without antagonism. We started fieldwork for this flora on 13 May

1987, by describing *Ceratocarpus claviculata*, which was flowering on Dunwich Heath in Suffolk, in a snowstorm. Gina returned to work officially in the Herbarium on 21 February 1991. Since then we have as far as possible spent one day a week working in the field or at the University Botanic Garden. We started writing Volume 5 in 1992 and completed it by Easter 1994. It was published on 10 April 1997, not in 1996 as stated in the volume itself.

I have done most of the writing and made the taxonomic and nomenclatural decisions. In the early days Gina did much of the measuring, sometimes sitting at the microscope dictating the description while I, surrounded by a pile of books, wrote it down. Gina also did most of the typing, drew most of the illustrations and organised much of our early fieldwork: without her this flora would not have happened. The illustrations, often diagrammatic, are intended mainly to give the shape of parts, which are often immensely variable in size, the range of measurements being given in the text. Volume 5 contained 28 families, 233 genera, 769 species, 93 subspecies, 148 varieties, 22 formae and 182 hybrids. Volume 4 contained an introduction and full accounts of seven families, 146 genera, 1098 species, 130 subspecies, 162 varieties, 27 formae and 51 hybrids. It dealt with a whole range of taxa from very variable species which we felt could not be further divided to species with geographical races, ecotypes, forms and cultivars. The taxa could be outbreeding, inbreeding, apomictic or spreading vegetatively. Volume 3 contained a number of difficult groups including *Euphrasia* and *Mentha* but no really large apomictic genera. It also contained the first major groups of introduced trees. The accounts are of 59 families, 299 genera, 996 species, 187 subspecies, 308 varieties, 102 formae and 235 hybrids. Volume 2 contained the large and difficult genera *Rubus*, *Rosa* and *Cotoneaster* and included 18 families, 148 genera, 1122 species, 65 subspecies, 221 varieties, 53 formae and 93 hybrids. Volume 1 contains a large number of introduced trees as well as a complete revision of the elms (*Ulmus*). Alan Leslie has supplied the first critical treatment of the apomictic *Ranunculus auricomus* aggregate for this country. Included are 72 families, 242 genera, 1077 species, 195 subspecies, 363 varieties, 61 formae and 267 hybrids. The whole series contains accounts of 184 families, 1068 genera, 5062 species, 670 subspecies, 1202 varieties, 265 formae and 828 hybrids, with a total of over 8000 subgeneric taxa.

David Briggs, who was Curator of the Cambridge University Herbarium from 1974 to 2001, published a book in 2009 called *Plant microevolution and conservation in human-influenced ecosystems*, which puts in perspective the vast number of subspecies, varieties, forms and hybrids, including intermediates, in this flora, but

unfortunately only talks of species and their variation and rarely mentions infraspecific names. We are in complete agreement with him that evolution, especially micro-evolution, is happening at the moment, but we cannot see how you can talk about it unless at least the more prominent taxa have names, for example the numerous cases discussed at the end of the Introduction to the present volume and described fully in the text. The other thing of importance is the vast number of species, subspecies, varieties, intermediates and hybrids which are being planted by conservationists and others but which are non-British variants. The origin and distribution of two varieties of the same species are often very different, as are their ecology and flowering time, especially if one of them is introduced. We strongly recommend David Briggs' book be read by all students of our flora.

Also, how wonderful and enlightening it would be if all the species in Volumes 1–5 of J. S. Rodwell's *British plant communities* (1991–2000) could have infraspecific names added and if the terminology of floristic elements as applied in Preston, Pearman & Dines' *New atlas of the British and Irish flora* (2002) was also applied to infraspecific taxa. These two developments would open up a whole new understanding of the origin and evolution of our flora, especially if their DNA was looked at as well. Arthur Chater's *Flora of Cardiganshire* (2010) gives numerous examples of the distribution of infraspecific taxa in that county.

My life has been almost a hundred per cent devoted to the flora and with occasional exceptions followed a strict routine. I was in Cambridge University Botanic Garden on most weekdays at 07.00 hrs. For the next hour I either looked at some particular species or made notes on a general walk around the Garden. A very large number of the plants described in this flora can be found in the Garden and seeing them day after day was extremely helpful. I then often briefly saw John Parker and he usually did his best to explain any cytological and genetical problems concerning the plants I was dealing with. At 08.00 hrs Gina picked me up and drove me to the Herbarium. On the way I brought her up to date with what I had seen that morning. I worked on the flora all day with only a brief break for lunch. I regularly put in two more hours in the evening at home. On Friday afternoons I used to go to Histon to walk the fields with Bryan and Rosemary Chapman. On Saturdays I went to Bassingbourn to walk the fields there with Bill Robinson.

My whole attitude towards the study of the British flora is based on what Agatha Christie called a life-long education in an English village at one end, which allowed me to understand what happened there from the Norman Conquest to the present day, and the inspiration and resources of a great university at the other. I am greatly indebted to the farmers of Bassingbourn, who have always allowed me to walk on their land.

The build-up of knowledge and experience required to write this flora took many years, with help and encouragement from many people, to whom I wish to give my sincere thanks:

To Arthur Harcourt, former headmaster of Bassingbourn Council School, who started it all by arranging work for me at the Cambridge University Herbarium when I left school, aged 14.

To Arthur Gray, Herbarium Technician for 50 years, who stayed on a year past his retirement date to instruct a 14-year-old boy in the skills and techniques of herbaria.

To Humphrey Gilbert-Carter, who taught me to identify plants properly and instilled in me a love of words.

To Frederick Thomas Brooks, who paid from his own pocket for me to be taught Latin.

To Bryan Golding, with whom I spent all my early days in the field, he bird-watching while I looked at the plants; we had the best of both worlds. We also had memorable trips to the south of France and the Carmargue, Malta, Flamborough Head, Pembrokeshire and Scotland.

To Max Walters, who encouraged me in everything I did and took me on a never to be forgotten 2000-mile tour of Ireland in 1952 with David Webb, Tom Tutin, Roy Clapham, Donald Pigott and Tige Böcher. He also took me on many excursions to Wales, Scotland, the south of France, Czechoslovakia, Yugoslavia and Majorca. We had a very informative trip to Upper Teesdale to collect all the *Alchemilla* species found there.

To Frank Harrup, with whom I spent three weeks in southern Spain and the Marismos.

To Charles and John Raven, who took me on a trip, driven by Dick Burges, from Gloucestershire, through Wales, up to the Yorkshire limestone, finishing at Langdon Beck in Upper Teesdale and seeing over 60 species of *Hieracium* as well as many rare plants.

To Cyril West, with whom I spent 30 years studying *Hieracium* and with whom I shared a remarkable trip to Sutherland with Norman Douglas Simpson.

To Eric George, who spent much of one summer taking me to most of the ponds, lakes and other open waters of the Fenland.

To James Dandy, who taught me nomenclature. As far as I know I was the only person he so instructed.

To Willie Stearn, who was a walking encyclopedia on the history of botany and whose *Botanical Latin* (1992) is a botanical bible.

To John Corner for much information and experiences received while working together.

To David Coombe, who between 06.00 and 22.00 hrs showed me many rare plants on the journey between Cambridge and Cornwall, and in the next 10 very long days showed me all the rare plants of the Lizard Peninsula.

To Charles Turner, who took me on a 4000-mile trip around Europe, through Belgium, Germany, Austria, Hungary, Yugoslavia, Italy, Switzerland and France.

To Archie Kenneth, who transformed my knowledge of the *Hieracia* of western Scotland, with two long field trips, especially in Ross-shire, which was practically unknown, and for an adventurous day on Arran.

To Ursula Duncan, who said "If you come to Clova I will show you all its rare plants", and she did.

To Caroline McCruddon, with whom I spent many happy days doing fieldwork in Norfolk and who took me

to Northumberland for a holiday after I had been ill. She also arranged for me to stay with her at Oxford so that I could work on the Druce herbarium.

Also thanks to all the young lady Technicians of the Cambridge Herbarium over the past 60 years who helped to make it such a very happy place to work.

The most constant help for the whole of this flora has come from a number of Cambridge scholars. Max Walters, former Curator of the Herbarium and Director of the Botanic Garden at Cambridge, fully supported us in all that we did up to his death in 2005 (Sell, 2007). He translated much German and Swedish for us and was always willing to give an opinion on taxonomic problems. Philip Oswald has not only written a very considerable amount of Latin for us, but has also translated Latin, Greek and French. In fact he used to say that, whenever he picked up the phone for a call from us, he would almost certainly have to fetch more than one dictionary. Chris Preston read much of the text of the early volumes and particularly helped us with plant distributions before *New atlas of the British flora* was published. Arthur Chater has been the great adjudicator of the flora, continually facing a multitude of questions on a wide range of subjects on which his opinion has been most helpful, particularly in that much of his fieldwork has been done on the opposite side of the country from most of ours. John Parker has given us an enormous amount of advice on genetics, which was especially useful because he knows his plants in the field. He also gave us complete freedom to work in the University Botanic Garden, of which he was Director. All the Botanic Garden and Office staff have given us much help over many years and some are mentioned in the text. Alan Leslie has not only written the account of the *Ranunculus auricomus* aggregate but has given us much help with aliens and garden escapes. James Cullen frequently made useful comments on what we were doing, particularly helping us with the account of the *Rhododendron ponticum* aggregate.

David Tennant and Desmond Meikle supplied much information on *Salix* and looked over our account of the genus. Charlie Jarvis has helped us with Linnaean types and has now published his full account of them (2007). Gina Douglas helped us while working at the Linnean Society in Burlington House. To Mrs J. E. Dandy we owe a special debt for giving us the second copy of her late husband's manuscript of his detailed nomenclatural work on the British flora. To Bill and Joan Robinson we are grateful for letting us frequently raid their garden and for allowing some of their vegetables to go to flower and seed so that we could make complete specimens. P. D. S. owes a very special debt to Brian and Rosemary Chapman, who took him around Histon on over a hundred walks. To Clive Stace we also owe a special debt: had he not written his *New flora of the British Isles* our task would have been insurmountable.

The late Richard Savage and the current librarian Christine Alexander in the Department of Plant Sciences have gone out of their way to track down rare and obscure publications for us. In the new Herbarium in the Botanic Garden Christine Bartram has been an immense help in

finding both plant specimens and books. Professor Enid McRobbie, Professor Roger Leigh, Professor John Gray and Professor Sir David Baulcombe have allowed P. D. S. to have full use of the Herbarium and Library of the Department of Plant Sciences after his retirement. Many other botanists, worldwide, have helped us at various times.

Lastly a very special thank you to Arthur Chater, Gwynn Ellis, Philip Oswald and Chris Preston for their combined work in preparing the texts of Volumes 1 and 2 for the press and to Sarah Holme, who has drawn most of the illustrations for these two volumes. We are also grateful to the late Roy Perry and to Jane Bulleid for assisting them in the work on Volume 2.

Having thanked a great many people about the botanical side of things, I wish to say that none of this flora would have happened without the immense support of my family. In my youth my mother and Uncle Maurice supported and helped me in everything I did. Whether I got covered in mud or tore my clothes, nothing was ever said. The only worry they ever had was that I would fall in the coprolite pit, which was one of my favourite haunts, for I roamed the fields of Bassingbourn from the age of four or five onwards. My early life spent on a working farm was very important when it came to the study of weeds. Two maiden aunts, Katie and Elsie, who lived in Ealing, came to Bassingbourn for all their holidays, and they bought me all my first books, for I was an avid reader. They also put me up when I later wished to visit London. In my old age my son Tim and his wife Judi somehow kept me going through much illness. To come home to the chatter of my three grandchildren, Alex, Ellen and Hannah, not forgetting the constant presence of the cats, Polly and Peggy, has been a very important factor in the production of the flora's two and a half million words. On top of it all Gina became almost an additional member of my family in the way that she looked after me at work. We have worked together in the Herbarium for 45 years, done an immense amount of fieldwork in East Anglia and made important trips to the New Forest, Wales, Cornwall, Dorset and Kent and many visits to the British Museum Herbarium, Kew and the Linnean Society.

Peter Sell  
 2010 (with updating by the editors in 2017)

## GINA'S PIECE

My association with the University of Cambridge started in the summer of 1966, when I accepted a post of Junior Technician in the Herbarium of the University Botany School. I was quickly introduced to a host of informed and learned plants people – Professor E. J. H. Corner, tropical botanist; Dr S. M. Walters, Herbarium Curator; Dr Peter Yeo, Botanic Garden Taxonomist; Peter Sell, Senior Herbarium Technician; the many Ph.D. students; and the other technical staff of the Herbarium. In addition there was daily interaction with local visitors, scholars

and eminent botanists from university departments and institutes around the world. The Herbarium was a hive of activity within a Department of Botany where everyone understood our ‘buzz words’, taxonomy and nomenclature. From early spring to the end of summer and throughout the University’s Long Vacation I attended field trips for plant collecting, teaching and identification. In the Herbarium I pressed, dried, mounted and incorporated into the main collections the plant specimens collected during those field trips. I became interested in the strong tradition of flora-writing and absolutely fascinated by plants, their collectors and the long history of botany in Cambridge.

During my first 10 years of employment all Herbarium staff were much involved in research, writing plant accounts, typing and publishing floras such as *Flora of Turkey*, *Flora of the Maltese Islands* and *Flora Europaea*. The five-volume *Flora Europaea* published by Cambridge University Press had a large number of editors, organisers, advisers and contributors who collaborated to produce the first general diagnostic and descriptive flora of the plants of Europe. The most modern evidence in plant morphology, geography, ecology and cytogenetics was considered when producing these volumes. Towards the end of the process Peter Sell and some of the *Flora Europaea* collaborators discussed the possibility of writing a similar but much more detailed flora of the British Isles, but with no grant funding available at that time this new project didn’t get started.

Near the end of 1986 I received a letter from Peter in which he detailed his proposal for a new British flora. He invited me to join him as co-author in producing, not a mere field guide, but a critical flora with full descriptions of native, naturalised and ‘alien’ or introduced species,

including those of apomictic genera and infraspecific variants. I accepted his offer eagerly, and we started our field research together on 13 May 1987 in a snowstorm on Dunwich Heath, Suffolk. Research in the field took us both to many and varied localities, not forgetting many visits to other major herbaria. Over the next 10 years, I filled 15 ledger files with detailed plant notes, descriptions and observational drawings while Peter wrote the flora manuscript almost continuously from these and his own copious field notes. We also visited the Balearic Islands as part of a Cambridge group field trip. Peter travelled in Austria, Czechoslovakia, France, Germany, Italy, Spain and Yugoslavia, while I have also been to the Canary Islands, Greece, Madeira, Portugal, Turkey and most recently Australia. Therefore we have both seen varied floras in a number of different countries.

I had no concept in 1987 of how life-changing or life-enhancing producing a flora would be, how much energy would be required or how long it would take us. Volume 5 of *Flora of Great Britain and Ireland* was published in 1997, Volume 4 in 2006, Volume 3 in 2009, and now with the help of others, Volumes 2 and 1 will follow. As I retire from my role as Senior Assistant Curator of the Cambridge University Herbarium, Peter enters his 67th year in botany. I have completed the typing of Volume 1, the manuscript for Volume 2 is written but is still to be typed and both have to be illustrated and put through the press. Thanks to a group of kind, generous botanical friends who are keen supporters of our work, I am very pleased to say that this will now be possible.

Gina Murrell  
October 2011

## *The Cambridge school of plant taxonomy*

A personal view  
 by  
 Peter Sell

Much of what is in this flora is owed to the great historic background to plant taxonomy here in Cambridge. One cannot but feel that one is following in a great tradition when studying the British and Irish floras in the Cambridge University Herbarium, its Library and the University Botanic Garden and when using them to work out the results of one's fieldwork.

When the modern western world took shape after the so-called Dark Ages it was France, Germany, Italy and the Low Countries that produced the pioneers of the science of botany. The medievalists were remote from any scientific appreciation of nature. An example of the work of a Cambridge scholar towards the end of that period is the book by John Maplet, *A greene forest, or A naturall historie vwherein may bee seene first the most sufferaigne vertues in all the whole kinde of stones & mettals: next of plants, as of herbes, trees, shrubs, lastly of brute beastes, foules, fishes, creeping wormes serpents*, published in 1567. It would be thought that by then the Renaissance and Reformation would have been established, but in thought this book is purely medieval. The breakdown of medieval ideas in England was to start at Oxford and then to be transferred to Cambridge, and it was the spirit of Erasmus in his writings, and above all in his edition of the New Testament, that gave an impetus to Greek studies and a new understanding of classical civilisation in the University.

Two men at Cambridge, William Turner and John Caius, can properly be said to have started the long line of field naturalists in Britain. Both studied in Italy and both were friends of the great Zurich naturalist Conrad Gesner. Of the two, William Turner was by far the more important botanically, being one of the most vigorous of reformers and our first scientific student of botany and zoology.

William Turner (1508–1568) was born at Morpeth in Northumberland and as a boy was said to notice the ways of animals and plants. In 1526 he went up to Pembroke Hall in Cambridge, where he stayed until 1537 and published a number of works. His teachings as a reformer got him into trouble and he went abroad, whether by order or his own choice is not known. He visited Belgium, Holland, Germany, Italy and Switzerland. He returned to England in the last year of Henry VIII's reign and stayed in the household of the Lord Protector, Edward Seymour, Duke of Somerset. He had brought over his Latin *Herball*, which he intended to publish, but the physicians he discussed it with advised delay. In fact at the request of the herbalists he first published in 1548

*The names of herbes in Greke, Latin, Englishe, Duche & Frenche wyth the commune names that Herbaries and Apotecaries use*. In 1551 the first instalment of *A new herball* was published in London. It is a small folio and contains 196 pages, with 196 woodcuts taken mainly from the octavo edition of Leonhart Fuchs's *De Historia Stirpium* published at Basel in 1546. The pictures have been copied and are reversed. The originals are beautifully designed and the depictions, although rough, can mostly be named if you know your plants well.

The death of Edward VI in 1553 again put Turner's life in jeopardy and he went to the continent in exile for a second time. He moved immediately to Germany and stayed there most of the time, but he also visited Switzerland. On Queen Mary's death in 1558 he returned to England. For some time he stayed in London, but he was finally reinstated to his position as Dean of Wells Cathedral, where he spent much of the rest of his life. His final edition of the *Herball* contains a fully revised edition of the 1551 volume, a reprint of Volume 2 of 1562 without correction, and a new third volume. His rather early death deprived English science of further work which was in preparation.

William Turner must be regarded as a true pioneer of natural history in England. When he started almost nothing was known of the ancient and scientific studies which Graeco-Roman culture bequeathed to Europe. His love for his country and his wish to impart knowledge to its people is shown by the fact that he published his *Herball* in English and not Latin as was standard at the time. Like most Cambridge taxonomists and ecologists he loved fieldwork and he spent much time in the Alps, along the Rhine, in Friesland, on the heaths and beaches of England, in the herb gardens of western Europe and in the parks of his patrons. Like any true scientist he found it necessary to name his plants accurately before he could try to understand their form and function. In his own day he stood alone as a scientific botanist in England. Charles Raven (1947) describes him as "a north-country man, outspoken in his comments upon men and things, contemptuous of ritual and clerical clothing, and defiant of ecclesiastical control". The description strikes a chord with some of the later Cambridge plant taxonomists.

Overlapping with William Turner was another Cambridge botanist, Thomas Penny. Born in Gressingham near Lancaster in 1530, Penny went up to Queens' College as a pensioner in 1546, but in 1550 he transferred to Trinity on a sizarship. He graduated in 1551, became

a Fellow in 1553 and Senior Bursar in 1564, and worked on divinity and medicine until 1565. He was ordained deacon at Ely on 8 June 1561, having been given the prebendary of Newington in St Paul's Cathedral in 1560. He was a strong supporter of the Reformation and was almost certainly a friend of William Turner, as he was of William's son Peter. He began to form a *hortus siccus* in his early years and later travelled widely in Europe, where he met Conrad Gesner and Mathias de l'Obel. His records were all published in other botanists' works, but his terse and exact descriptions with precise terminology portray all his species clearly. He died in 1588 and was buried in London.

The great advance towards modern science in the seventeenth century was brought about by the large number of men of genius who were the effective leaders of the first generation of the Royal Society. Inspired men of widely different tempers and beliefs such as John Wilkins (poly-math), William Petty (statistician, economist and doctor), Christopher Wren (architect and scholar), Robert Boyle (chemist), Isaac Barrow (mathematician and scholar), Nehemiah Grew (botanist) and Isaac Newton (physicist) came together, and Cambridge botany produced the great John Ray.

John Ray was born at Black Notley in Essex in 1627. He was educated at Braintree School, came up to Cambridge in 1644 and entered Catharine Hall as a pupil of Daniel Duckfield. In 1646 he transferred to Trinity as a pupil of James Dupont, graduated B.A. in 1647/1648, was elected a Minor Fellow in 1649, was appointed a Greek Lecturer and obtained his M.A. in 1652, became Mathematical Lecturer in 1653 and Humanities Lecturer in 1655 and was ordained in 1660. Little is known of his childhood except that he was the son of a blacksmith; living at Black Notley his world would have been very limited. He took no interest in politics and he made no comments about the fact that he was living in one of the most exciting periods of English history. He made a deliberate choice to be a student in his home village and not to be bothered by worldly affairs. Charles Raven (1942) has remarked: "Even if he did no scientific work until after his election to a fellowship in 1649 he must have been profoundly interested in nature; for his breadth of range, his power of acute and accurate observation, his flair for discriminating the vital from the superficial, bespeak not only natural gifts but of early habit. He had the authentic love of living things, animals, birds, insects and plants, of the countryside and its denizens, which marks the real naturalist." He had the very unusual gifts which do not usually go together of "the poet's sense of wholeness and life combined with the craftsman's concern for details of construction and process". He followed the best of traditional practices, but did his utmost to improve them.

Ray's study of botany began in 1650 when, convalescing from illness, he found the leisure to look at the plants growing around Cambridge, a pleasure which led to him to look at their characteristics and differences. In 1660 he published his *Catalogus plantarum circa Cantabrigiam nascentium*, a list of plants growing around Cambridge,

of which a new and extensively annotated edition was recently published by Philip Oswald and Chris Preston (2011). Ray wrote to his friends and acquaintances who knew the names of plants, asking them to send him lists of those which grew where they lived or visited. This enquiry led to his *Catalogus plantarum Angliae* in 1670 and that in turn to his *Synopsis methodica stirpium Britannicarum* in 1690. His knowledge was gained not only from correspondence but from extensive travel in the country on appalling roads and often in treacherous weather.

The main crisis in Ray's life was in 1662 with the enforcement of the Act of Uniformity, which implied that an oath was not binding, and some 2000 clergymen, among them Ray, forfeited their livings and appointments. This left Ray in extreme poverty, but he had befriended a young landowner, Francis Willughby (1635–1672), who now came to his aid and, by solving his pecuniary problems, freed him to give an immense contribution to European natural history. Together Ray and Willughby travelled many thousands of miles around England and Wales and, between 1663 and 1666, through the Low Countries, Rhineland Germany and Austria to Italy; Ray then went to Sicily, Malta, Switzerland and France. Willughby died prematurely at the age of 36, but he left Ray an annuity, which allowed him to carry on the good work.

For the rest of his life Ray prepared and published works on birds, fishes, insects and plants. The most important for the botanist was the massive three-volume *Historia plantarum* published in 1686, 1688 and 1704, which incorporates the results of his European travels. This work and Dillenius's edition (1724) of Ray's *Synopsis methodica stirpium Britannicarum* provided much of the information for Carl Linnaeus's *Species plantarum*, especially concerning the species which occurred in Britain and where Ray travelled in Europe. In all Ray added some 200 species to the British list. Ray's most popular book, *The wisdom of God manifested in the works of the creation*, was not published until 1691, in English. The Ray Society published a new edition in 2005, with an introduction by Max Walters published as a separate booklet. Charles Raven (1942, p. 452) wrote of Ray's book: "it supplied the background for the thought of Gilbert White ... and more than any other single book it initiated the true adventure of modern science...". Ray died in 1705 and was buried in his native village.

The first Professor of Botany in Cambridge was Richard Bradley (c. 1688–1732), who accepted a newly created Chair in 1724, a post which he held until his death in 1732. Bradley was a most prolific writer, mostly about agricultural and horticultural subjects, but his five volumes of *Historia plantarum succulentarum*, published in 1716–1727, are a considerable contribution to botany. Bradley's trouble seems to have been social, with gaps in his classical education as well as money problems. John Martyn and his son regarded him as disreputable and best forgotten, a view which lasted until the present century. The only lengthy accounts of him are by Max Walters (1981) and John Edmondson (2002).



Our second Professor of Botany, John Martyn, was born in 1699, the son of a wealthy merchant trading in London and Hamburg. His first botanical interests seem to have developed from field excursions with young friends organised by the Society of Apothecaries and centred on the Chelsea Physic Garden, where Philip Miller (1691–1771) was to write his famous *Gardeners' dictionary*, which ran to eight editions. Martyn developed a course of lectures, which he gave to the Botanical Society, formed in 1721. Eventually more than 20 scholars invited him to give a course of lectures in the Anatomy School in Cambridge in 1727. The introductory lecture was published as a booklet in 1729 and was clearly designed to teach young medical students plant morphology as a preliminary to learning to identify individual species. The booklet's value is much increased by its copious illustrations. Martyn was elected a Fellow of the Royal Society in 1727. In May 1730 he was admitted to Emmanuel College with the intention of taking a degree in medicine, but he abandoned it; he did, however, practise medicine, first at Bishopsgate and then after his marriage in 1732 at Chelsea. He was elected to the Chair of Botany at Cambridge in 1723, but from 1735 until his retirement from the Chair in 1762 he seems to have shown little interest in botany. His greatest usefulness to botanical taxonomy at Cambridge was the final bequeathing by his son of his herbarium and library to the University.

John Martyn's son Thomas was born in Church Lane, Chelsea, in 1735. When he was 17 years old his father arranged for his admission to his own college, Emmanuel. He was elected a Fellow of Sidney Sussex College in 1758. He married the Master's sister in 1773 and resided at Thriplow until 1776. His smooth succession to the Professorship at the age of 26 on his father's retirement must have owed much to grooming by his father. Despite his long tenure of 63 years, Thomas Martyn added no new specimens to his father's herbarium. Memoirs of the Martyns were published by Gorham (1830).

The successful foundation of a Botanic Garden in Cambridge came about when the Vice-Master of Trinity College, Richard Walker, purchased a plot of ground on 16 July 1760 and gave it to the University on 25 August 1762 in trust "for the purpose of a public Botanic Garden". This original Garden was laid out by Free School Lane on the site of the ancient Monastery of the Austin Friars. In 1771 Thomas Martyn published *Catalogus horti botanici Cantabrigiensis*, and in a small *Mantissa* of 31 pages published the following year he included a plan of the Garden.

The old Mansion House, which Walker had bought with the land, was sold in 1784. In 1787 the University erected a lecture room and ancillary building. In this way the New Museums Site gradually became the centre of Natural Science in the University. The most famous Curator of this first Garden was James Donn, who had trained under William Aiton at Kew and who published seven editions of his famous *Hortus Cantabrigiensis* between 1796 and 1812. These catalogues included plants from other gardens as well as from Cambridge.

The fourth Professor of Botany, John Stevens Henslow (1796–1861), was one of our great teachers and he was to lead the way to a rejuvenation of botany in Cambridge. He was born in Rochester, Kent, and went to a private school in Camberwell. He was said to have found his studies easy and entered St John's College, Cambridge, in 1814. He also took lectures in chemistry and mineralogy, which were not relevant to his Tripos studies. Zoology was his main pursuit; botany he had hardly taken up. The geologist Adam Sedgwick greatly influenced Henslow, who was first elected to the Chair of Mineralogy. Why he moved to the Chair of Botany is not clear, as he then knew little about the subject. He and Adam Sedgwick thought it would be useful to have a society to promote the study of science in Cambridge and so in 1819 the Cambridge Philosophical Society was founded. One of the undergraduates influenced by Henslow was Leonard Jenyns of Bottisham Hall. Through their friendship Henslow met his future wife, Harriet, Jenyns' sister. They were married in 1823 and set up house in Cambridge.

Henslow was ordained and became a Curate at Little St Mary's Church in 1824. He obtained the living of Cholsecum-Moulsford in Berkshire in 1832 and spent the Long Vacations there. He remained in Cambridge until 1839, two years after being presented by the Crown with the valuable living of Hitcham in Suffolk. His Easter Term Course was apparently given without a break for 25 years between 1825 and 1850, though it had a relatively poor attendance in later years when his great influence as a teacher in Cambridge was coming to an end.

Henslow's most famous pupil was Charles Darwin and his role in recommending Darwin for the post of naturalist on the voyage of the *Beagle* was crucial in Darwin's development of the theory of evolution by natural selection. Henslow not only gave lectures but introduced the practical class and the demonstration bench. While building up his British herbarium at Cambridge he had a network of botanical friends in different parts of the country who sent him specimens. These he mounted beautifully on herbarium sheets to show as much variation as possible, and, if they were small plants and he could fit several on a sheet, he would arrange them to show a gradually changing series. He would surely have used some of these specimens in his teaching and they would have been seen by his student Darwin (see Kohn et al., 2005). In the Botanic Garden several groups of mature trees are planted together to show variation and hybridisation and it is difficult to believe that Henslow was not responsible. They were very useful when we were writing this flora. Henslow's friendship with Darwin brought most of the natural history material collected on the voyage of the *Beagle*, including the plants, to Cambridge University. There are over 900 herbarium sheets from this voyage.

It is almost certain that it was Henslow's influence which brought four other great collections to the Cambridge Herbarium. John Lindley's (1799–1865; Anon., 1865) 58,000 sheets were bought by the University, Charles Morgan Lemann's (1806–1852) over 50,000 sheets, all

named by George Bentham, a large number of Joseph Hooker's duplicates from Kew, and Sir Charles James Fox Bunbury's (1809–1886; Anon., 1887; Lyell, 1906) large private herbarium were also acquired. The Lindley, Lemann and Hooker herbaria are very important for this flora as they contain original specimens of many of the plants introduced into our gardens and show what they were like before any selection took place. Biographies of Henslow have been written by Russell-Gebbett (1977) and Walters & Stow (2001).

Samuel Frederick Gray (1766–1828) and his son John Edward Gray (1800–1875) may possibly have little connection with Cambridge, but they were the first botanists to introduce to the British flora the natural arrangement of the French botanists. A two-volume work entitled *A natural arrangement of British plants, according to their relations to each other, as pointed out by Jussieu, De Candolle, Brown, &c. including those cultivated for use; with an introduction to botany, in which the terms newly introduced are explained* was written by S. F. Gray with the assistance of his son and published in 1821. The connection with Cambridge seems to be that Henslow in *A catalogue of British plants arranged according to the natural system* in 1829 and Babington in his *Manual of British botany* in 1843 were the next British botanists to take up this classification. Most British botanists still used the Linnaean system, led by J. E. Smith, who bought the Linnaean Herbarium. J. E. Gray was vetoed by a large majority from becoming a Fellow of the Linnean Society, probably because he did not use the Linnaean system. The enlightened Cambridge attitude may well have been the reason for his wife leaving her collection of algae and her husband's collection of British flowering plants to Cambridge, despite J. E. Gray working at the British Museum all his life. The 1821 work includes many new taxa including varieties, although the names are often illegitimate. I cannot help feeling that this little-known book (eclipsed by J. E. Smith's *English flora* of 1824–1828) had a great influence, both as regards variation and the new classification, on the young Henslow, leading to Darwin being taught the "natural system" by Henslow.

Taxonomy, like other branches of natural history at this time, radiated from three groups which Noel Annan (1955) has called "The Intellectual Aristocracy". The first includes the families of Buxton, Barclay and Cadbury, another contains the family names of Macaulay, Trevelyan and Babington, and the third radiates from the Hookers of Kew. J. D. Hooker's first wife was Henslow's daughter, and Henslow's wife was the sister of Leonard Jenyns, who married into the family of Daubeny, the Professor of Botany at Oxford. Charles Darwin, Henslow's pupil, was in constant touch with Joseph Hooker while writing *On the origin of species*. George Bentham was working at Kew with Hooker. John Lindley's long association with the Royal Horticultural Society and his working relationship with George Bentham brought about the exhibition of flowers and fruits which continues to this day as the

Chelsea Flower Show. The close connections of this intellectual elite have much to do with the formation and value of the historic Cambridge University Herbarium and thus with plant taxonomy in Cambridge.

Charles Cardale Babington (1808–1895; Britten, 1895), who succeeded Henslow as the fifth Professor of Botany, was born in Ludlow, Shropshire. Part of his education was at Charterhouse, but he himself considered that he learned most at a private school in Bath, where his family moved in 1822. Here he first began his study of botany and to collect plants and insects, which gave rise to his first published book, *Flora Bathoniensis*, in 1834. He was one of the first converts to Henslow's botany course and attended his first lecture in 1827. He became friends with Henslow and helped him before and after his lectures, attending six successive series of Easter Term lectures and taking part in most of the local excursions. As Henslow occupied the only Chair that interested Babington, it is not surprising that, after taking his M.A. in 1833, he settled down to a comfortable bachelor existence in his rooms in St John's College. Here he wrote his books and went into the countryside to do much fieldwork, gradually becoming Henslow's assistant and deputy. By the time he became Professor of Botany he had a nationally established reputation as a taxonomist, who, in his published works, had endeavoured to include important finds made by the German botanists W. D. J. Koch (1771–1849), H. G. L. Reichenbach (1793–1879) and J. Sturm (1771–1848). From the time of his appointment to the Professorship in 1861 until about 1883 he worked with great vigour building up the University Herbarium. In 1865 the Herbarium was moved from the building which had originally stood in the old Botanic Garden to a new and larger one built on nearly the same site. It remained there until moved to the present Department of Plant Sciences, which was built as the University Department of Botany in 1904. Babington held the Professorship until he died in 1895, but Sir Francis Darwin was Deputy Professor from 1891 to 1895. Some of Babington's memoirs were published after his death (Babington, 1897). As he grew older Babington developed a suspicion and mistrust of the young men who surrounded him and troubled his old age with new ideas and interests. Although he described quite a lot of varieties in the nine editions of his *Manual of British botany*, he did not seem to have Henslow's understanding of variation. Babington's herbarium of some 55,000 sheets and his library were presented to the University on his death. The library contained many early European floras, which have been invaluable in the writing of this flora.

A new Botanic Garden had been much wanted by Henslow. It eventually came about and took effect in three phases, the purchase of the land on Trumpington Road in 1831, the establishment of the Garden's main features, which included the planting of the Arboretum and the transference of hardy herbaceous plants from the Old Garden to the new Systematic Beds, and finally the building of the glasshouse range and the transfer of the

remaining stock from the old greenhouses to the new, three processes which spanned over a quarter of a century. The first Curator, Andrew Murray (1812–1878), was responsible for its detailed design, which was finished under his successor James Stratton. In 1864, on the death of Stratton, William Mudd (1830–1879) was appointed Curator. Completely self-taught, he had to educate himself after reaching mature life but rapidly became an authority on the local flora and in 1861 produced his classic work *A manual of British lichens*.

By the time Richard Irwin Lynch (1850–1924) was appointed Curator in 1879, the Garden was functioning in the way in which it has continued to do until fairly recently. Born in Cornwall in 1850, Lynch was 29 years of age when he took up his appointment. He put in order the woody collections, redesigned the bog and water garden area, reconstructed the rock garden, made an ornamental bamboo collection and established his collection of hardy cacti. In 1904 he published *The book of the Iris*. On the whole he brought order to all areas of the Garden; his reputation as a plantsman grew rapidly and before the end of the nineteenth century Cambridge Botanic Garden under Lynch had a reputation second only to Kew. A more detailed account of the origin and development of the Botanic Garden is given by John Parker (2006).

The long fight, in which Sydney Howard Vines (1849–1934) had taken a leading part, against considerable opposition, to find a place for experimental botany in Cambridge, ended with the death of Babington and the appointment to the vacant Chair in 1895 of Harry Marshall Ward (1854–1906), a pupil of Thomas Huxley. The long tradition of taxonomic botany in the University was broken, and the dawn of the last century saw a new Botany Department in Downing Street, in which, however, the Herbarium was still housed. To Marshall Ward himself taxonomic botany was not completely dead, as he published five excellent volumes on trees. However, as pointed out by Arthur George Tansley (1871–1955) in his Presidential Address to the Botany Section of the British Association in Liverpool in 1923, there was a distressingly rigid separation between phylogenetically obsessed morphology and physico-chemical plant physiology. Tansley made a plea for a broadly based elementary botany dealing with form and function together. Marshall Ward's son, Frank Kingdon Ward (1885–1958), became one of the most famous of the great plant collectors of the Sino-Himalayan regions.

In 1880, William Hillhouse (1850–1910) was appointed the first Curator of the Herbarium, and there has been a series of Curators, with some intermissions, ever since. Hillhouse was succeeded by Thomas Hughes Corry (1859–1883) from 1882 to 1883, Michael Cresse Potter (1858–1948) from 1883 to 1890 and Isaac Henry Burkill (1870–1965) from 1891 to 1895. Burkill seems to have done the most work, rearranging the whole Herbarium in accordance with George Bentham and Joseph Hooker's recently published *Genera plantarum* in three volumes.

Under the Professorships of H. Marshall Ward and Sir Albert Charles Seward (1863–1941) the Curators were Henry Harold Welch Pearson (1870–1916) from 1898 to 1899, Richard Henry Yapp (1871–1929) from 1900 to 1903, Robert Heath Lock (1879–1919) from 1905 to 1907, Charles Edward Moss (1870–1930) from 1907 to 1917, Humphrey Gilbert-Carter (1884–1969) from 1921 to 1930 and John Scott Lennox Gilmour (1906–1986) from 1930 to 1931. Moss was the most active, preparing two volumes of his *Cambridge British flora*, the illustrations for which were drawn by Edward Walter Hunnybun (1848–1918); many of them were never published and are still housed in the Herbarium. They are copiously annotated by Moss and it is a great pity that this excellent British flora was not finished. During this period Edward Shearburn Marshall (1858–1919; Britten, 1920) left his exceptionally fine critical British herbarium to the University.

In 1907, the University instituted a Readership in Forestry and appointed to it Augustine Henry (1857–1930). Born at Cookstown in Co. Antrim, he had travelled widely in Asia collecting plants before becoming Reader at Cambridge from 1907 to 1913. While occupying this post he wrote, in collaboration with Henry John Elwes (1846–1922), who had also travelled extensively in Asia collecting plants, *The trees of Great Britain and Ireland* (1906–1913) in seven volumes. When the Forestry School at Cambridge was abandoned, a large collection of herbarium specimens of trees, labelled “H. J. Elwes and A. Henry, *Trees of Great Britain and Ireland*”, came to the University Herbarium. Although Henry's main herbarium is at Dublin and Elwes's at Kew, it is likely that the very substantial collection which came to the University Herbarium was their working set while writing *Trees of Great Britain and Ireland*. It was an exceedingly useful set of specimens when we were writing the accounts of trees for this flora.

When Lynch resigned from the Curatorship of the Botanic Garden in 1919 the Botanic Garden Syndicate altered the direction of the Garden away from horticulture towards scientific botany. Humphrey Gilbert-Carter (1884–1969; Gilmour & Walters, 1975) was made Director and Frederick George Preston Superintendent. Gilbert-Carter went to Tonbridge School and from there to Edinburgh University, where he read medicine. After postgraduate study in Marburg he turned to botany as a career, came to work in Cambridge as an advanced student under C. E. Moss in 1909 and there developed a lifelong friendship with Sir Arthur Tansley. As a teacher he was supreme; if his subject did not hold your attention his idiosyncrasies did. Through his local excursions in the field, his conversations in pubs and his tea parties in the Director's house he imparted a wealth of knowledge. It was undoubtedly his linguistic abilities that imparted to his teaching and writing a unique quality which held his audience. Latin, Greek, French, German, Danish, Spanish, Hindu, Urdu, Persian and Arabic all were within his grasp. When I was a young lad he taught me to identify my first plants, leisurely and absolutely clearly. Gilbert-Carter

influenced and in a real sense educated many of the leading botanists of the period after the First World War. James Edgar Dandy (1903–1976; Cannon, 1977) was one of these students, who went on to work at Kew and then the British Museum (Natural History), where he eventually became Keeper of the Herbarium. His knowledge of botany was wide, but British botanists will remember him particularly for his long series of erudite papers with George Taylor on the genus *Potamogeton*. He brought up to date all the *Potamogeton* specimens in the University Herbarium during this study. He was known worldwide for his expertise on nomenclature and on my visits to the Natural History Museum I would seek him out to get his opinion on difficult nomenclatural problems. If I had not done the basic work before asking him questions he could be caustic in the extreme, but he eventually seemed to take me under his wing. In my opinion he tried to understand exactly what the author of a name had done and so often it seemed to me to be perfectly logical. Today there seems to be too much fiddling of names to bring about the results that are wanted. The three authors of *Flora of the British Isles* (first published in 1952), A. R. Clapham, T. G. Tutin and E. F. Warburg were all Gilbert-Carter students, and the six editors of *Flora Europaea*, T. G. Tutin, V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters and D. A. Webb, were either his students or Cambridge-trained. In the 1930s the young William Thomas Stearn, then working in a Cambridge bookshop, used to spend his lunch hours working in the University Herbarium while he ate his sandwiches. He was to become Librarian of the Lindley Library of the Royal Horticultural Society, and later Senior Principal Scientific Officer in the Herbarium of the British Museum (Natural History). His output of publications was enormous (Stearn, 1976, 1992) and he became the leading authority on the history of botany (e.g. Stearn, 1975) and on botanical Latin (Stearn, 1992). Two large and important British herbaria were given to Cambridge during the 1930s, those of Spencer Henry Bickham (1841–1933; Thompson, 1933) and Joseph Edward Little (1861–1935; Thompson, 1935).

When I entered the Herbarium as a Technician in 1944, a young lad of 14, it was a dead and dreary place enlightened only by Humphrey Gilbert-Carter's regular but short visits. The Professor was Frederick Thomas Brooks (1882–1952), a mycologist. The Technician in charge of the Herbarium was Arthur W. Gray (1877–1954), who had been there for nearly 50 years and was due to retire. Although he knew little about taxonomy, he had a vast knowledge of the historical side of the Herbarium and he stayed on for a year past retirement to teach me about it. I was then left to run the Herbarium on my own. The first thing I did was find out what was in every cupboard.

In those days many of the old taxonomic books were housed on open shelves in one of the bays. One day I was sitting on the floor of this bay trying to understand one of John Ray's appendices to his Cambridgeshire flora, when a quiet, amused voice told me that he knew of only two other copies of the book I was studying in existence. Charles Earle Raven (1885–1964; Dillistone, 1975) was one of

the all-time greatest scholars of Cambridge University. Canon of Liverpool Cathedral, Chaplain to the Queen, Professor of Divinity, Master of Christ's College and Vice-Chancellor of Cambridge University, he was also an ardent botanist and ornithologist and became President of the Botanical Society of the British Isles. He was the most brilliant lecturer I have ever heard. A personal lecture on *Hieracium* was delivered at me once while we were having breakfast together.

Charles's son, John Earle Raven (1914–1980; Lipscomb & David, 1981), classical scholar and Lay Dean of King's College, was one of the finest field botanists I have known, who would work out where a given plant occurred from the literature and a study of maps and with unerring instinct go straight to it in the field. Father and son between them painted almost all of the British and Irish species of plants, not just *Hieracia*.

In 1953 I travelled with them, finding and naming over 60 species of *Hieracium* while father painted the leafy part and son the inflorescence, which required more patience. I have an abiding memory of Charles making up a rocky slope at a great pace, followed by John begging him to slow down because of his weak heart, to rediscover, after 50 years, *Hieracium rectulum*, which he had seen through his binoculars exactly where John said it would be. Every time I see scowling, taut faces peering into the screen of a VDU, I think of the look of immense joy on the faces of those two great Cambridge scholar as a result of their find. They brought an enthusiasm and appreciation to field botany which seems to be missing from 'hard drive' sciences.

One of my first tasks in the Botany Department was to put the photographic slides through a lantern projector for Harry Godwin's lectures on the Quaternary Period and on Algae, but the most important job he did as far as I was concerned was to run the Long Vacation Field Course. This was where I learned the bulk of my common plants as well as much ecological information about them. Over 600 species could be seen on the excursions, which went to Therfield Heath (chalk grassland), Hardwick Wood (boulder clay), Tuddenham and Cavenham (Breckland heath and valley wood), Wicken Fen, Holme saltmarsh and Dersingham Fen (acid bog). In the first year the students would learn the names of some plants, in the second do some elementary ecology and in the third year do more detailed ecology with Alex ('Sandy') Watt. This supplied an excellent background to whatever sort of botany they wished to pursue. Soon after the Second World War we went to the Gog Magog Hills instead of Therfield Heath, with over a hundred students. Everyone in the Department who knew some plants was called on to demonstrate and even I at 17 could help with the common species. With Humphrey Gilbert-Carter, Paul Richards, Val Chapman, Ken Sporne and John Corner as well as Harry Godwin there was a wealth of talent to help out.

On returning in 1950 from National Service duty I was to find taxonomy had received a large boost. Max Walters had been made Curator of the Herbarium and John Corner Lecturer in Tropical Botany. Professor George Edward

Briggs (1893–1985) had become Head of Department and the whole building was being renovated. At the east end of the building was a museum, which was disbanded. I was just in time to search it for type specimens and incorporate them into the Herbarium. The Herbarium was transferred from the west end of the building to the site of the old museum. Some old cupboards were renovated and some new cupboards fitted and all painted white, so that we had a bright and spacious new Herbarium. The site of the old Herbarium became the new Library. Only books constantly used were kept in the main aisle of the new Herbarium and the old and exceptionally valuable books were locked up in the new Library.

Max Walters had taken his Ph.D. working on *Eleocharis* and had now turned his mind to *Alchemilla*. I had chosen *Hieracium* as my critical genus and was soon joined by Cyril West (1887–1986; Sell, 1987), who had the same idea. A physiologist all his professional life, his hobby had been the study of the British flora. He was 60 years old when he started studying *Hieracium*, but he was to spend his summers for the next 30 years collecting them all over the British Isles, and four days of every month during the winter he came up to Cambridge to work with me in the Herbarium. A memorable trip with West and Norman Douglas Simpson to Sutherland gave me a taste for leisurely field botany, which is a kind of botany which has long disappeared. John Corner was to work on his huge revision of the Asiatic species of *Ficus*.

A visitor to the Herbarium at this time was the Cambridge chemist, William Hobson Mills F.R.S. (1873–1959), who used to sing hymns while naming *Rubus* specimens. During this period I prepared and put through Cambridge University Press William Charles Richard Watson's (1885–1954) manuscript of *Handbook of the Rubi of Great Britain and Ireland* (1958). Watson had burnt much of his herbarium, but what was left of it came to Cambridge. A young Cambridge student, Beverley Alan Miles (1937–1970), took up the study of the genus and soon amassed a large collection of specimens, beautifully pressed and mounted with very detailed field notes. He also carefully mounted the remainder of the Watson herbarium. With the help of Mills I put the whole collection in order. The Babington collection of British *Rubi* had been loaned to the British Museum of Natural History. Miles brought the nomenclature of this up to date and returned it to Cambridge bit by bit and we incorporated it. On the death of Mills and the very early decease of Miles both their fine herbaria were added to the general collection of *Rubi*. Miles had also made a superb collection of the British alpine *Hieracia*, which also came to Cambridge. The early death of this formidable young scholar was a great blow to British botany (Sell, 1971). With the large continental collection of *Rubi* made by Gaston Genevier, bought and presented to the University by Babington, which the German batologist Heinrich E. Weber said was the finest historical collection of European *Rubi* in the world, Cambridge is an ideal place to study this genus.

David Allen was another young student who, though not reading Natural Sciences, was constantly working in

the University Herbarium, taking a particular interest in infraspecific taxa. We still see him from time to time when he comes to look at our collection of *Rubi*. He referred to his time at Cambridge in his inaugural address as President of the Botanical Society of the British Isles (Allen, 1987).

The Council of the Botanical Society of the British Isles met in May 1950 to discuss the possibility of preparing and producing a series of maps of the British flora, a proposal suggested at its second conference, reported in *The study of the distribution of British plants* (Lousley, 1951). The 'Maps Office' was set up at Cambridge University Botanic Garden in April 1954 with Max Walters as its Director, Franklyn Perring as its Senior Worker, Audrey Matthews as its Secretary and Sylvia Fincham as its Punch-card Operator (Walters, 1954). The records poured in from all parts of Great Britain and Ireland and amongst them was much of interest, including specimens of critical plants still needing to be identified. The University's Herbarium and its libraries were in constant use by Frank Perring for identifying plants and he used any other help he could get. *Atlas of the British flora* was finally published in 1962. Many critical genera were not dealt with in this atlas and Frank Perring immediately set about accumulating records for them with help from many specialists. *Critical supplement to the Atlas of the British flora* was finally published in 1968. My obituary of Frank Perring (Sell, 2006) in particular outlines his Cambridge days; see also Preston & Oswald (2006).

In July 1954 in a brasserie on the banks of the Seine an informal meeting of Tom Tutin, Roy Clapham, John Gilmour, Alan Burges, David Valentine and Vernon Heywood took a decision that a flora of Europe could and should be written. In January 1955 David Webb was added to the group and in March 1956 Max Walters was invited to join the committee. In 1957 an agreement was reached with the Linnean Society of London for them to act as sponsors of the *Flora Europaea* project. An offer to publish the work by Cambridge University Press was accepted. It was to be in English. Although the Secretariat was first at Liverpool and then at Reading, much of the time in the next 20 odd years in the Cambridge Herbarium was spent working on *Flora Europaea*. We are told in the introduction to the final volume that the manuscript of Volume 1 was delivered to Cambridge University Press on 16 January 1963. What we have not been told is that Arthur Chater then withdrew the manuscript on the authority of Heywood and the rest of the Editorial Committee, but against the wishes of Tutin, the Chairman. Arthur and I worked on it for six weeks from 08.00 hrs often until 22.00 hrs, Saturdays and Sundays included, to perfect it. I had been preparing standard abbreviations for authors and references. This task I handed over to Arthur and I concentrated on the index, which was not an ordinary index but much of it synonymic.

I had first known Arthur when he was a student, but we became much better acquainted when we had sessions on *Carex*. This major effort in preparing Volume 1 of *Flora Europaea* proved that we could work together under immense pressure without friction, and we have remained

firm friends ever since. Volume 1 was published in 1964, Volume 2 in 1968, Volume 3 in 1972, Volume 4 in 1976 and Volume 5 in 1980. The fact that I was continually in Cambridge and that I dealt with the index meant that I acted as a sort of co-ordinator. The corrected proofs came to me, I corrected the index and passed any new author names on to Arthur and he passed back the corrected version. Frequently corrections arrived after the proofs had been handed in, so I would meet with the Press subeditor and we would wangle it as best we could. Sometimes an author would want to put a whole line in, which meant a whole line had to come out and there was no time to consult the author. The only person I ever consulted was Arthur and we never had to withdraw a manuscript again. Only once did I nearly get overwhelmed when I had the huge index to Volume 4 to prepare and 50 pages of proofs to check, but again Arthur came to the rescue. *Flora Europaea* was one of the most important taxonomic works published in the last century and it brought to the Cambridge Herbarium visiting botanists from all over the world and with them all kinds of information not found by just reading published works. The final conference, held at King's College, Cambridge, between 31 August and 4 September 1977, brought a total of 131 visitors from 30 countries. A short history of the project is published in Volume 5 of *Flora Europaea*, but it is a pity that no detailed account of the whole of the *Flora Europaea* project has ever been written. My experience with *Flora Europaea* gave me much help when setting out on and publishing this flora.

The Biological Records Centre at Monks Wood was opened in 1964 and Frank Perring set up the recording system for plants and animals which has continued until recently, Chris Preston replacing him as botanist in 1980. The University's Herbarium and its libraries continued to be used for reference, being the nearest available, and many voucher specimens of new records, especially those recorded by Chris Preston, are now in the Cambridge Herbarium. Chris also used the very large collections of *Potamogeton* when writing his fine B.S.B.I. handbook of that genus (1995) and personally added greatly to that collection. Recording at Monks Wood has now ceased and their herbarium has come to the Cambridge one for incorporating into the British collection.

While accumulating the Cambridgeshire records for the *Atlas*, Frank Perring put all the records he could find for the county in a notebook in the form of 10 km square grid references. Using this book, the Cambridge Natural History Society card index and the Herbarium, I drafted *A flora of Cambridgeshire*. This was then read and commented on by Max Walters and Frank Perring and finally we all met to discuss any difficulties. In the 1930s Paul Richards had started collecting records of Cambridgeshire Bryophyta, and this was continued by M. C. F. Proctor and H. L. K. Whitehouse. This flora was published in 1964 with an account of the Bryophyta by Harold Whitehouse.

While these scientific tomes were being produced John Gilmour and Max Walters were writing *Wild flowers* (1954) and John Raven and Max Walters *Mountain flowers* (1956)

in the more popular New Naturalist series. John Corner wrote *The life of plants* in 1964, which sold worldwide in several languages, and *The natural history of palms* in 1966. His love of trees and his vast experience of the tropical forest had been brought together in the two volumes of *Wayside trees of Malaya* (1940), which was subsequently revised and twice reprinted, in 1952 and 1988.

In October 1964, Sylvia Haslam, a research student of Alex Watt, took up a lectureship in Biology in the Royal University of Malta, but found that there was no modern flora of the island to take into the field. We discussed this on her return to England on holiday and decided to try to produce one, making *Flora Europaea* the basis for the work. During 1966, Pat Wolseley, a friend of Sylvia, also became interested and agreed to illustrate the work. It was finally published in Malta in 1977. Sylvia Haslam was later to publish a whole series of books on the vegetation of the rivers of western Europe.

There were many subsidiary papers concerned with these major works to get through the press, and Max Walters and I contributed large accounts to the *Flora of Turkey*, which was being written under the guidance of Peter Davis at Edinburgh. There were huge batches of manuscript and proofs to check with Professor Corner, and two of his books I was to put through the press while he was in Borneo and in the Solomon Islands. Two or three Technicians were kept busy dealing with loans and mounting and incorporating specimens. Professor Corner's loans came by the crate-load, sometimes two or three crates at a time. Funding was plentiful and we had much part-time employment to help out. Dorothy Soden, who first came to work with us part-time when she was 60, continued to do so until she was nearly 90. She put in order the large collection of Bryophyta made by William Nicholson (1866–1945; Richards, 1946). In the 1970s things steadily began to change. In 1972 Professor Corner retired, but he continued to churn out a whole series of monographs on the fungi, having finished his work on *Ficus*, and prepared two volumes of *The seeds of dicotyledons* (1976).

Edred John Henry Corner (1906–1996) was arguably one of the greatest botanists Cambridge has ever produced and he won his fame by the published results of his personal research. Administration did not interest him at all. Son of a Harley Street surgeon, he was educated at Rugby, where he was an outstanding rugby union football player. He came up to Sidney Sussex College, Cambridge, where he received a double first in the Natural Sciences Tripos and went on to do research under F. T. Brooks and A. H. Church. It is typical of the man that he could not be bothered to register for a Ph.D., considering it a waste of time. He was persuaded by Brooks to try for, and got, the post of Assistant Director of the Singapore Botanic Garden, which he took up in 1929, a year after his graduation. He remained in Singapore for 16 years. His behaviour during the Japanese occupation, when he was under house arrest and continued to curate the herbarium, has been much questioned, and his own account is published in *The Marquis: a tale of Syonan-to* (1981). After the Second

World War, before returning to Cambridge in 1948, he left the Colonial Service and served for one year as Principal Field Officer, Latin America, for UNESCO, working primarily in Brazil. At Cambridge he became Lecturer in Botany in 1949, Reader in Plant Taxonomy and Fellow of Sidney Sussex College in 1959 and Professor of Tropical Botany in 1966.

His output of publications was enormous in almost every year from 1929 until his death. Corner's scientific accomplishments were recognised throughout the world and included Fellow of the Royal Society of London (1955), Darwin Medal of the Royal Society (1960), Patron's Medal of the Royal Geographical Society (1966), Gold Medal of the Linnean Society of London (1970), Companion of the British Empire (1972), Victoria Medal of Honour of the Royal Horticultural Society (1974), Allerton Award of the Pacific Tropical Garden, Hawaii (1981), International Prize for Biology of the Japanese Academy of Sciences (1985), the Golden Key of the City of Yokohama (1985) and the International Mycological Association de Bary Medal (1996). These honours are even more remarkable when you consider how abrasive he could be. He did not suffer gladly what he considered to be fools and his comments on almost everything were blunt and very much to the point, and yet to the young ladies of the Cambridge Herbarium who helped him with his work he was the perfect gentleman. I spent many, many happy hours with him, particularly when checking proofs, and his vast knowledge of the earth's flora would come to me through a great many pungent remarks and tit-bits. Two pieces of advice he gave me I have followed all my life. If you do the little things you will never do the big things, and only 10 per cent of all research is interesting and the remaining 90 per cent is hard grind, but if you give it to somebody else to do you are sure to miss something which is important. His fellow scientists would normally regard him as a tropical botanist, but when he gave me advice it seemed to be based on the world flora and there will have been much done in this flora which is due to his wise guidance.

Professor Harry Godwin (1901–1985; Godwin, 1985) had replaced Professor Briggs on the latter's retirement in 1960 and during his term of office the whole range of botanical subjects came together and the Botany Department taught everything from the rapidly expanding molecular and cell biology, mycology, cytology and genetics to ecology and taxonomy; it included a large Subdepartment of Quaternary Research. Also, the Botanic Garden was at the height of its post-war expansion owing to the munificent Cory Bequest. Sir Arthur Tansley's wishes had been granted because of the wide interests and expertise of his pupil, Sir Harry Godwin. As if to celebrate it 36 Cambridge biologists got together to write *The Cambridge encyclopedia of life sciences* in 1985.

On John Gilmour's retirement in 1971, Max Walters was appointed Director of the Botanic Garden, and on the retirement of Bob Younger as Superintendent, Peter Orris replaced him. Peter Frederic Yeo (1929–2010; Sell, 2010) had been appointed Taxonomist at the Garden in 1953, a

post which he retained until his retirement in 1993. He was an acknowledged authority on the genera *Euphrasia*, *Aster* and *Geranium* and published many papers on them as well as on the taxonomy and nomenclature of garden plants. The Botanic Garden became one of the best labelled in the country. Yeo was also to write, with Michael Proctor, a large text book, *The pollination of flowers* (1973), with a much enlarged second edition in 1996, which was in effect a completely new book in which the two authors were joined by Andrew Lack, entitled *The natural history of pollination*.

The combination of Corner, Sell, Walters and Yeo formed a powerful botanical taxonomic contingent at Cambridge, who published some 15,000 pages and described over a thousand taxa new to science in the 65 years after the Second World War. Three of them were Honorary Fellows of the Linnean Society at the same time. They were always supported by the ecologists Alex Watt, Donald Pigott, David Coombe, Oliver Rackham and Peter Grubb, who also knew their plants in the field. For over 20 years Max Walters attended to all the Herbarium correspondence, sat on many taxonomic committees dealing with European plants, had much to do with conservation, did a large amount of taxonomic teaching, wrote numerous papers and took students on field trips to various parts of Great Britain and Europe.

The taxonomic research students since the Second World War included Jayne Armstrong, Peter Ashton, Eklas Bari, Chris Cook, Quentin Cronk, Barbara Croxall, Gordon DeWolf, John Dransfield, David Frodin, Shahina Ghazanfar, Keith Goodway, Geoffrey Halliday, Vernon Heywood, Frances Jarrett, Joachim Kadereit, Ruth Kiew, Chu Wee Lek, Alan Leslie, David Maberley, David Ockendon, Honor Prentice, Gordon Smith, Engkik Soepadmo, Suzanne Warwick, Tim Whitmore and Fenella Wrigley.

In 1975 the collection of local floras made by Norman Douglas Simpson (1890–1974) came to Cambridge. Simpson had also been a Gilbert-Carter student and, being of independent means, had built up a collection of books and pamphlets of 3600 items. These he left in the care of his executors, Patrick Brenan and William Stearn, who offered them to Cambridge University on condition that they were kept as a separate collection and were not sold. The executors also arranged for a sum of money to be invested so that all relevant new books could be bought. This wonderful collection of books, with those of Henslow and Babington and the large number bought second-hand when funding was available, has meant that almost every book on local flora needed to write our accounts in this work was available to us. I was appointed Assistant Curator of the Herbarium in 1972, and David Briggs became Curator in 1974. David Briggs, a geneecologist, worked on the variation of plants, the effect of herbicides and lawn-cutting on them, and their conservation. His research has resulted in his book entitled *Plant microevolution and conservation in human-influenced ecosystems* (2009). On Max Walters's retirement Donald Pigott became Director of the Botanic Garden and a good deal of his time was spent on preparing

a monograph of *Tilia*, the study of which he has continued in his retirement. On Pigott's retirement, John Parker took over the Directorship. Peter Yeo retired in 1996 and I retired in 1997.

Local amateurs have always been encouraged to use the Herbarium and Library, and foremost amongst these is Gigi Crompton, who, with a large number of helpers, extracted all the information on Cambridgeshire specimens in the Herbarium and annotated books in the Library. Mary McCallum Webster (1906–1985; Stewart & Sell, 1987) did much work in the Herbarium and gave us many specimens. Dick David (1912–1993; Davies, 1994), one-time London Manager of Cambridge University Press and later Publisher to the University, was a frequent visitor to look at *Carex* and *Crocus*. His last big task before his death was to go through the huge collection of *Carex* in the British collection in the Herbarium and bring every sheet up to date. John Trist (1908–1996; Wells, 1997) did the same with the Poaceae and his fine personal collection was left to the Herbarium, where it was incorporated by his widow. Max Walters continued to come regularly into the Herbarium until just before his death in December 2005. He wrote, amongst other things, *The shaping of Cambridge botany* (1981), with David Briggs *Plant variation and evolution* (1969, 1984, 1997) and with E. A. Stow *Darwin's mentor* (2001). Gina Murrell became Assistant Curator of the Herbarium in 2002. As I write, the Herbarium is being moved to the Sainsbury Laboratory at the University Botanic Garden and a new era begins.

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## Introduction

Taxonomy and nomenclature are the most important branches of every science and for that matter everything we do. Get it wrong and a surgeon could operate on a lung instead of a kidney, or a shopper could buy arsenic instead of sugar. Most of us are very bad with names and scientists are no exception. Some of us get better at our particular subject but remain slapdash about all associated subjects. Ecologists develop a broad range of knowledge but sometimes their knowledge of taxonomy is not precise enough to explain the subtleties of why one variant is in a particular place but not another or why a particular insect only visits a particular variant of a plant. Television shows us some wonderful documentary films on nature and describes in great detail the birds and animals but hardly mentions a plant and, when it does, often gets it wrong. It is infuriating for someone interested in both plants and poetry to hear Wordsworth's famous poem on Daffodils quoted and then to be shown an image of the cultivated 'February Gold' which has nothing to do with the Daffodil of the Lakes. When P. D. S. sat on conservation bodies in Cambridge he was always supported by the late John Smart, an entomologist, because Smart said that if the botany is all right it is all right for the insects.

### HISTORICAL BACKGROUND OF OUR FLORA

The first real flora of these islands was John Ray's *Catalogus plantarum Angliae, et Insularum adjacentium* in 1670. The first flora to use the Linnaean binomial system of nomenclature was William Hudson's *Flora Anglica* nearly a hundred years later in 1762. This was followed in 1776 by William Withering's *A botanical arrangement of all the vegetables naturally growing in Great Britain*, the first of many floras written primarily for the amateur.

James Sowerby's *English botany*, the text of which was written by J. E. Smith, was first published between 1790 and 1814. It presented for the first time a complete set of coloured illustrations of our plants, illustrations which are still unsurpassed for line and colour. The third edition, published between 1863 and 1886, has inferior illustrations, but its text, rewritten by James Boswell Syme, is still important for its nomenclature and infraspecific taxa. S. F. Gray's *A natural arrangement of British plants, according to their relations to each other, as pointed out by Jussieu, De Candolle, Brown, &c. including those cultivated for use; with an introduction to botany, in which the terms newly introduced are explained*, published in 1821, was the first flora of our islands to use this classification. It is a little-known flora, probably because it did not use the Linnaean system.

Three especially famous floras were produced in the nineteenth century. George Bentham's *Handbook of the British flora* in 1858 was written as a before-breakfast relaxation. In it keys appeared for the first time in a British flora. It was revised by J. D. Hooker in 1886.

J. D. Hooker's *The student's flora of the British Islands*, first published in 1870 and finally revised in 1884, had very clear and concise descriptions and was the main flora used by many generations of botanists up until the 1950s. It is also important in that Hooker was one of our first authors to make frequent use of the category of subspecies.

Charles Cardale Babington's *Manual of British botany* first appeared in 1843 and the tenth edition, revised by A. J. Wilmott, was published in 1922. It contains many critical species and varieties not in other floras, but the descriptions are not clear and without keys it is difficult to use.

C. E. Moss's *Cambridge British flora* (1914–1920) was very detailed and would have supplied a much needed critical flora, but alas only two volumes were published.

The arrival of 'C. T. & W.', A. R. Clapham, T. G. Tutin and E. F. Warburg's *Flora of the British Isles* in 1952 heralded the beginning of a different era in the study of British plants in which species were regarded as all-important and little was said about variation. It was the first up-to-date treatment of species and genera in the twentieth century. A much revised second edition appeared in 1962 and a third in 1987, when D. M. Moore replaced E. F. Warburg, who had died in 1966, on the title-page. This last edition included information from *Flora Europaea 1–5* (Tutin et al., 1964–1980). The nomenclature had been brought up to date by J. E. Dandy in his *List of British vascular plants* in 1958 and the work he did on this for *Flora Europaea*. Thus for the first time taxonomy and nomenclature of species in Great Britain and Ireland had been brought in line with that of Continental Europe. Nothing, however, was done to take account of the vast amount of work on variation and apomorphic taxa undertaken in both Great Britain and Europe.

The Botanical Society of the British Isles' publication of the *Atlas of the British flora* in 1962, edited by F. H. Perring and S. M. Walters, and the *Critical supplement to the Atlas of the British flora* in 1968, edited by F. H. Perring, gave us a much better idea of the distribution of our species. *New atlas of the British & Irish flora* (2002) arrived after Volume 5 of our flora was published and when most of Volume 4 had been prepared for the press, but the fact that Chris Preston had checked most of our distributions meant that they were not much out of date. For Volumes 3 and 2 and this volume the *New atlas* was available to us and we were able to bring all distributions up to date. The publication in 2003 of *The vice-county census catalogue of the*

*vascular plants of Great Britain, the Isle of Man and the Channel Islands*, edited by C. A. Stace et al., has greatly helped us to get the distributions up to date.

The publication of Clive Stace's *New flora of the British Isles* in 1991, with a second edition in 1997 and a third in 2010, and of D. H. Kent's *List of vascular plants of the British Isles* in 1992, brought about the end of the C. T. & W. era and has given us a completely up-to-date account of the species of our flora, but still little or nothing concerning variation. Major changes included the moving over of the main classification to A. Cronquist's *An integrated system of classification of flowering plants* (1981) and the inclusion of almost as many alien species as native ones. Stace's *Hybridization and the flora of the British Isles* (1975) did much to explain that aspect of the flora. The third edition of Stace's flora in 2010 has partially moved the classification over to that of the Angiosperm Phylogeny Group in *Botanical Journal of the Linnean Society* 161: 105–121 and 128–131 (2009), but it has still not adequately addressed variation in species. All these books were in constant use when preparing this flora. In addition the continental floras Ascherson & Graebner, *Synopsis der mitteleuropäischen Flora*, Hegi, *Illustrierte Flora von Mitteleuropa*, Hayek, *Prodromus florum peninsulae balcanicae*, Parlato, *Flora italiana*, and Săvulescu, *Flora Republicii Populare Române* were checked for most species, particularly to understand any variation which might occur.

The aim of our flora is to supply full descriptions of all the species in Stace's flora, to include all the large apomictic genera and as many infraspecific variants as practicable, and to add more information about hybrids. When it is a question of occasional, often sterile, hybrids very little in the way of description is given. If, however, they are trees or shrubs which occur frequently, much fuller descriptions are given. Pseudogamous plants of hybrid origin which rarely if ever reproduce by seed, like the elms, are treated as species. The theme of the flora, which became more developed as we went along, is set out in the two quotations at the beginning of this volume. Although Darwin got it right about species, races, varieties and lesser varieties, as in the quotation, the title of his book, *On the origin of species*, seems to place an undue emphasis on species rather than other taxa. If the title of Alfred Russel Wallace's (1858) paper, *On the tendency of varieties to depart indefinitely from the original type*, had been followed things might have been very different.

Why do our present-day scientists not want names for variants? If a farmer orders wheat to grow in his fields he does not grow any old wheat. He asks for it by name, the variant that he knows grows best on his land and which brings him the highest returns. Gardeners of course take names of variants to even greater extremes, but not scientists. Plant ecologists mention variation in their 'Biological flora' accounts under the appropriate heading, then forget about it as they write about the plants, and particularly their associations with animals, birds and insects. You need names for variants when you talk about the relationships of various biota. That is what evolution is all about.

## THE CONTENTS OF THE FLORA

This flora includes all the vascular plants, that is the Lycopodiophyta (clubmosses), Equisetophyta (horsetails), Polypodiophyta or Pteridophyta (ferns), Pinophyta (gymnosperms, mostly conifers) and Magnoliophyta (angiosperms or flowering plants). The list of plants is made up of all our native species, including apomicts, and all the introduced plants given in Stace, with some more added, particularly planted trees. E. J. Clement's and M. C. Foster's *Alien plants of the British Isles* arrived in 1994 after we had written Volume 5, but we went through it and added as much information as possible. It has been used continually while preparing the remaining volumes. These alien taxa may be found to be more widespread when full attention is given to them. In his coverage of alien taxa Stace considers that inclusion is merited when an alien is either naturalised (i.e. permanent and competing with other vegetation or self-perpetuating) or, if a casual, frequently recurrent so that it can be found in most years. These criteria were applied as much to garden escapes or throw-outs as to the unintentionally introduced plants, and rarity was not taken into consideration for any of them. Cultivated species were included if they are field crops or forestry crops, or, in the case of trees only, ornamentals grown on a large scale. Stace's aim has been to include "all taxa that the plant-hunter might reasonably be able to find in the wild in any one year". To these we have added ornamental trees and shrubs which are planted along streets, roadsides and motorways in large numbers and in parks and estates, and which we consider to be part of the landscape. We have also tried to include all the trees and shrubs planted in 'new woods' and those taxa included in wildflower seed, including taxa sown around fields by farmers. These are rapidly being spread by grass-cutting machines and construction vehicles all over the country. Usually plants in gardens are not mentioned at all, but some species that seed freely and spread over areas of garden and lawn where they are not planted are included. Most of the species which Stace has mentioned but not numbered or included in his keys are here included, while a few have been left out altogether. We started with Volume 5 because *The European garden flora* had already covered the Monocotyledons and this made it easier for us to deal with the garden escapes; we then followed it with Volumes 4, 3, 2 and 1. Because new information is being published all the time we have found it immensely difficult to keep up to date. When a large account has been written, taking three or four years, it is often harder to add information than to write the account in the first place. The following list of references supplies the historical background to our flora.

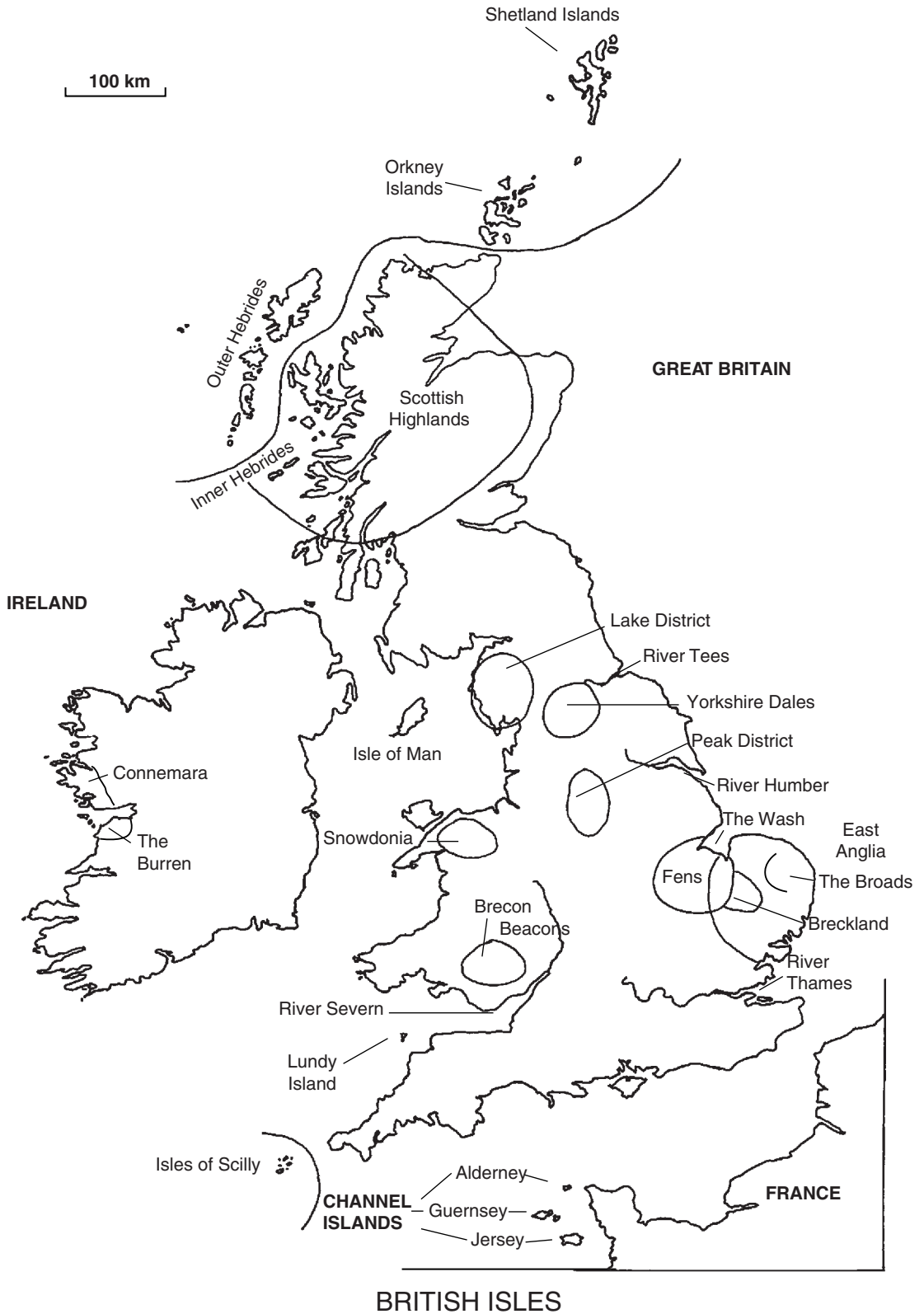
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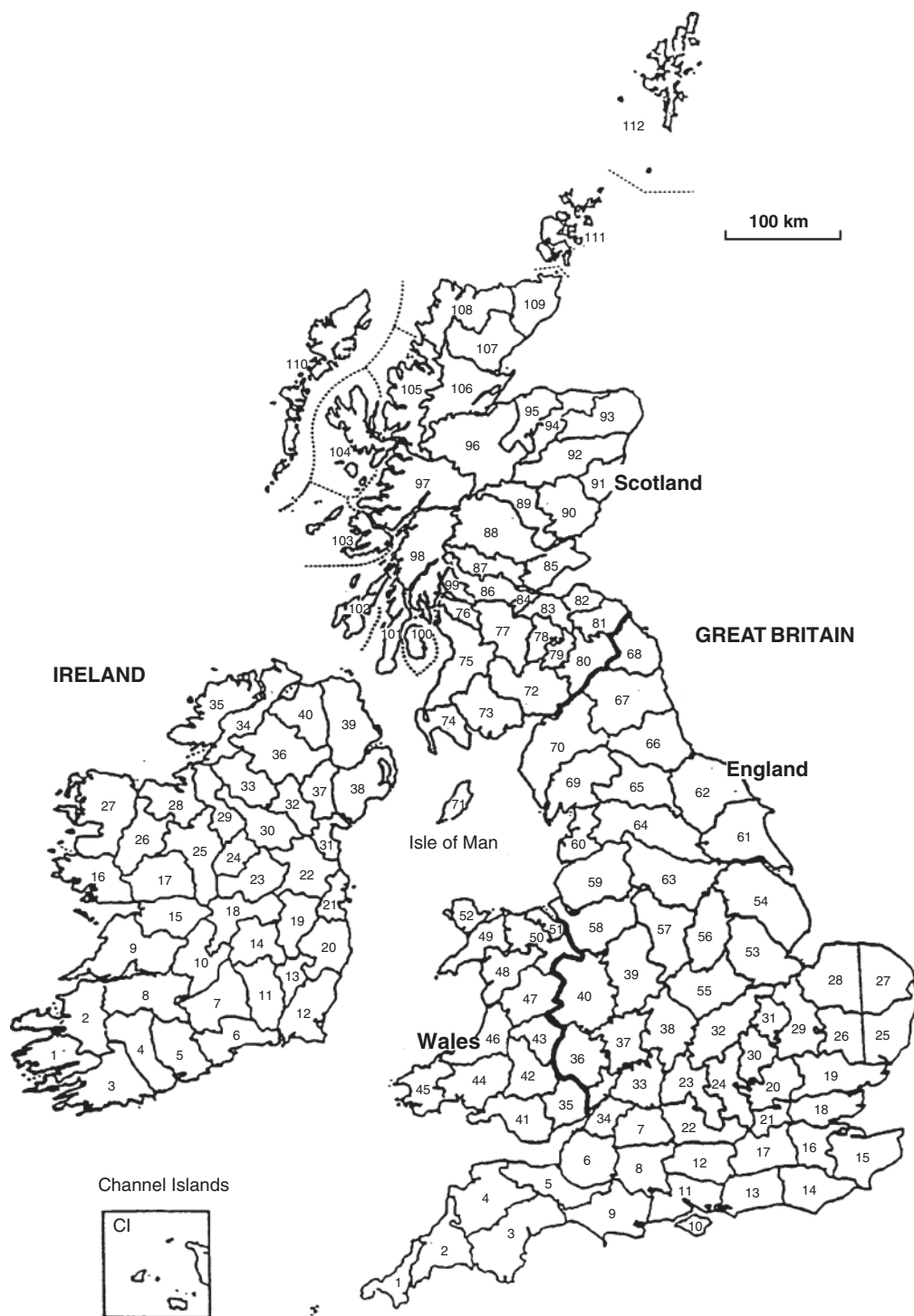
## GEOGRAPHICAL AREA

The flora deals with the British Isles and includes England, Scotland and Wales, collectively known as Great Britain, Northern Ireland and Eire together forming Ireland, the Isle of Man and the Channel Islands, which include Jersey, Guernsey, Alderney, Sark, Herm and various small islands. In these respects it follows Stace (1991, 1997, 2010).

The smallest geographical area usually referred to is the county, for which we have tried to use the name that Dandy (1958) used, especially if it ends in ‘shire’. We have dropped the prefixes that he uses when dividing the large counties into vice-counties. Sometimes in our sense the name includes more than one botanical vice-county. For Great Britain we have used the county boundaries adopted by H. C. Watson in 1873 in *Topographical botany* and for Ireland those adopted by R. L. Praeger in 1901 in *Irish topographical botany*, again disregarding subdivisions into vice-counties. These are the boundaries used by botanists, which have the benefit of not changing as do the boundaries of political counties. With rare or local species the actual place or area may be given. The extra-limital distributions are those given in Clapham, Tutin and Moore (1987) with as much correcting as we and Chris Preston have been able to give them. Russia and Yugoslavia have been used in the sense of the old USSR and Yugoslavia before political disruptions.



Adapted from Stace, C. A. (2010). *New Flora of the British Isles*. Edn 3. Cambridge University Press, Cambridge. Reproduced with permission.



VICE-COUNTIES OF THE BRITISH ISLES

Adapted from Stace, C. A. (2010). *New Flora of the British Isles*. Edn 3. Cambridge University Press, Cambridge. Reproduced with permission.

## ENGLAND, WALES, SCOTLAND, ISLE OF MAN

- |                          |                           |                          |
|--------------------------|---------------------------|--------------------------|
| 1. West Cornwall         | 39. Staffordshire         | 77. Lanarkshire          |
| 2. East Cornwall         | 40. Shropshire            | 78. Peebles-shire        |
| 3. South Devon           | 41. Glamorganshire        | 79. Selkirkshire         |
| 4. North Devon           | 42. Breconshire           | 80. Roxburghshire        |
| 5. South Somerset        | 43. Radnorshire           | 81. Berwickshire         |
| 6. North Somerset        | 44. Carmarthenshire       | 82. East Lothian         |
| 7. North Wiltshire       | 45. Pembrokeshire         | 83. Midlothian           |
| 8. South Wiltshire       | 46. Cardiganshire         | 84. West Lothian         |
| 9. Dorset                | 47. Montgomeryshire       | 85. Fifeshire            |
| 10. Isle of Wight        | 48. Merionethshire        | 86. Stirlingshire        |
| 11. South Hampshire      | 49. Caernarvonshire       | 87. West Perthshire      |
| 12. North Hampshire      | 50. Denbighshire          | 88. Mid Perthshire       |
| 13. West Sussex          | 51. Flintshire            | 89. East Perthshire      |
| 14. East Sussex          | 52. Anglesey              | 90. Forfarshire          |
| 15. East Kent            | 53. South Lincolnshire    | 91. Kincardineshire      |
| 16. West Kent            | 54. North Lincolnshire    | 92. South Aberdeenshire  |
| 17. Surrey               | 55. Leicestershire        | 93. North Aberdeenshire  |
| 18. South Essex          | 56. Nottinghamshire       | 94. Banffshire           |
| 19. North Essex          | 57. Derbyshire            | 95. Morayshire           |
| 20. Hertfordshire        | 58. Cheshire              | 96. East Inverness-shire |
| 21. Middlesex            | 59. South Lancashire      | 97. West Inverness-shire |
| 22. Berkshire            | 60. West Lancashire       | 98. Main Argyllshire     |
| 23. Oxfordshire          | 61. South-east Yorkshire  | 99. Dunbartonshire       |
| 24. Buckinghamshire      | 62. North-east Yorkshire  | 100. Clyde Islands       |
| 25. East Suffolk         | 63. South-west Yorkshire  | 101. Kintyre             |
| 26. West Suffolk         | 64. Middle-west Yorkshire | 102. South Ebudes        |
| 27. East Norfolk         | 65. North-west Yorkshire  | 103. Middle Ebudes       |
| 28. West Norfolk         | 66. Co. Durham            | 104. North Ebudes        |
| 29. Cambridgeshire       | 67. South Northumberland  | 105. West Ross-shire     |
| 30. Bedfordshire         | 68. Cheviotland           | 106. East Ross-shire     |
| 31. Huntingdonshire      | 69. Westmorland           | 107. East Sutherland     |
| 32. Northamptonshire     | 70. Cumberland            | 108. West Sutherland     |
| 33. East Gloucestershire | 71. Isle of Man           | 109. Caithness           |
| 34. West Gloucestershire | 72. Dumfries-shire        | 110. Outer Hebrides      |
| 35. Monmouthshire        | 73. Kirkcudbrightshire    | 111. Orkney Islands      |
| 36. Herefordshire        | 74. Wigtownshire          | 112. Shetland Islands    |
| 37. Worcestershire       | 75. Ayrshire              |                          |
| 38. Warwickshire         | 76. Renfrewshire          |                          |

## IRELAND

- |                      |                        |                      |
|----------------------|------------------------|----------------------|
| H1. South Kerry      | H15. South-east Galway | H29. Co. Leitrim     |
| H2. North Kerry      | H16. West Galway       | H30. Co. Cavan       |
| H3. West Cork        | H17. North-east Galway | H31. Co. Louth       |
| H4. Mid Cork         | H18. Offaly            | H32. Co. Monaghan    |
| H5. East Cork        | H19. Co. Kildare       | H33. Fermanagh       |
| H6. Co. Waterford    | H20. Co. Wicklow       | H34. East Donegal    |
| H7. South Tipperary  | H21. Co. Dublin        | H35. West Donegal    |
| H8. Co. Limerick     | H22. Meath             | H36. Tyrone          |
| H9. Co. Clare        | H23. West Meath        | H37. Co. Armagh      |
| H10. North Tipperary | H24. Co. Longford      | H38. Co. Down        |
| H11. Co. Kilkenny    | H25. Co. Roscommon     | H39. Co. Antrim      |
| H12. Co. Wexford     | H26. East Mayo         | H40. Co. Londonderry |
| H13. Co. Carlow      | H27. West Mayo         |                      |
| H14. Laois           | H28. Co. Sligo         |                      |

## CLASSIFICATION AND NOMENCLATURE

The classification follows that of Stace (1991, 1997) and Kent (1992), which is taken from A. Cronquist's *An integrated system of classification of flowering plants* (1981), with the exception that the main groups are called Divisions and the second groups Classes, following H. C. Bold, C. Alexopoulos & T. Delevryas in *Morphology of plants and fungi* (4th edition, 1980) and A. Cronquist, A. Takhtajan & W. Zimmermann in 'On the higher taxa of Embryobionta' in *Taxon* **15**: 129–134 (1966) and as set out by one of us, P. D. S., in *The Cambridge encyclopedia of life sciences* in 1985. We have not changed the classification to that of the Angiosperm Phylogeny Group, but we would have followed it exactly if we were starting the flora now.

One of us, P. D. S., has specialised in nomenclature for many years and it is here made as accurate as possible according to the latest *International code of botanical nomenclature*. The names of genera and species differ little from those in Stace (1991, 1997) and Kent (1992). When a name is given in a scientific paper, at least when first used, it should always bear the name of its author. Recent changes in the *International code* have been used to get rid of some names which have been a long-standing source of confusion. New taxa and such changes in nomenclature and taxonomy as do occur are published at the end of each volume.

No rules have been made about the number of synonyms given, as many as possible being included, but an attempt has been made to include all names used in British and Irish floras. The abbreviation *auct.* following a name means only that the name has not been accepted for the plant; it does not mean that the type has been checked and the name rejected. Only in the case of a later homonym, which has been checked, does the word *non* and an author follow the name and author. This inclusion of numerous synonyms often shows how a species has moved from one genus to another over the years, especially for example in the Asteraceae. One of the greatest challenges is finding the earliest name of infraspecific taxa, especially as it is difficult and time-consuming to see their types. Sometimes we have taken up names because we are more sure of them, usually because we have checked the type, knowing that there is almost certainly an earlier one which we have been unable to check.

The English names for the species follow Stace (1991, 1997) as far as possible, and where they are missing for additional species they have been created.

Some of the volumes contain some very large keys. Such keys are not very easy to use and the modern idea is to break them up into a number of smaller ones. This is purely psychological, giving the impression that it makes things easier. It does not! The initial breaks, whether in one large key or in an introductory key or grouping, are the most difficult. The more one knows about the genus, the more useful the key becomes, and such knowledge often enables one to take a short cut. Where natural groups appear in the key, this has been indicated so that, as users

become more proficient, they can immediately move to the group which matters. In whatever way you arrive at your identified species, your plant should fit more or less exactly the detailed description in the text. If a difficult plant has any chance of being identified, very detailed notes of every character should be made in the field.

## COLLECTING PLANT SPECIMENS

With conservation foremost in the minds of most botanists, the collecting of wild plant specimens is often considered to be wrong. As regards rare plants we would agree with this attitude and also about collecting in well-known areas from which specimens already exist in herbaria. However, there are many common species where the picking of a good specimen (with permission of the landowner) will do no damage whatsoever, particularly in the case of weeds, trees and shrubs.

During the days of the former Botanical Exchange Club and Watson Botanical Exchange Club (late nineteenth century) many local collections of plants were formed including specimens to show variation. On the death of their owners these collections found their way into local and national museums. In many of these herbaria the nomenclature still needs to be brought up to date. As regards Great Britain and Ireland the largest collection is undoubtedly that of the British Museum of Natural History (**BM**). At Cambridge (**CGE**) we have been extremely lucky in that J. S. Henslow (1796–1861), who put together the original collection, went out of his way to show variation. C. C. Babington (58,000 sheets) also added a great many sheets to show variation. The fine collections of E. S. Marshall and S. H. Bickham have brought us most of the plants sent through the two exchange clubs. We have personally carefully built up most critical genera, especially *Hieracium*, and we have added to the British collection some 50,000, usually copiously annotated sheets. In *Rubus* we have the collections of C. C. Babington, W. H. Mills and B. A. Miles, backed by the European collections of Gaston Geneviev, bought by Babington and given to the University. Herbaria need constant curatorial attention, even though funding for specialist staff may be difficult. The scientific value of voucher specimens in herbaria should be realised as an essential back-up for today's experimental work in chromosome and DNA research. When collecting for the Cambridge Herbarium we have been meticulous, using numbered jeweller's tags on each specimen and detailed notebook entries for each plant made in the field. One of the worst scenarios is to leave specimens in plastic bags to return to them days later, hoping to rely on memory for plant locality and field observation. Tags remain on our specimens right through the plant-pressing stage, while drying and after mounting onto a herbarium sheet.

P. D. S. has almost always avoided field meetings, not because he disliked the company of other botanists, but because in taking copious field notes he was always delayed, so bringing up the rear or trying to catch up with the main group just as they disappeared over the next hill.



We have tried to make this flora for scientists; there is no ‘dumbing down’ to make it user-friendly. If a plant is in some way difficult, despite frequent requests from fellow botanists we have not used aggregate species, except in *Dryopteris* and *Rosa*, where we feel we lack knowledge. We are not in favour of using morphs, which are categories that geneticists do not wish to name, e.g. *Dryopteris* apomicts, as we find that botanists ignore them.

## ORIGIN OF THE BRITISH AND IRISH FLORA

All traces of the Tertiary forests of Great Britain and Ireland were swept away by a succession of cold periods known as the glaciations. During the last few million years, known as the Quaternary Era, there have been alternating periods of warmer temperature and cold stages. Most important for the origin of our flora are those species which survived through the cold stages. Evidence for these in Great Britain and Ireland has been brought together by Richard West (2000).

Before the formation of the Dover Strait, Great Britain remained connected to Europe by means of a structural ridge known as the Weald–Artois anticline, which extended from south-east England to north-west France. A large proglacial lake in the southern North Sea was impounded by the coalescent Fennoscandian and British ice-sheets in the central North Sea and the Weald–Artois barrier across the Dover Strait, and this was fed by the Rhine and Thames drainages as well as from the melting ice-sheet itself. Around 425,000 years ago the build-up of water burst through the Weald–Artois anticline into what is now the English Channel. After the draining of the North Sea lake that resulted from this flood, the Thames and Scheldt were realigned through the newly formed Dover Strait into the Channel River; the Rhine and the Meuse, however, returned to flow into the North Sea after the glaciers withdrew.

The Little Ouse and Waveney Rivers form the northern boundary of Suffolk. The river valleys are the sites of many nature reserves and the exceptional flora of the Breckland sands are to the west. The slate of the landscape was swept clean by the ice of the glaciation that advanced across Suffolk from west to east half a million years ago, the ice of the Anglian Glaciation. After the retreat of this ice, a valley system developed. Richard West (2007) describes in detail how it came about at Lopham Ford that the Little Ouse River runs west to the Wash and the Waveney River runs east to the North Sea. During the warm interglacial period which followed the Anglian Glaciation the watershed between the Waveney and the Little Ouse was not at Lopham Ford as it is today, but near Brockdish, where the plateau of boulder clay extended across the present Waveney valley to form the watershed.

After the interglacial a further glaciation produced ice which blocked the valley of the Ouse near Brandon, resulting in a linear lake forming in the Little Ouse Valley and its tributaries. While the lake was in existence, it carried

sediment from the ice front in Fenland and sediment from the feeding rivers. This resulted in wide expanses of sand to the west of the Chalk escarpment around the Fenland margin and in a sand-filled Little Ouse Valley, in places several metres in depth. It is this sand which is the source of Breckland sand today. These sands have become widely distributed by wind action to give Breckland the heaths that it has at present.

In the valleys there was a copious supply of water rising in artesian springs and seepages from the Chalk aquifers underlying the Little Ouse Valley and headwaters of the Waveney, and also subsidences caused by solution of the underlying Chalk through water movement. This brought about large hollows that became lakes, which evolved into fens as sediment accumulated in them – hence the valley fens.

Eighteen thousand years ago ice-sheets extended southwards to central England, north of which was an uninhabited polar waste. During the cold stages the build-up of ice-sheets brought about eustatic lowering of sea levels so that the English Channel, Irish Sea and large areas of the North Sea were land and Great Britain and Ireland became a peninsula of Europe. There can be no assumption that the climate was uniform. When it was more severe the vegetation would have been mainly herbaceous. At such times, with the advance of ice-sheets, sediments such as till or boulder clay would have been produced. Such an advance appears to have been gradual. Amelioration, however, seems to have been more abrupt. How the cold stage floras spread or contracted during such periods is questionable. The end of these ice-sheets brought a tundra-like landscape, which was colonised later by Birch, Aspen and probably Sallow. Pine probably invaded Kent and Hampshire. The trees either formed deciduous woodland or grew as groves in favoured spots. It needs to be remembered that our plants from then on came from two main directions, from Spain and France (and earlier from along the Mediterranean) and across what became the North Sea from central Europe (and earlier from Asia). This applies not only to species but to variants as well (see *Viburnum lantana* below). DNA research may well show that taxa from these different areas are of completely different origins. Later, as the ice-sheets receded further, some species came from further north in northern Europe (see *Tripleurospermum maritimum* below).

Between 12,000 and 10,000 years ago the climate rapidly became warmer and woods became common over most of Great Britain. Birch and Pine were widespread, but abundant only in the south. Hazel became abundant in the north-west and in the next 7000 years extended southwards into England and Ireland, while Oak increased and Lime became common in the southern half of England.

By 10,000 years ago temperatures had risen substantially and insects and other animals appeared, followed by Man. As the climate ameliorated further the mixed deciduous forest got denser and Hazel, Oak, Lime and Elm replaced Birch and Pine, but Alder and Willow occurred in wet places. By 8500 years ago the melting of the ice caused a rising sea which made Great Britain and Ireland

islands. Rivers that had flowed into the newly submerged land silted up and brought about the formation of the East Anglian fens.

Civilisation has been built on settlement, agriculture and the keeping of livestock for food. Since the very first day that Man set foot in our islands he has steadily and remorselessly altered it in a multitude of ways, sometimes deliberately and sometimes accidentally. Man has come from many areas, at first the Celts from Spain and Portugal up through France into the west country and Ireland, then the Romans, Saxons, Danes, Vikings and Normans. At first Man did much of the work himself. Gradually he developed implements pulled by bullocks, then horses, and finally we came to the machine age. Pastures were created for his horses, cattle and sheep to graze on and areas were fenced to prevent the animals from straying. Streams were altered so that his mills worked more efficiently. Woodland was managed. Orchards were created to grow his fruit. Trade with Continental Europe started from very early times and spread until we became the greatest sea-faring nation of all time, trading with the whole world. We must also not forget that trade came right across Asia and into Europe. All the great houses began to plant foreign trees over their estates. The Enclosure Acts brought another great change: large open fields became small fields surrounded by new hedgerows. Oliver Rackham (1994) suggests that a thousand million or more hedging plants were needed to make some 200,000 miles of new hedges. We know of no records of the place of origin of the hedging. The biggest change of all came after the Second World War. Machines got bigger and bigger and more and more efficient, so that no longer was there a need for so many people to work on the land. Stackyards, a haven for wildlife, disappeared. Hedgerows were trimmed by machine and many cut down altogether. Fields were ploughed up immediately after harvest and much food for wild birds had gone. Perhaps the most devastating change was the ever greater use of herbicides and pesticides. Run-off from fields has also polluted our waterways, and fish, frogs and toads have all but disappeared in mainly agricultural areas. Many of our smaller waterway ditches are not cleared of rubbish and silt, which accumulate further after the banks are cut by machine and the cuttings fall into the ditch, adding to the build-up.

Conservation bodies are now greatly influencing the running of our countryside, while all sorts of other groups and local authorities are joining in. Trees and shrubs are being planted everywhere in new woods, along roads, in amenity areas and even implanted in old hedgerows. A large number of these trees and shrubs are not native. Wildflower seed is sown and even plug plants planted on roadsides, in new woods, by tracks and in field margins. Grass-cutters and construction vehicles moving between sites introduce plants to new areas. The timing of cutting of grass verges etc. is crucial for flower conservation; ideally it should be in late summer, when flowering is over and ripe seed has developed. Many are now cut in May and again in July before they can set seed. Flood plains need minor conservation, as there is usually little agriculture.

Some areas which are conserved do need attention, such as woodlands, but the planting of shrubs and plug plants together with sowing of wildflower seed has established a whole new foreign flora. We have endeavoured to include as many of these introduced plants as possible into our flora, particularly varieties and subspecies. To realise how these plants of all kinds may have been moved from one area to another throughout the ages we recommend reading the chapter 'How weeds and aliens are dispersed' in Sir Edward Salisbury's *Weeds & aliens* (1961).

We finish by quoting the words of Bill Bryson in the introduction to his book *The English landscape* (2000):

The English countryside is an exceptional creation – a corner of the world that is immensely old, full of surprises, lovingly and sometimes miraculously well maintained, and nearly always pleasing to look at. It is one of the busiest, most picked over, most meticulously groomed, most conspicuously used, most sumptuously and relentlessly improved landscapes on the planet.

## VARIATION

The recording of variation is most important for the study of the origin of our plants and their ecology and conservation, and also for gardeners, who go out of their way both to create and to conserve prominent variants.

Intraspecific variation is recorded by the recognition of subspecies, varieties, formae and cultivars. These taxa differ chiefly in ecology and distribution. A **forma** is a plant with a one- or two-gene difference which occurs with one or more other formae in a mixed population for most or all of its range. Zoologists and occasionally botanists (but not we ourselves) call it a morph. The term **variety** is used when one of these formae becomes more or less dominant in a particular ecological area; that is it forms an *ecotype*. The term **subspecies** is used when one of these formae becomes dominant in a geographical area; that is it forms a *race*. A **cultivar** is a forma which is selected by horticulturalists and perpetuated, usually vegetatively. Selection is really the wrong term for the origin of new taxa. What happens is that one genetic sport proves more successful in a certain set of circumstances than another and takes off. Variants often flower at different periods, so their pollinators may be different and, if climatic conditions alter, one ecotype may be better able to survive than another. Variation thus becomes very important in conservation. Because the accounts published as the 'Biological flora of the British Isles' have lumped all their information under species they can be highly misleading when applied to individual populations. It is unfortunate that many botanists tend to ignore variation completely, and they will certainly ignore it if it has no name at all; subspecies are usually more often recognised than varieties. Sometimes it is more important to conserve one variety rather than another. For example the Chilterns *Orchis militaris* var. *tenuifrons* is endemic, while the Suffolk var. *militaris* occurs in Continental Europe; *Liparis loeselii* var. *ovata* is rare in distribution but frequent where it occurs, whereas var. *loeselii* is rare in Britain but occurs on the continent.

Sometimes the variant will tell us whether the plant is native or not; for example *Leucojum aestivum* subsp. *aestivum* is native while subsp. *pulchellum* is a naturalised garden escape.

All apomicts, where possible, are treated as species, long experience showing that any sort of lumping deprives them of being recognised as having an interesting ecology or distribution. Hybrids are dealt with as fully as possible, especially those that spread vegetatively. In some cases no serious attempt has been made to decide on the correct infraspecific rank as taxa are often both ecological and geographical. Uniformity of infraspecific rank is often presented in a species or genus, but usually the only important thing considered is that a morphologically recognisable infraspecific taxon with its own ecology and distribution should have a name.

Where species grade gradually into one another over large distances, as the species of *Larix* do around the northern hemisphere, and at given points the whole population is uniformly intermediate, this is regarded as a **cline**. Where two populations with differing ecological preferences grow adjacently, as in *Geum rivale* and *G. urbanum*, there is often an area in which variable intermediates occur. This is also often called a cline, but it is really only so statistically, and we prefer to call it a **variable hybrid zone**. It is surprising how often such situations can, on careful investigation, be found to exist, and species, even apomicts, are not so clear-cut as we are made to believe.

Some of the most important work on plant variation was done long ago by Alexis Jordan (1814–1897). Philip Oswald has translated the following account of him from A. Boreau's *Flore du centre de la France et du bassin de la Loire* (1857, XI–XIV):

Two schools are today in opposition: a fairly large number of botanists, faithful to former bad habits, recognise clear-cut species, around which they group, under the title of *varieties*, other forms which seem to them less characteristic and which they suppose to have been originally derived from them. Most often these are organisms the distinctive attributes of which it has not proved possible to grasp and which are classed thus by analogy; but no definite rule determines these groupings, which are all the more evidently arbitrary because each author conceives them in a different way, following the point of view that he adopts. Some of them even, perhaps as a logical consequence, have reached the point of denying completely the existence of species: if, by that word, one must understand organisms perfectly isolated in nature and exclusively distinct from other organisms, we would acknowledge with them that such species have no existence at all. All organisms indeed are bound together by a multitude of connections; they form part of a great whole, which, although possessing unity in its essence, is no less infinitely varied and manifests itself everlastingly in all the forms that life can take on, forms that nature constantly reproduces, leaving to human science the task of analysing and distinguishing them without its ever being able to flatter itself that it has exhausted the subject.

These are the forms, neglected up to now, that the botanists of the new school are endeavouring to characterise, by subjecting them to close attention. Monsieur Jordan has opened for himself a broad path in this field of enquiry, where I should have liked to follow him with a surer tread. I know that his works, despite the conscientious exactitude that has directed them, will not be

immune from criticism; but denials or jests are not proofs and they have no power against facts. Experience has shown that the polymorphy or instability of forms attributed to certain species had in no way been based on reason; the studies which have in recent times illuminated the aquatic *Ranunculi*, the *Rubi* and several other genera lead to results which can no longer be denied by anyone; is there not then a positive presumption in favour of the trials undertaken on some other groups too much neglected by observers up to now?

Monsieur Jordan has described these new species only after having reproduced them from their seeds and tested them by long cultivation; he has brought a noble challenge to the incredulous, by disseminating dried specimens of these plants to herbaria and by communicating seedlings or seeds of them to the botanists in a position to verify for themselves the truth of his assertions. After more than twenty years of regular relations with this honourable scientist, who has enriched my collections with so many precious plants, after proofs without number of his good faith and of his scientific probity, free of those signs of charlatanism from which scientists unfortunately do not always know how to preserve themselves, my conviction would not perhaps have been completely established if I had not had before my eyes, each year, a large number of these contentious species, which, reproduced far from their place of origin, have corresponded exactly to the descriptions that their author had sketched out for them. I have had to submit to the evidence and, despairing of saying anything better, I have often contented myself with translating or abridging the master's descriptions. As for the species that Monsieur Jordan has communicated to me before having published them, I have tried hard to grasp their characters and, if they have not been adequately brought to light, it is my deficiency alone that ought to be called into question. I shall always pay homage to the patient investigations of this botanist, who has not recoiled before so stupendous a task, who, with so outstanding a talent for discrimination, has made proof of such soundness of judgement that, after having analysed minutely so many diverse plants, he has known how to refrain from the easy credit of modifying generic divisions. Appealing only to observation of the facts, he has been careful not to attribute the origin of contentious species to adulterous [i.e. hybrid] breeding – a theory born of hypotheses which experience daily refutes but which has led to the creation of a hybrid and barbarous nomenclature, likely to divert the most devoted vocations from the pleasant science [of botany] and against which the weapon of ridicule could perhaps be usefully employed if the science itself did not have to be compromised by it.

But, someone will say, distinguishing so large a number of forms indicated by minute characters tends to make the study of botany more and more difficult and can do harm to the philosophical considerations that derive from a science of which it is necessary to be able easily to grasp both the whole and the synthesis. This objection would merit serious consideration if the number of species could be increased or reduced arbitrarily, as some naturalists still think. Those that have been called 'bad species', placed in the herbaria by superficial botanists, do not exist in nature; but the real species exist, and the naturalist's duty is to distinguish and describe them. So henceforth the question can be summed up thus: *should one study a conventional nature such as is represented in our books or should one see nature as it is?* [our italics] Should one be content with a superficial examination, highlighting only very easily grasped characters, or should one analyse each organ minutely and distinguish everything that is capable of being so? There lies the whole question, and, if the reply cannot be in doubt for any man of good faith, no one, I hope, will any longer reproach us for having described too large a number of organisms and for remaining with the regret of not having had the

time and opportunity to describe yet many more that will certainly be distinguished in the future.

Some botanists believe that they can avoid the difficulty by suggesting that there exist many varieties that are constant and provided with hereditary characters. There is simply a battle of words there: characters that are easily grasped and transmissible by heredity are the only means that observation can employ to distinguish species in the natural state (for organisms in which long domestication has modified their functioning cannot be taken as a point of comparison), and it becomes impossible thereafter to fix a limit between species and these supposed varieties.

Moreover, however extensive our researches and observations may be able to be, they will never reach a limit; our books will never be other than the alphabet of the great book of nature that humanity is called upon to unroll successively and page by page; always man will find himself in the presence of this great mystery that the infinite being presents to us, single and multiple at the same time, ceaselessly manifesting itself in entities that are as varied as they are innumerable; always the spirit will be suspended over the abyss: *Semite Dei in abysso!*... [The footpaths of God in the abyss!...]

Most of Jordan's species are either apomictic or self-pollinating, or else they are infraspecific geographical or ecological races. He was sensible enough to make many specimens, which he distributed to various herbaria, and we are lucky enough to have many of them at CGE. We would encourage modern botanists who carry out chromosome or DNA research to deposit voucher specimens in the same way. What Boreau said about Jordan is still applicable today.

Dick Brummitt and Arthur Chater, writing in *Watsonia* 23: 161 (2000) about the genus *Calystegia*, say:

The whole genus, in which some 25 species world-wide may conveniently be recognised, is taxonomically difficult, and few if any of the species are morphologically clear-cut. They mostly vary considerably over their ranges and merge geographically one into another, and division into species and subspecies is of necessity somewhat arbitrary.

We find this true of many groups, including species, especially when their whole range is considered.

Sir Arthur Tansley, writing in *The British islands and their vegetation* in 1939, said on page xi:

The separation and study of ecotypes is another line of investigation that is urgently needed to elucidate the behaviour of important species. We very often suspect that it is the existence of different ecotypes of a species which accounts for its various behaviour in different habitats, but there can be no certainty and no real advance in knowledge until each case has been properly investigated; and this means a great deal of laborious cultural and genetical work. ... The field is enormous and scarcely more than its fringes have been touched.

This is still almost as true.

Charles Raven wrote in *The changing flora of Britain* (Lousley, 1953, pp. 15–17):

At the risk of seeming to go beyond the scope of our programme – I must add that, while the changes in our flora by invasion give rise to a number of fascinating ecological, physiological and chemical problems which deserve full investigation, for my own part I must draw attention to changes which raise rather different issues. Here is the point to which I specially desire to draw attention – the

changes taking place in our flora not by introduction from outside, nor by changes in the status and distribution of native species, but by the extreme variability of many of our most familiar groups. In Britain we have a relatively small area, widely varied in soil, altitude, character and climate, closely studied over a long period, and the home of a remarkable number of still varying aggregates. ... By all means let us collect and identify and classify our flora and note additions to it, and calculate their chances of survival. But let us remember that this is only preliminary investigation: we do not learn from it anything of scientific value, unless we use our experience to throw light upon the problems of the relationship of the plant to its environment, of its adaption and survival, and of the parts played by nature and nurture in its constitution.

In the same book (p. 175) E. F. Warburg wrote: "I would like at this point to put in a plea that more study should be given to woody aliens of all kinds and that where specimens are preserved they should be accompanied by full data of the occurrence and amount of regeneration".

In the past an immense amount of work has been carried out on variation, but since the Second World War, except for a paper here and there, everything seems to have been dumbed down to the rank of species, often aggregate species. With changing climate and great changes in agriculture, ecological and distributional studies will need to take more account of variation within species. The vast number of foreign variants which have arrived in Great Britain in the last 50 years and the large numbers still coming in will completely change our landscape over the next decades. Thirty years ago Professor David Valentine remarked that in 50 years Britain would be one large garden. It is well on its way.

Oliver Rackham wrote in *Woodlands* (2006, p. 346):

Conservation of 'biodiversity' is usually thought of in terms of species: it might not matter much if Hungarian *Quercus robur* were to replace Welsh *Q. robur*. However, this is more a convention of how ecologists think than an expression of biological reality. It is hard to argue that species are worthy of conservation and lesser units – subspecies and varieties – are not: that the native pine of Scotland is 'only' a subspecies and not worth protecting. These categories are inventions of the human mind, not measured units of genetic difference, and taxonomists are forever changing their minds about which is which.

As Sell points out, the biological reality has only recently come to light and is not fully understood, especially with trees. Many trees widely distributed in the northern hemisphere exist as *clines*, varying gradually from western Europe to east Asia or even into America. Travellers to the Caucasus or Japan might describe the local variants as species distinct from those of western Europe, without realising that they were connected by intermediates. Conventional taxonomy is not good at handling clines: the authors of *Flora Europaea* repeatedly refused to name a geographical variant on the grounds that it is connected to the named 'typical' variant by intermediates. (If developers or polluters were to exterminate the intermediate forms, would this increase the world's biodiversity by creating a new species?)

Importing false natives arbitrarily mixes up variants from one point on the cline with those on another point. (Whether the variants are regarded as different species or not is a historical accident.) The consequences vary according to whether the introduction performs better or worse than the true native, whether it hybridises with it, and whether it has the same relation to associated plants, animals and fungi.

Intermediates occur between all taxa, including species, if you look at the full range of a taxon, and sometimes these intermediates reproduce themselves. It has been suggested that our keys to varieties would be better placed under the parent species, but this would not show when a variety approached another species or even keyed out next to it. One can best understand all this by considering how the variation of *Homo sapiens* developed on a world scale. In *The tribes of Britain* (2005) David Miles tells of what happened in our islands and also shows how plants could have been moved about by Man, deliberately or accidentally, and Bryan Sykes in *Blood of the isles* (2006) explains the genetical aspects of the mixture of tribes or non-mixture of tribes.

## DNA

The exciting, comparatively new method of looking at the origin and progress of life through the investigation of DNA did not develop early enough for us to consider it for the arrangement of families in this flora. We believe that the project is still in its infancy and much more work lies ahead before it can compare with the classifications made by a large number of botanists over a very long period: see the account of the Second Systematics Debate at the Linnean Society in *The Linnean* **23**(2): 8–9 (2007). However, if we were just starting our flora now we would follow the arrangement set out below.

The identification of plants from their DNA is a different matter. If one has a plant in the hand its DNA can be tested. If you walk into a meadow and want to find a certain plant DNA will not help you, unless you test every plant in the meadow. Even if you use this method for confirmation, are you just going to consider one plant or all the other plants like it in the meadow? The morphologist can walk about the meadow and check all the plants in a fairly short time. Is the DNA researcher just going to test one plant and rely on the morphologist to say if the rest are the same? For sheer practicality the DNA specialist and the morphologist have surely to work together.

A more complex problem arises when plant characters slowly change from Europe to China or from India down the Malay peninsula and archipelago to Australia and you find that plants at the two ends have different DNA. What about the taxa in between? Returning to our own flora, if western variants which came from Spain and western France differ from those which came from central Europe into East Anglia, will their DNA be different? We look forward to the results of study by researchers in these difficult areas.

The following is a linear sequence of the angiosperm families which occur in our *Flora of Great Britain and Ireland* as set out by E. Haston, J. E. Richardson, P. F. Stevens, M. W. Chase & D. J. Harris of the Angiosperm Phylogeny Group in *Botanical Journal of the Linnean Society* **161**: 128–131 (2009), with orders inserted as defined by this group in the same volume on pages 105–121 (2009).

- Nymphaeales** Salisb. ex Bercht. & J. Presl
  - Cabombaceae** Rich. ex A. Rich.
  - Nymphaeaceae** Salisb.
- Piperales** Bercht. & J. Presl
  - Aristolochiaceae** Juss.
- Magnoliales** Juss. ex Bercht. & J. Presl
  - Magnoliaceae** Juss.
- Laurales** Juss. ex Bercht. & J. Presl
  - Lauraceae** Juss.
- Acorales** Link
  - Acoraceae** Martinov
- Alismatales** R. Br. ex Bercht. & J. Presl
  - Araceae** Juss.
    - (*Lemnaceae*).
  - Tofieldiaceae** Takht.
  - Alismataceae** Vent.
  - Butomaceae** Mirb.
  - Hydrocharitaceae** Juss.
    - (*Najadaceae*).
  - Scheuchzeriaceae** F. Rudolph
  - Aponogetonaceae** Planch.
  - Juncaginaceae** Rich.
  - Zosteraceae** Dumort.
  - Potamogetonaceae** Bercht. & C. Presl
    - (*Zannichelliaceae*)
  - Posidoniaceae** Vines
  - Ruppiaceae** Horan.
- Dioscoreales** R. Br.
  - Nartheciaceae** Fr. ex Bjurzon
  - Dioscoreaceae** R. Br.
- Liliales** Perleb.
  - Alstroemeriaceae** Dumort.
  - Colchicaceae** DC.
  - Smilacaceae** Vent.
  - Liliaceae** Juss.
- Asparagales** Link
  - Orchidaceae** Juss.
  - Iridaceae** Juss.
  - Xanthorrhoeaceae** Dumort.
  - Amaryllidaceae** J. St-Hil.
  - Asparagaceae** Juss.
    - (*Agavaceae*)
- Arecales** Bromhead
  - Arecaceae** Bercht. & J. Presl
- Commelinales** Mirb. ex Bercht. & J. Presl
  - Commelinaceae** Mirb.
  - Pontederiaceae** Kunth
- Poales** Small
  - Typhaceae** Juss.
    - (*Sparganiaceae*)
  - Bromeliaceae** Juss.
  - Xyridaceae** C. Agardh
  - Eriocaulaceae** Martinov
  - Juncaceae** Juss.
  - Cyperaceae** Juss.
  - Poaceae** Barnhart
- Ceratophyllales** Link
  - Ceratophyllaceae** Gray
- Ranunculales** Juss. ex Bercht. & J. Presl

- Papaveraceae** Juss.  
 (*Fumariaceae*)  
**Berberidaceae** Juss.  
**Ranunculaceae** Juss.  
**Proteales** Juss. ex Bercht. & J. Presl  
**Nelumbonaceae** A. Rich.  
**Platanaceae** T. Lestib.  
**Buxales** Takht. ex Reveal  
**Buxaceae** Dumort.  
**Gunnerales** Takht. ex Reveal  
**Gunneraceae** Meisn.  
**Saxifragales** Bercht. & J. Presl  
**Paeoniaceae** Raf.  
**Grossulariaceae** DC.  
**Saxifragaceae** Juss.  
**Crassulaceae** J. St-Hil.  
**Haloragaceae** R. Br.  
**Vitales** Juss. ex Bercht. & J. Presl  
**Vitaceae** Juss.  
**Fabales** Bromhead  
**Fabaceae** Lindl.  
**Polygalaceae** Hoffmanns. & Link  
**Rosales** Bercht. & J. Presl  
**Rosaceae** Juss.  
**Elaeagnaceae** Juss.  
**Rhamnaceae** Juss.  
**Ulmaceae** Mirb.  
**Cannabaceae** Martinov  
**Moraceae** Gaudich.  
**Urticaceae** Juss.  
**Fagales** Engl.  
**Nothofagaceae** Kuprian.  
**Fagaceae** Dumort.  
**Myricaceae** A. Rich. ex Kunth  
**Juglandaceae** DC. ex Perleb  
**Betulaceae** Gray  
**Cucurbitales** Juss. ex Bercht. & J. Presl  
**Cucurbitaceae** Juss.  
**Begoniaceae** C. Agardh  
**Celastrales** Link  
**Celastraceae** R. Br.  
 (*Parnassiaceae*)  
**Oxalidales** Bercht. & J. Presl  
**Oxalidaceae** R. Br.  
**Malpighiales** Juss. ex Bercht. & J. Presl  
**Euphorbiaceae** Juss.  
**Elatinaceae** Dumort.  
**Passifloraceae** Juss. ex Roussel  
**Salicaceae** Mirb.  
**Violaceae** Batsch  
**Linaceae** DC. ex Perleb  
**Hypericaceae** Juss.  
**Geraniales** Juss. ex Bercht. & J. Presl  
**Geraniaceae** Juss.  
**Myrtales** Juss. ex Bercht. & J. Presl  
**Lythraceae** J. St-Hil.  
**Onagraceae** Juss.  
**Myrtaceae** Juss.  
**Crossosomatales** Takht. ex Reveal  
**Staphyleaceae** Martinov  
**Sapindales** Bercht. & J. Presl  
**Anacardiaceae** R. Br.  
**Sapindaceae** Juss.  
 (*Aceraceae*  
*Hippocastanaceae*)  
**Rutaceae** Juss.  
**Simaroubaceae** DC.  
**Malvales** Juss. ex Bercht. & J. Presl  
**Malvaceae** Juss.  
 (*Tiliaceae*)  
**Thymelaeaceae** Juss.  
**Cistaceae** Juss.  
**Brassicales** Bromhead  
**Tropaeolaceae** Juss. ex DC.  
**Limnanthaceae** R. Br.  
**Resedaceae** Martinov  
**Capparaceae** Juss.  
**Cleomaceae** Bercht. & J. Presl  
**Brassicaceae** Burnett  
**Santalales** R. Br. ex Bercht. & J. Presl  
**Santalaceae** R. Br.  
 (*Viscaceae*)  
**Loranthaceae** Juss.  
**Caryophyllales** Juss. ex Bercht. & J. Presl  
**Frankeniaceae** Desv.  
**Tamaricaceae** Link  
**Plumbaginaceae** Juss.  
**Polygonaceae** Juss.  
**Droseraceae** Salisb.  
**Caryophyllaceae** Juss.  
**Amaranthaceae** Juss.  
 (*Chenopodiaceae*)  
**Aizoaceae** Martinov  
**Phytolaccaceae** R. Br.  
**Montiaceae** Raf.  
**Basellaceae** Raf.  
**Portulacaceae** Juss.  
**Cornales** Link  
**Cornaceae** Bercht. & J. Presl  
**Hydrangeaceae** Dumort.  
**Loasaceae** Juss.  
**Ericales** Bercht. & J. Presl  
**Balsaminaceae** A. Rich.  
**Polemoniaceae** Juss.  
**Primulaceae** Batsch ex Borkh.  
**Diapensiaceae** Lindl.  
**Sarraceniaceae** Dumort.  
**Clethraceae** Klotzsch  
**Ericaceae** Juss.  
 (*Empetraceae*  
*Pyrolaceae*  
*Monotropaceae*)  
**Garryales** Lindl.  
**Garryaceae** Lindl.  
**Gentianales** Juss. ex Bercht. & J. Presl  
**Rubiaceae** Juss.  
**Gentianaceae** Juss.  
**Loganiaceae** R. Br. ex Mart.

- Apocynaceae** Juss.  
**Boraginales** Bercht. & J. Presl  
**Boraginaceae** Juss.  
 (*Hydrophyllaceae*)  
**Solanales** Juss. ex Bercht. & J. Presl  
**Convolvulaceae** Juss.  
 (*Cuscutaceae*)  
**Solanaceae** Juss.  
 (*Nolanaceae*)  
**Lamiales** Bromhead  
**Oleaceae** Hoffmanns. & Link  
**Calceolariaceae** Olmstead  
**Gesneriaceae** Rich. & Juss.  
**Plantaginaceae** Juss.  
 (*Callitrichaceae*  
*Hippuridaceae*)  
**Scrophulariaceae** Juss.  
**Lamiaceae** Martinov  
**Phrymaceae** Schauer  
**Pawloniaceae** Nakai  
**Orobanchaceae** Vent.  
**Lentibulariaceae** Rich.  
**Acanthaceae** Juss.  
**Bignoniaceae** Juss.  
**Verbenaceae** J. St-Hil.  
**Aquifoliales** Senft  
**Aquifoliaceae** Bercht. & J. Presl  
**Asterales** Link  
**Campanulaceae** Juss.  
 (*Lobeliaceae*)  
**Menyanthaceae** Dumort.  
**Asteraceae** Bercht. & J. Presl  
**Escalloniales** R. Br.  
**Escalloniaceae** R. Br. ex Dumort.  
**Dipsacales** Juss. ex Bercht. & J. Presl  
**Adoxaceae** E. Mey.  
**Caprifoliaceae** Juss.  
 (*Dipsacaceae*  
*Valerianaceae*)  
**Apiales** Nakai  
**Griselinaceae** J. R. Forst & G. Forst. ex A. Cunn.  
**Pittosporaceae** R. Br.  
**Araliaceae** Juss.  
**Apiaceae** Lindl.

## EXAMPLES OF VARIATION

Since 'tis nature's law to change,  
 Constancy alone is strange.

John Wilmot, Earl of Rochester  
 (1647–1680).

The following are examples of different kinds of variation, which should highlight the challenges involved in recognising only species. Some botanists do not recognise some taxa because they say that the variation is continuous. Almost all variation is continuous even between species, especially if you look at their world distribution,

and sometimes each part of a continuous line reproduces itself. This is what evolution is all about. The inclusion of variants in the same key as the species in our flora helps to point this out. Since the country has been flooded with foreign variants, variation has become ever more difficult to understand.

## Coastal variants

In 2004, M. O. Hill, C. D. Preston and D. B. Roy published *Plantatt*, which contained attributes of British and Irish plants – status, size, life history, geography, habitats, etc. One of the ecological factors given is a 0–3 value on salt tolerance. On 4 August 2005 we made the following list of plants on the shingle between Thorpness and Aldeburgh in Suffolk: *Ammophila arenaria*, *Crambe maritima*, *Eryngium maritimum*, *Euphorbia paralias*, *Glaucium flavum*, *Honckenya peploides*, *Lathyrus japonicus* and *Silene uniflora*, all of which are given a salt tolerance of 3 in the above work. Growing intermixed with these species were *Carduus crispus* var. *glareicola*, *Carduus nutans* var. *litoralis*, *Cerastium fontanum* subsp. *vulgare* var. *lucens*, *Cirsium arvense* var. *maritimum*, *Cirsium vulgare* var. *litorale*, *Crepis capillaris* var. *capillaris*, *Galium verum* subsp. *maritimum*, *Ononis spinosa* subsp. *maritima*, *Plantago lanceolata* var. *angustifolia*, *Senecio jacobaea* var. *condensatus*, *Solanum dulcamara* var. *marinum*, *Sonchus arvensis* var. *maritimus* and *Sonchus asper* var. *sabulosus*, which as species are given a salt tolerance of 0. As well as having a different salt tolerance the shingle plants mostly have a different habit and are probably native. The variants that are inland weeds, however, are mostly taller plants, which were either derived from the coastal plants after Man opened up the terrain or were brought in by Man himself. In all these cases, if you speak only of species, they should have a salt tolerance of 0–3.

### *Sonchus*

*Sonchus arvensis* var. *maritimus*, *S. asper* var. *sabulosus* and *S. oleraceus* var. *litoralis* are all restricted to sand and shingle by the sea. They are shorter plants with fewer capitula and are salt-tolerant; they are probably native. *S. arvensis* var. *arvensis*, *S. asper* var. *asper* and *S. oleraceus* var. *oleraceus* are inland weeds of cultivated and waste places. They may have been derived from the coastal plants after Man opened up the terrain, or Man may have brought them in from Continental Europe. *S. asper* subsp. *glaucescens* and *S. asper* var. *integrifolius* are probably later introductions.

### *Galium verum*

Sometimes when two populations of the same species grow on different soils, but adjacently, there are no intermediates. *Galium verum* subsp. *verum* is a plant of calcareous grassland. *G. verum* subsp. *maritimum* occurs on sand and shingle by the sea and on sandy heaths inland. At Grimes Graves in Norfolk there is a sandy heath with an outcrop of chalk pushing through at the top of a rise. All

over the sandy heath *G. verum* subsp. *maritimum* occurs in abundance, while on the chalk outcrop it is replaced by *G. verum* subsp. *verum*. The line between them is clear-cut and they do not seem to grow on each other's territory. Subsp. *maritimum* is a dwarf plant with dense leaves and inflorescences and occurs in large patches. Subsp. *verum* is erect and more open. To further confuse the issue, elsewhere there is a large erect form with pale flowers, which may be referable to subsp. *wirtgenii* and which is similar to the hybrid *G. mollugo* × *verum*. This plant may have been introduced with wildflower seed.

### ***Galium aparine* and *Valerianella locusta***

*Galium aparine* subsp. *agreste* var. *marinum* and *Valerianella locusta* subsp. *dunensis* are both probably native, coastal variants with short prostrate or ascending stems. *V. locusta* subsp. *locusta* is an inland arable weed, possibly brought in by Man, with a single erect stem. *G. aparine* subsp. *agreste* var. *agreste* occurs in the stubble of cereal crops after the crop has been harvested. It is very like var. *marinum*, but that plant has fleshy leaves, stems more spreading and smaller nutlets. Var. *agreste* was once abundant throughout the cultivated regions, but is now much reduced by herbicides and early ploughing. It could still be seen in abundance in early stages of set-aside. Both these varieties retain their characters in cultivation. *G. aparine* subsp. *aparine* is probably native and could be one of the *Galium* taxa whose pollen is recorded from the Quaternary cold stages. *Valerianella locusta* var. *oleracea* is a large plant with large fruits cultivated in gardens for salads and may escape in the future.

### ***Achillea millefolium***

This species is well recorded from the Quaternary cold stages, mainly in grasslands, where it occurs now (West, 2000). However, there are three different coastal variants distinguished by their habit and hairiness. *A. millefolium* var. *compacta* occurs on the western coasts and apparently also in the mountains. Var. *villosa* occurs on the north coast of Scotland south to Argyll, in the islands and on the west coast of Ireland. Var. *densiloba* occurs in sandy areas of the East Anglian coast. Did these varieties originate from the inland populations or did they come from three different directions, from France and Spain, from Scandinavia and from across the North Sea? Their relatives suggest that they came from three different directions, though they all tend to grade into the variable inland var. *millefolium*. Were the inland populations in the past derived from the coastal ones when Man opened up the terrain? Were they already there in the cold stages, or did Man and his animals bring most of them in? All these varieties belong to subsp. *millefolium*. Introduced with wildflower seed from central Europe is *A. millefolium* subsp. *sudeta* (Opiz) Weiss, which we had not identified when Volume 4 went to press. It is probably widespread, especially where wildflower seed has been sown on roadsides and field margins. From there it is also probably distributed on grass-cutting machines. The leaves are illustrated in *B.S.B.I. News* 101: 21 (2006).

### ***Tripleurospermum maritimum***

This group raises the question of what rank to give the various taxa. The coastal plants are often called *T. maritimum* and the inland ones *T. inodorum*. The former occupy coastal sand and rocks; the latter are weeds of cultivated and waste places. Where arable land is close to the coast there often occur many variable fertile intermediates. These two plants would thus normally be regarded as varieties of the same species. Unfortunately, *T. maritimum* can be divided into a number of geographical races, which would normally be called subspecies. This would mean that plants less distinct morphologically would be given a higher rank. On top of this we were confronted with a nomenclatural mess. We finally decided to treat all the taxa as subspecies of one species. The coastal plant of northern Scotland, the Orkney Islands, Fair Isle and the Shetlands, which is also in the Faeroes and Iceland, has always been called subsp. *phaeocephalum* (Rupr.) Hamet-Ahti, but this name applies to the plant of the Arctic, which is shorter with differently shaped involucre bracts. We thus had to give our plant a new name, subsp. *nigriceps*, referring to its blackish capitula. The coastal plant of southern England, north to the Wash and west to Cornwall and the Channel Islands, which continues down the coast of France to Spain and Portugal, was called *T. maritimum* var. *salinum*. Unfortunately its type specimen was referable to the inland plant, so yet another new name was needed – subsp. *vinicaule*, referring to its usually deep purple stem. The nominate coastal race, subsp. *maritimum*, is found in the remaining coastal areas of Great Britain and Ireland, and also in Continental Europe in coastal areas of the North Sea and Baltic. All these coastal variants are probably native, but they may have different origins, as their continental distributions suggest. The inland subsp. *inodorum* was probably introduced by early Man, but after being an abundant weed it is now much reduced by herbicides. All our plants, as far as is known, are sexual diploids with  $2n = 18$ . Plants from eastern and central Europe, apparently morphologically indistinguishable from subsp. *inodorum*, have  $2n = 36$ . One example of a plant with  $2n = 36$  has been recorded from Great Britain. In view of so many other species from central and eastern Europe being found in wildflower seed it might be worth counting the chromosomes of plants of such origin.

### **Inland variants**

These variants usually occur in different habitats, but much of their distribution is brought about by Man and his animals. Some of the variants occur in what can be described as inland 'islands', i.e. in woods or on mountain tops. Some have developed in particular crops and others are simply introduced.

### ***Aethusa cynapium***

After the corn has been cut at harvest a small umbel grows to the height of the stubble, with flowers and fruits. It is Fool's Parsley, *Aethusa cynapium* subsp. *agrestis*. Earlier



in the year, on waste ground, a taller plant of the same species, but subsp. *cynapium*, occurs. The two subspecies grown from seed in the same soil in Cambridge Botanic Garden retained their differences, and subsp. *cynapium* flowered and fruited before subsp. *agrestis* came into flower. On 18 July 1998 at Bassingbourn in Cambridgeshire a plant occurred of this species about two metres high, which was common all over a field of wheat. It was a continental variant, subsp. *gigantea*. Possibly it was introduced with Pig slurry or dung, which had been put on the land before sowing. In the same year it occurred in a field of wheat at Histon in the same county. If there was any connection with wheat this was not understood, and it has not been seen in either locality since. This brought to mind another plant collected in Bassingbourn in 1994, where *Narcissus* bulbs had been planted along the edge of a medieval moat. These bulbs had been given to the village by a local farmer. A search of the field where the bulbs were obtained produced more plants of the *Aethusa* variant. Plants were then found in two different years in a garden in the same village. These plants were slightly different from the plants growing in the wheat fields and were referable to *A. cynapium* subsp. *cynapioides*. It is interesting that a representative from the firm which sold the herbicides to the farmer to spray the field containing subsp. *gigantea* thought the plants were Hemlock. Because of the plants' size P. D. S. assumes that he meant *Conium maculatum*, but it should be pointed out that the native village people call *Anthriscus sylvestris* 'Hemlock'. All four of the subspecies of *Aethusa cynapium* were probably brought in by Man. The recently published account in Volume 6 of *Flora Nordica* (Jonsell et al., 2010) has more or less the same taxonomy but different nomenclature.

### *Anthriscus sylvestris*

Cow Parsley, *Anthriscus sylvestris*, tells an interesting story. Anyone who has seen it in Scotland or Wales and knows it well in East Anglia will know that they are very different-looking plants. G. C. Druce called them var. *angustisectus* and var. *latisectus*, relating to the shape and division of the leaf segments, but he seemed to take little interest in their distributions. Roy Clapham (in Lousley, 1953, p. 34), suggested that var. *latisectus* was introduced by Man, and we would go along with that suggestion. On a journey from Aberystwyth to London, Arthur Chater collected specimens at intervals. These showed a tendency for the western material to be var. *angustisectus* with some intermediates, but further east some, but not many, specimens were more or less var. *latisectus*. In East Anglia the great bulk of the material is var. *latisectus*. However, we thought that if we considered carefully where to look we ought to find populations of var. *angustisectus* in East Anglia. On an ancient way at Histon in Cambridgeshire called Gun's Lane we found it through much of its length, but near the built-up area of Histon the plants were var. *latisectus*. We then found var. *angustisectus* by the Royston Road from Litlington, a comparatively new road that ran through the ancient heath that was not ploughed up until after 1800. Curiously the adjacent Therfield ('Royston')

Heath held only var. *latisectus*, which may be because of Man's long activity there. Var. *angustisectus* also occurs on the ancient trackway of Ashwell Street in Cambridgeshire. *Anthriscus sylvestris* is recorded from the Quaternary cold stages (West, 2000).

### *Cerastium fontanum* subsp. *scoticum*

This provides an extreme example of an endemic inland 'island' variant. It is known only on two small serpentine outcrops at about 860 m at the head of Glen Clova in Forfarshire. Other variation occurs in this species in the lowlands.

### *Oxytropis halleri* and *O. campestris*

Both species of *Oxytropis* have variants which show inland 'island' distributions. *O. halleri* var. *halleri* occurs in Fifeshire, Ross and Cromarty, Perthshire and Argyllshire and each colony tends to be slightly different from every other colony. Var. *grata* occurs at two localities in Sutherland. *O. campestris* var. *kintyrica* occurs only at one locality in Kintyre, var. *perthensis* grows at two localities in Perthshire and var. *scotica* at Glen Clova, Forfarshire.

### *Ranunculus bulbosus*

The common Bulbous Buttercup, *Ranunculus bulbosus*, in Great Britain has at least three variants – plants that grow on the chalk, on the sand and on the clays. The one growing on the sand is easily distinguished from the other two by having dense, spreading hairs on the stems and petioles, while the other two have rather sparse, ascending, semi-adpressed hairs. The plants of the chalk and clays are distinguished from one another by the different divisions of the leaf segments and the size of the flowers. Intermediates can be found and rarely even an intermediate population reproducing itself. For those who favour using statistics, P. D. S. witnessed an interesting incident. He took two of the Technicians from the Cambridge Herbarium to the meadows by the River Cam to measure the parts of the three common buttercups, *Ranunculus bulbosus*, *R. acris* and *R. repens*. When they got back to the Herbarium one of them picked up the account of these buttercups in 'Biological flora of the British Isles' and compared the measurements of *Ranunculus bulbosus* given there with hers. She was quite indignant to find that the measurements given there were completely outside hers. P. D. S. realised that the 'Biological flora' description was that of the plants of the sand while hers were those of the clays. Although the 'Biological flora' does consider variation, its authors often don't take it into consideration when writing the descriptions. The plants on the chalk and sands often come into flower in March, whereas the plant on the clays does not come into flower until well into April and sometimes as late as May. You have to be careful when considering the distribution of the three taxa, particularly the one on the sand, as sand is frequently used in making road and railway banks and even lawns, and seeds get taken with it. How long they will exist in the wrong type of habitat is not known. The plant of the sand is in the most natural habitats, particularly by the sea and on heaths, and

is probably native. The plants of the chalk and clays, however, may have come about as a result of grazing by Man's animals. Cows and horses grazed the clays and sheep the chalk. A Bassingbourn meadow was a sea of buttercups in the 1950s, when it was grazed by two cows. When the cows no longer grazed it for 20 years, although it was cut for hay, the buttercups almost disappeared. Then it became horse-grazed and the buttercups returned. In the 1950s there were over 50 buttercup meadows in the civil parish of Bassingbourn-cum-Kneesworth; now there are almost none. Up until the 1950s horses were regularly tethered on roadsides for grazing, and patches of buttercups would appear in such places.

*Ranunculus bulbosus* is a good example of how difficult it is to find the correct name for infraspecific variants. The lectotype of *Ranunculus bulbosus* L. was originally chosen by L. Benson in the Linnaean Herbarium, but he could not even have looked at it, as it does not fit his diagnosis and is not *R. bulbosus*. The new lectotype is the plant of the sand, which therefore becomes *R. bulbosus* var. *bulbosus*. In general many lectotypes have been chosen without any thought about infraspecific taxa at all. The names for the *R. bulbosus* of the chalk and clays have to be chosen from a mass of epithets used in Continental Europe, many of which do not refer to any of our plants. Var. *bulbifer* appears to be the plant of the chalk, var. *albanaevis* the plant of the clays.

### ***Senecio aquaticus*, *S. jacobaea* and *S. erucifolius***

A fascinating series of problems is brought about by the three species *Senecio aquaticus*, *S. erucifolius* and *S. jacobaea*, all of which are very variable and between which hybridisation is said to occur. *S. jacobaea* subsp. *jacobaea* var. *jacobaea* starts flowering early in June and continues through the summer in grassy places inland. It could have been introduced by Man. *S. jacobaea* subsp. *jacobaea* var. *condensatus* replaces var. *jacobaea* on coastal sands in much of Great Britain and Ireland, except the extreme north. Sometimes, when inland soil is brought to build up the coastal defences, it brings with it var. *jacobaea*. *S. jacobaea* subsp. *jacobaea* var. *condensatus* is replaced on coastal sand in Sutherland, Orkney and Shetland in Scotland and in Co. Kerry, Co. Wexford and the west coast in Ireland by the discoid *S. jacobaea* subsp. *dunensis*. When all the above taxa have mainly finished flowering *S. jacobaea* subsp. *jacobaea* var. *nemosus* comes into flower in wet places in August and September and is a large and handsome plant. When numbers of var. *nemosus* appeared at Wicken Fen National Nature Reserve in Cambridgeshire, its natural habitat, it was pulled up as it was thought to be an invasive weed from grassland nearby, but that grassland plant was var. *jacobaea*. *S. jacobaea* subsp. *jacobaea* var. *nemosus* is the plant most likely to hybridise with *S. aquaticus* subsp. *aquaticus* var. *aquaticus*, as it grows in the same habitat and flowers at the same time. Although it reproduces itself from seed we have wondered whether var. *nemosus* could be part of the hybrid *S. aquaticus* × *jacobaea*. However, it often occurs where *S. aquaticus* has never been recorded, it reproduces

itself from seed and hundreds of plants occur together, all exactly alike. The variant of *S. aquaticus* which grows with *S. jacobaea* subsp. *dunensis* is subsp. *ornatus*, but we have seen no intermediates between them. *S. aquaticus* subsp. *aquaticus* var. *aquaticus* (as in John Hill's (1761) illustration; there is no type specimen) is what is usually known as var. *pennatifidus* Gren. & Godr., which has often been considered to be part of the hybrid with *S. jacobaea*. What British botanists normally call *S. aquaticus* is var. *barbareifolius* Wimm. & Grab. *S. aquaticus* subsp. *erraticus* is known only from old records from Guernsey and southern England. All the variants of *S. jacobaea* may be native, but grazing animals have probably helped the spread of *S. jacobaea* subsp. *jacobaea* var. *jacobaea*.

The nominate variant of *S. erucifolius* is a slender plant with narrow leaves which are greyish- or whitish-hairy beneath and it grows mainly on chalk grassland. It is presumably native. The plant which most frequently grows with *S. jacobaea* subsp. *jacobaea* var. *jacobaea* is *S. erucifolius* var. *communis*, a large plant with leaves broadly ovate in outline. Although these two taxa often grow in large mixed communities we have found no hybrids, though they have been recorded. We once spent a whole day in a huge mixed colony at Histon in Cambridgeshire without finding a single plant thought to be a hybrid. On the other hand you could regard all the plants referred to var. *communis* as hybrids, as they are somewhat intermediate with *S. jacobaea*, but they reproduce themselves and there were no plants of *S. erucifolius* var. *erucifolius* present. *S. erucifolius* var. *latilobus* is a very distinct plant known from Great Britain only from a specimen collected in Southampton in 1836; it was probably introduced. One other variant occurs in Great Britain, *S. erucifolius* var. *viridulus*. On the Gog Magog Hills near Cambridge it seems to have been introduced with wildflower seed. The native plant there is var. *erucifolius*. It is also on roadsides, where the normal plant is var. *communis*. Arthur Chater, however, has var. *viridulus* on a boulder-clay slope near the sea in Cardiganshire, where it is probably native. As it also occurs in France it may be that the Welsh plants are part of its natural distribution.

## Variation and hybridisation

### ***Geum urbanum* and *G. rivale***

In eastern England *Geum urbanum* grows in grassland and along ditches in the open, while *G. rivale* grows in woodland; thus they are normally isolated from one another. If woodland is cut down *G. urbanum* moves in and hybridisation occurs until the woodland grows up again. These hybrids are fertile, but because the two parents are very distinct morphologically they have always been regarded as species. In addition there is an upland taxon, subsp. *subalpinum* (Neuman) Selander, in an area where *G. urbanum* does not grow. The hybrids between the species are fertile and back-cross, so that there are some plants nearer one parent and some nearer the other. This situation does not really differ from that of *Medicago sativa*. In central

Europe the hybrid between the two *Geum* species occupies a large area.

### *Medicago sativa*

*Medicago falcata*, with yellow flowers and a straight or curved legume, is probably native in East Anglia and occurs as an introduction elsewhere. *M. sativa* was formerly a common crop plant, which was introduced by Man from the Mediterranean region. It has mauve to violet flowers and a spiral legume. *M. × varia* is a variable hybrid between the two and is fertile and back-crosses. Stace (1997) has made them three subspecies of *M. sativa*, with which we are in agreement. *Medicago × varia* has been planted around field margins in south Cambridgeshire.

### *Anthyllis vulneraria*

The ultimate variation in a species is shown by James Cullen's account of *Anthyllis vulneraria* in *Flora Europaea*, from geographical to ecological to intermediate populations, to hybrids and to introduced taxa, with 24 subspecies listed. The intermediates are often given names because they seem to have produced uniform populations which reproduce themselves. Even then not all populations are described. Fleshy-leaved plants in coastal regions of central Portugal are obviously a coastal variant of subsp. *maura* (G. Beck) Lindb. Under subsp. *polyphylla* (subsp. *carpatica*) it is stated that intermediates occur between it and every other subspecies it comes in contact with; five are then given. As it was cultivated for fodder, it could cross boundaries with any other subspecies that it was introduced next to. *Anthyllis vulneraria* is recorded in Great Britain from the Quaternary cold stages (West, 2000).

Tim Rich (in *Watsonia* 23: 469–480) has argued for lumping *A. vulneraria* subsp. *corbieri* into the northern subsp. *vulneraria* because there are intermediates and it differs in only one character. Cullen says that, if it is to be lumped, it should be into the south-east European and Turkish subsp. *hispidissima* (Sagorski) Cullen, to which it is connected geographically by subsp. *vulnerarioides* (All.) Arcangeli from north-east Spain, the south-west Alps and the central Apennines. All three key out together in *Flora Europaea*. Interestingly, the common plants of the Welsh coast are subsp. *vulneraria* var. *langei*, which are an intermediate population between subsp. *vulneraria* and subsp. *iberica* (W. Becker) Jalas from France, Spain and Portugal.

We have constantly found this sort of example very difficult, when you get one answer when looking at British plants and another if you consider Europe and the rest of the plant's distribution. You can sometimes only look with bewilderment in Ascherson & Graebner's *Synopsis der mitteleuropäischen Flora* (1896–1938) and Rouy & Foucaud's *Flore de France* (1893–1913), which cover the two main areas from which plants entered Great Britain and Ireland after the last ice age!

### *Euphrasia*

The genus *Euphrasia* subsection *Ciliatae*, which includes nearly all our species, is distributed all around the northern

hemisphere. All its taxa are ecologically or geographically replacing, or both. There are two levels of chromosomes involved, diploid and tetraploid. Within each chromosome number all the taxa which grow within reach of each other can hybridise. There is at least one taxon, *E. vigursii*, that has evolved by hybridisation between taxa with different chromosome numbers and now acts as a distinct entity, reproducing itself from seed. Other such taxa seem to occur but have not been named. The normal action would be to call them subspecies or varieties of one or at the most two species, but this would create chaos in the nomenclature and present no easy way of naming hybrids. Left as they are, with nearly all taxa treated as species, their nomenclature remains intact and it is easy to present information on hybrids.

Sometimes these species occupy huge areas and all the plants are exactly alike, as in the case of *E. micrantha*. In other cases several species may be present, as on the north coast of Sutherland, with hybrids scattered between them. The larger-flowered species appear to be pollinated by bees and other insects, but the smaller-flowered ones are usually selfed. It must be this selfing that helps to keep the various taxa more or less intact, together with some geographical and ecological isolation. However, hybrids and hybrid swarms occur commonly, while sterile hybrids are comparatively rare. Populations frequently occur in which only one character falls outside those of a species and apparent hybrids occur independently of the parents. If you look at populations as a whole, however, they become interesting and meaningful. *Euphrasia* is not recorded from the Quaternary cold stages.

### *Epilobium*

The species in this genus vary greatly in morphology as well as frequently hybridising. This can best be seen when a large area of waste ground or a set-aside field is available to them for several years. Hybrids can often be recognised by their larger and more branched stature, unusually large or small flowers, more darkly coloured tips of the petals, partially or entirely abortive seeds and a longer flowering season. Variation in species involves stature, degree of branching, leaf size and hairiness, particularly the type of hairs. In set-aside fields in particular you could find patches of plants scattered over the land with every plant in each patch identical and each patch differing slightly from every other patch. This is presumably brought about by self-pollination, which, as in *Euphrasia*, helps to keep the species distinct. In his monograph C. Haussknecht (1884) describes these patches as formae. Introduced species from the southern hemisphere and North America are also hybridising with our native plants.

### Polygonaceae

There has been much variation in the number of genera recognised in Polygonaceae during the last 50 years. It seems there are two main alternatives, either to lump most of them in one big genus with subgenera or to split them as far as possible. Most accounts have taken an intermediate course. We have split as far as we can. There then seem

to be no hybrids between genera and most genera can be recognised at a glance.

### *Reynoutria*

*R. japonica* is an introduced species which is common in waste places, on tips and by roads, railways and rivers; it was first found wild in 1886. It spreads vegetatively. Almost all the plants in Great Britain and Ireland are female octoploids and almost all set seed as a result of crossing with other species.

In southern England *R. japonica* × *sachalinensis*, *R.* × *bohemica*, occurs in scattered localities. Most of these hybrid plants are hexaploid, with  $2n = 66$ . Some are  $2n = 44$  and may be *R. compacta* × *sachalinensis*.

The hybrid of *R. japonica* with Russian Vine is more difficult to deal with as we have accepted two species in that aggregate. *R. baldschuanica* has larger flowers and fruits, the plant becomes much suffused with red, it flowers earlier and it is a much more handsome plant than *R. aubertii*, which is practically free of red coloration, has smaller flowers and fruits and is a much more sombre plant. Fortunately both grow in Cambridge Botanic Garden, but not near one another. Both, however, grow near to *R. japonica*. Seeds were taken from a plant of *R. japonica* growing very close to *R. baldschuanica* and grown in a tray, and they came up like mustard and cress. Twelve were grown on in separate pots, which we arranged in order with one end very like *R. japonica* and the other more like *R. baldschuanica*. Several plants produced flowers but they soon withered and fell off. Seeds of a plant of *R. japonica* growing directly beneath *R. aubertii* were also grown. Fewer seedlings appeared from this batch of seeds and all were very near to *R. japonica* when grown on. None of them produced flowers. It is difficult to write a description of either of the hybrids which would distinguish them from the parents. Some of the plants growing in the neighbourhood of the parent *R. japonica* looked as though they might be hybrids.

### *Centaurea debeauxii*

Growing along the site of the old railway at Histon in Cambridgeshire on 28 June 2002 was a long line of large patches of this species. The individual plants in each patch were identical with one another in height, morphology and time of flowering, but each patch was different from every other patch. Some had finished flowering and were in fruit, some had shed their fruit, some had just come into flower, some were in full flower and some were going over, but every plant in each patch was in exactly the same condition. All would have run down in this flora to *C. debeauxii* subsp. *nemoralis*. The patches, some of which were very large, looked as though they might be the result of vegetative spread, but each plant pulled up showed no connection with the rest. If they were apomictic or self-pollinating the answer would have been simple, but the group is notorious for producing hybrid swarms. However, the plants in this group of taxa have not been seen to behave like this anywhere else. Was it connected with the time that each patch had flowered?

### Fabaceae: general comments

Although the flowers are very prominent in the family Fabaceae, hybrids appear to be rather scarce, perhaps owing to the structure of the corolla. Much artificial hybridisation and selection has been carried out on many genera for use in agriculture. *Lotus corniculatus* var. *sativus* (Common Bird's-foot Trefoil), *Medicago lupulina* var. *major* (Black Medick), *Medicago sativa* subsp. *sativa* (Lucerne or Alfalfa), *Onobrychis viciifolia* subsp. *viciifolia* (Sainfoin), *Trifolium campestre* var. *majus* (Hop Trefoil), *Trifolium hybridum* subsp. *hybridum* (Alsike Clover), *Trifolium incarnatum* subsp. *incarnatum* (Crimson Clover), *Trifolium pratense* var. *americanum* and var. *sativum* (Red Clover), *Trifolium repens* var. *grandiflorum* (White Clover) and *Vicia sativa* subsp. *sativa* (Common Vetch) have all been grown for hay or green manure or used as wildflower seed. Some remain here and there as a remnant of past crops and all now occur frequently in wildflower seed and are widely planted on roadsides, in nature reserves and around the margins of fields. These places are regularly mown with grass-cutters, which seem to take the seeds of the plants from one locality to another.

*Onobrychis* is an interesting case. The variant found in wildflower seed is *O. viciifolia* subsp. *decumbens*. There is a magnificent plate of it in Richard Mabey's *Flora Britannica* (1996, p. 220). The plant that used to be grown as a hay crop was subsp. *viciifolia*. Our native plant is subsp. *collina*, which is prostrate. Subsp. *viciifolia* is robust and erect. Subsp. *decumbens* is slender and ascending. All three grow true from seed. A rare bee is said to visit only subsp. *collina* and to ignore the other two.

## SELF-POLLINATION

### *Viola arvensis* and *V. tricolor*

P. D. S. first took an interest in variants of *Viola arvensis* in the early 1950s, before herbicides had almost eliminated them. He was intrigued by the fact that the plants in cereals, the plants in root crops and the plants in autumn stubble were different from one another, but within each habitat at any one time and place all the plants were the same. They reproduced themselves from seed and were probably all self-pollinated. He assumed that all the fields had a stock of mixed seed in the soil, but how did they know when it was their turn to grow, or did some that germinated die if it was the wrong crop? These plants are all given varietal names under *Viola arvensis*. They can no longer be properly studied, as most have been eliminated from crops by herbicides, at least in East Anglia. They still occur here and there, in waste ground and gardens, but not in the enormous quantity in which they occurred in the past.

More recently P. D. S. has taken an interest in the *Viola tricolor* group. In Cambridge Botanic Garden there was a large bed covered with plants of this group, which varied enormously in colour and shape of flower. We watched a mass of insects moving from one plant to another. We then took seed from 12 different-looking plants and grew

them in separate trays in the same soil in a glasshouse and visited them nearly every morning. They did not all develop at the same time, some being in bud while others were in fruit, but each plant in a tray eventually developed the same flower colour pattern and each tray was different from every other tray. It was, however, impossible to write a description which would distinguish all plants in a tray at any one time. Despite all the insects visiting them, it is probable that they were all self-pollinated.

Most plants intermediate in characters between the *V. arvensis* and *V. tricolor* groups were more or less fertile and reproduced themselves. They are probably best treated as varieties of whichever of the two species they are nearest to. True sterile hybrids appear to be rare.

### **Arctium**

In the 1950s Frank Perring and P. D. S. grew half an acre of *Arctium* in Cambridge Botanic Garden. We grew a whole series of plants which seemed to form a continuum between the large-headed *A. lappa* and the small-headed *A. minus*. All the plants were bagged and seemed to produce almost one hundred per cent good achenes. Each type of plant reproduced itself from seed, including what seemed to be intermediates between extremes. We went on to emasculate them, after which they produced no seed. This caused us to assume that they were self-pollinating but not apomictic. They could of course have been pseudogamous but we did not know how to prove or disprove that.

For this flora we have made all the recognisable taxa subspecies of *A. lappa*. *A. lappa* subsp. *minus* often grows on its own in south-west England, where it tends to be very small-headed, and it is absent from Scotland, northern England and northern Ireland. Subsp. *nemorosum* is the only taxon in much of northern Great Britain and northern Ireland. The rest of the area contains a mixture of subsp. *lappa* and subsp. *minus* and intermediates between them, which we call subsp. *pubens*. Subsp. *nemorosum* gets into the area of these subspecies and intermediates with them cannot be distinguished from the intermediates that we call subsp. *pubens*. The introduced *A. tomentosum* may also be confused with subsp. *pubens*.

### **Capsella, Cochlearia, Draba and Erophila**

The species normally accepted within these four genera of the Brassicaceae are probably all self-pollinating with occasional hybrids. Across Europe many species of *Draba* have restricted localities but are retained as species because they are in natural habitats. There are two schools of thought on *Cochlearia*. In one hybrids are prominent; in the other most are described as distinct taxa. In *Erophila* many species have been described but they are now more or less restricted to those plants with different chromosomes. Several hundred species have been described in *Capsella*, but they have all been lumped by us into one. Unless someone makes a thorough study of their distribution and ecology we will not know whether these *Capsella* species are meaningful. All four genera occurred in the Quaternary cold stages (West, 2000).

### **Fumaria**

Of all the genera of the plants of Great Britain and Ireland which are known to be self-pollinated, *Fumaria* is the most completely so. The arrangement of the four petals stops all but the occasional bee from getting to the reproductive parts by the legitimate route, although bees can still bite through the side of the flower. In the 1970s P. D. S. made a special effort to see all the species and infraspecific taxa in the field. In only one case did he find morphological intermediates and that was between *Fumaria officinalis* subsp. *officinalis* and subsp. *wirtgenii*. This was even more curious because they have different chromosome numbers and the intermediates seemed to reproduce themselves. They are best included within subsp. *officinalis*.

In 1985 at Bassingbourn P. D. S. found a five-acre field of onions which was so thick with plants of *Fumaria* that you could not see the onions. For at least 20 years before this field had grown cereals and only a few fumitriads occurred yearly, but somehow a huge amount of seed had accumulated in the soil. *F. officinalis* subsp. *officinalis*, *F. officinalis* subsp. *wirtgenii* var. *wirtgenii* and var. *minor*, *F. densiflora*, *F. vaillantii* var. *vaillantii* and *F. parviflora* var. *acuminata* were all present (P. D. Sell, *B.S.B.I. News* 41: 16–17). As the farmer was a friend, P. D. S. was able to search the whole field thoroughly, but he was unable to find any intermediates, even between the varieties in the same species. *Fumaria* is not recorded from the Quaternary cold stages (West, 2000).

### **Polygonaceae**

Much of our treatment of genera in this family is supported genetically in the paper by Galasso et al. (2009).

### ***Polygonum aviculare* aggregate**

The important characters to distinguish the species are habit (whether the stems are prostrate, ascending or erect, or prostrate for a short way and turned up at the ends), the shape of the leaves and the length of the internodes. The flowers and fruits are less constant, being very variable even on the same plant.

This aggregate has been variously divided into species and other taxa, but we believe it has never been divided enough, except perhaps by Alexis Jordan. Most of the seed seems to be moved about on the wheels of vehicles. Over a period of about 10 years we studied almost all of the taxa on an almost daily basis in the car park and around the glasshouses in Cambridge Botanic Garden. The construction vehicles brought in for building works brought a fresh wave of these plants. All the species remained constant with no intermediates. Most of the species have also been found at Bassingbourn and Histon. Arthur Chater has found almost all the same species in Cardiganshire. The aggregate formerly occurred widely in agricultural areas, especially in gateways, on tracks, around stackyards and where crops were poor. A large area of concrete, well out in the open fields of Bassingbourn, was used to pile up dung from the cattle yards. Every crack in the concrete and around the edges of the area was filled with plants of this aggregate,

presumably brought there by the tractors, which were constantly back and forth with loads of dung.

This group of plants is very important for seed-eating birds. J. P. Nunn of Royston in Hertfordshire, writing under the pseudonym of Rambler in the *Naturalist's Journal* of 1893, described thousands of House Sparrows feeding in his fields. Shooting a number of them and examining the contents of their crops, he was surprised to find that the main content was the seeds of *Polygonum aviculare* aggr. One of the reasons for the decline of the Grey Partridge has been a decline in a leaf-cutting beetle, *Gastrophysa polygona*, whose larvae were one of the main foods of their chicks. These beetles fed on the leaves of *Polygonum aviculare* aggr.

In 2001 there was heavy spring flooding in Bassingbourn and all the hollows in the fields were flooded. By the time they dried out it was too late for the farmers to spray with a herbicide. The area became covered with two species of the *Polygonum aviculare* aggregate, *P. chamaechyton* and *P. denudatum*. Both are more or less prostrate and have branches up to a metre long. Signs of the presence of the leaf-cutting beetles were on many of the plants. In the past there was much more flooding and more numerous waste areas providing an abundance of food for seed-eating birds. Herbicides have cleared many areas that are left. P. D. S. has been interested in birds since he was a small boy and has read an enormous amount of literature on the subject worldwide. Information is missing on the precise scientific naming of the food of many bird species, especially concerning food for their young. Many birds are driven out of fields by modern agriculture into village or town gardens, where they often resort to visiting bird tables. How do we know we are feeding them a suitable diet? Most *Homo sapiens* after all are not eating what is good for them. The R.S.P.B. does not seem to consider the exact food of birds when trying to conserve them.

### Chenopodiaceae

The limits of genera in this family have probably been reasonably well settled by the work of W. H. Blackwell (1977) and A. J. Scott (1978).

Over the last 40 years we have been collecting steadily to try to bring up to date these complex groups. *Chenopodium* has been particularly collected from game-cover crops, set-aside, building sites and road works. What is not understood is their breeding mechanisms. We have not found plants that we think are hybrids. Many taxa will reproduce themselves exactly, even taxa very close morphologically. Sterility is common, especially late in the year. Even when a number of plants are morphologically alike, some will bear seeds and some not. Much reliance has been placed by botanists on the character of the ripe seed, but, because many late-flowering plants do not produce seed, the descriptions and keys are here based mainly on vegetative characters, which work particularly well if one can compare taxa.

We have spent hundreds of hours studying the coastal species of the genera *Suaeda*, *Salicornia* and *Atriplex* in East Anglia and occasionally elsewhere. *Suaeda* and

*Salicornia* seem to behave in much the same way as *Chenopodium*, but in the former two genera the taxa are called varieties and in the latter they are called species. *Atriplex* is a mixture of varieties, species and supposed hybrids. The whole situation in the family is unsatisfactory, but we have been able to double the number of taxa in the family without having to describe any new ones; all have already been recognised somewhere else.

### Chenopodium

Before starting work on the huge collection of *Chenopodium* in the Cambridge Herbarium we borrowed the Ida Haywood collection from Edinburgh, which had been looked at by both P. Aellen and P. Uotila. A few of these taxa are not known from modern records, but they are likely to occur and have been included. The site around a new building in Cambridge Botanic Garden produced an amazing number of species, which were available as living material while the account was being written. Some arose from seeds in the recently disturbed soil; others were brought in from other sites on the wheels of construction vehicles. When the building works were complete, weed-suppressant matting was used between shrubs in newly created beds. *Chenopodium* ignored the matting, grew up through it and covered the whole area.

Two plants for which Cambridge Botanic Garden purchased seed are *C. quinoa* and *C. giganteum*. The first seed bought was the correct *C. quinoa*, which is also the plant occasionally grown as a crop. When seed was reordered a completely different plant arrived, called in this flora *C. quinoa* subsp. *milleanum*. It may be a different species or a subspecies of *C. hircinum*. It is the plant illustrated by S. Francis in *British field crops* (2005, p. 63) and may now be the plant grown as the crop Quinoa. The first seed purchased by the Botanic Garden as *C. giganteum* was the correct Asiatic species. The second seed they obtained under that name was *C. strictum*. A field of potatoes at Bassingbourn had a headland which had remained unploughed for at least two years. On 7 October 2006 it had at least a thousand plants of *C. strictum*, all about a metre high and looking exactly alike. In the same year at Bassingbourn a new path was created from Kneesworth to the Army barracks, and *C. strictum* appeared in the disturbed earth. The seeds could have been brought in by the construction vehicles. *C. strictum* has been lumped with *C. striatum* in British floras, but the two have a completely different appearance, especially when seen growing. *C. striatum* is common in Pheasant cover.

A friend, Bill Robinson of Bassingbourn, was determined to rid his garden of some weeds and dug a patch three times. When he started it was covered with *C. bernbergense*. Then followed *C. striatiforme*, then *C. pseudostriatum* and finally *C. probstii*. Each time *Capsella* was with them, but it was not thought to check if it was the same variant each time. Nor until *C. probstii* grew was it realised how interesting this was. However, the four species grew in other parts of the garden and were collected for herbarium specimens. *C. album* sensu stricto, *C. lanceolatum* and *C. ficifolium* also occur in that same garden. All

these species occur on the farm where Bill has worked all his life and he probably brought seeds home on his boots.

### *Suaeda maritima*

To understand *Suaeda maritima* it is important to visit a mature saltmarsh in autumn, when the vegetation has fully changed colour and all the varieties of *Suaeda* occupy their own niches in the marsh, forming an impressive mosaic of colour. In an immature marsh, just being formed, or one tampered with by Man, varieties are much more mixed, but there are no intermediates. The species is usually said to be wind-pollinated. This does not make sense unless they cannot cross-pollinate or are self-pollinated at an early stage before having the chance to cross-pollinate. The smallest variety, var. *aestuaria*, grows up to only 20 cm, is unbranched and bright red in autumn. It can occur in thousands in the upper and driest part of the saltmarsh, often with no other species growing with it. The tallest plant, var. *jacquini*, grows along the edge of the channels within the saltmarsh, can be over a metre high, is much branched and stays a dull green. Other variants which are variously branched occur in different parts of the marsh and are procumbent to erect and turn yellow, purple, pink or brown. *Suaeda* taxa are impossible to grow in cultivation. Herbarium specimens can be made, but detailed notes on colour need to be written and, if possible, coloured photographs taken. Size of seed has been regarded as a good character for identification, but every variant can have two seed sizes, often on the same plant.

### *Salicornia*

The *Salicornia* challenge is almost identical to that of *Suaeda maritima*, except that the taxa are usually regarded as species. They occur in different parts of the saltmarsh, are variously branched and change colour in the autumn. One big difference is that they have two different chromosome numbers. They also lose their colour when preserved as herbarium specimens or pickled, which makes field notes and colour photographs all the more important for identification. It is probable that not enough taxa have been described to date, with more research required on western coasts.

### *Atriplex*

*Atriplex* growing on the coast behaves differently from the preceding genera. It is composed of fairly clear-cut species, numerous varieties and variable supposed hybrids, all of which can grow intermixed. Despite this, they all appear to reproduce themselves, including the variable hybrids, presumably by self-pollination. Inland the situation is very similar to that of *Chenopodium*, seeds being taken from one locality to another on the wheels of vehicles. No serious study has been made along motorway verges where salt accumulates after winter de-icing to see if any coastal taxa grow there.

## TREES AND SHRUBS

The thorough study of trees and shrubs requires frequent visits to the same plants at all seasons. Fortunately, many

of our species are growing in Cambridge Botanic Garden and most of them are mature. At Bassingbourn there are eight 'new woods', which contain a large number of the taxa now widely introduced. Enclosure hedgerows are common in Cambridgeshire and have been examined in detail. It doesn't matter what landscape you are looking at in Great Britain and Ireland, you must bear in mind that the trees and shrubs you are looking at may not be our native plants. Man has always liked planting trees and shrubs; he has used them to enclose his animals, but has not always sourced them locally, especially in recent years. Either it is now too expensive or perhaps we are too lazy to grow our own, so plug plants grown on a huge scale are pouring in from Continental Europe. We cannot do better than quote *verbatim* from Oliver Rackham's book *Woodlands* (2006, p. 335):

People have planted trees in orchards and gardens probably since Neolithic times, and since Roman times have imported fruit trees from Europe. Planting *areas* of trees for timber or underwood was very rare before the seventeenth century. In the twentieth century, tree-planting took off on a far larger scale. The Forestry Commission established, or encouraged others to establish, timber plantations, first on heath, moorland and poor agricultural land, and then in the third quarter of the century on the sites of existing woods. Then from 1973 ('Plant a Tree in '73') the conservation movement took up tree-planting on an increasing scale, mainly in non-woodland situations. Between them these people have probably planted more trees in Britain, outside gardens and orchards, than in the whole of history before 1900. Most of the Commission's trees were exotics such as Sitka spruce and Corsican pine. Most of the conservationists' were thought to be native.

### Maples

In the last few years we realised that a great many maples were being planted in the countryside and that they were very variable. We collected a large number of specimens with flowers, fruits and leaves from the same tree. Those we considered to be native Field Maples had small leaves, hairy fruits and the wings of the fruit sloping down. This variant turned out to be the type of *Acer campestre* and is therefore subsp. *campestre* var. *campestre*. Other trees, which have the same hairy fruits but larger leaves and more spreading wings to the fruit, are var. *lobatum* with obtuse leaf lobes and var. *oxytomum* with pointed ones. They are probably not native. One of the most commonly planted trees has glabrous fruits and larger leaves. It is subsp. *leiocarpum* from central and east Europe. This left one tree with very large leaves up to 13 cm, which is probably *A. miyabei* from Japan. All the introduced taxa come into flower about three weeks before our native plant and are in young fruit before the flowers of our native plants open. There is another difference. The native trees that P. D. S. had known since he was a boy, although covered with fruit, never seemed to produce new trees. On the other hand the introduced trees have produced many young trees and these young trees are producing flowers and fruit while they are little more than bushes. This may account for Oliver Rackham saying that *Acer campestre* reproduced poorly up to 1970 but had done better

since. Most of these introduced maples have been planted in the last 40 years on Council holdings of land, private fields, 'new woods', housing estates and amenity areas and along new roads. Some, however, have been planted in hedgerows a long way from any house or road. I was with my friend Bill Robinson one day in as remote a part as you could find between the villages of Bassingbourn and Wendy, and there was a magnificent tree of *A. campestre* subsp. *leiocarpum*. Bill was able to tell me he had planted it there 40 years ago. It was given by the County Council to the farmer who owned the land, who gave it to Bill to plant. With it he planted another fine tree of *Alnus incana*. In Bassingbourn alone, subsp. *leiocarpum* is in all the 'new woods', implanted in old hedgerows by Spring Lane and along Ashwell Street, around the village college playing fields, by Knutsford Road and in large numbers by the Royston by-pass, where there are many seedlings and young trees.

### Sycamores

Having finished with the maples it occurred to us that the sycamores might be as variable. We discovered there were five different species.

Two have rounded buds with green and brown scales and their twigs form a close network at the ends of branches. They have a very rough bark and a cylindrical, pendulous inflorescence. One, *Acer pseudoplatanus*, has little hair on the undersurface of the leaves, except in the axils of the veins, and the leaves are large with pointed lobes. The other, *A. villosum*, is often densely felted on the undersurface of the leaf and the leaves are smaller with more rounded lobes. Old, very large trees of both these species are common and have long been introduced. *A. villosum* is a native of the Mediterranean region and *A. pseudoplatanus* is a native of the Balkans and perhaps central Europe. If the Romans were the first to introduce sycamore, it could well have been *A. villosum*.

The remaining three species have all brown, pointed buds and the twigs at the ends of the branches are longer and more open and do not form a network. Their inflorescences are more or less erect and ovoid, their bark is smooth and they have large leaves. *A. vanvolxemii* is easily distinguished by its very large leaves up to 25 cm, with almost no hairs beneath. *A. velutinum* looks just like *A. pseudoplatanus* at a glance, but it has the undersurface of the leaves felted like *A. villosum*. Its different arrangement of twigs cannot be seen when the tree is covered with leaves. *A. trautvetteri* has more divided leaves than any of the other species, but it could still be passed as *A. pseudoplatanus* at a glance. These three trees are planted in large gardens, parks and estates, in amenity areas and along roads.

If you have all the characters of a sycamore it is not hard to place it as one of these five species, but there are difficulties. All the species grow in Cambridge Botanic Garden, where we have studied them for several years. In some years no flowers or fruits are produced and sometimes they change sex. The amount of hairiness of the backs of the leaves varies from year to year. There are

three trees of *A. trautvetteri* in the Botanic Garden and, although not one of them is referable to another species, all are slightly different in leaf shape. Hybrids between these trees have not been recorded, but among the large number of living trees that we have examined some have been named with considerable doubt and with the feeling that they are tending to verge towards one of the other species.

The only species which P. D. S. is sure produces a large number of seedlings is *A. pseudoplatanus*. In the area in which he was living, the various roads off Hills Road, Cambridge, sycamore seedlings are the commonest weeds in the gardens. They show an immense variation of leaf shape and lobing, but the trees from which they could have come all seem to be *A. pseudoplatanus*.

### Larix

The species of *Larix* stretch all around the northern hemisphere, gradually replacing one another with intermediates in the connecting areas. *L. decidua* was the first larch to be introduced into Great Britain and Ireland for forestry. Later came the plant of Japanese mountains, *L. kaempferi*, which hybridised with *L. decidua* and the hybrid became the tree of forestry. Despite the intermediates which occur in the genus *Larix*, they are still regarded as species rather than subspecies.

Sometimes zoology and botany are similar. The Lesser Black-backed Gull (*Larus fuscus*) and Herring Gull (*Larus argentatus*) also replace one another around the northern hemisphere. Some call them species, some subspecies. The Carrion Crow/Hooded Crow complex is very similar to *Geum urbanum* and *G. rivale*, both having a large hybrid area in central Europe. Both have lesser variants, *G. rivale* in mountains, Hooded Crow on islands.

### Pinus contorta

In the north of Scotland many thousands of acres were planted with the American Lodgepole Pine. The trees were *Pinus contorta* subsp. *contorta*, which were short and stubby and quite useless for forestry. Presumably the trees which should have been planted were *P. contorta* subsp. *latifolia*, which are fine forestry trees and which the American Indians used as the main post for their lodges. Unfortunately the name Lodgepole Pine is used to cover the whole species with three subspecies. Getting the wrong subspecies can be an expensive mistake!

### Betula

When we started studies on *Betula*, which we had been collecting for some time, we thought our main challenge was the hybrid complex of *B. pendula* and *B. pubescens*, with a few introduced taxa. As well as the general collection in the Herbarium we had the large, carefully selected collection of E. S. Marshall for comparison. We were shocked when we started looking at material from plantings in new woods and along streets, and even more shocked when we received a parcel of *Betula* collected by Arthur Chater in Cardiganshire. Michael Crawley in *The flora of Berkshire* (2005) lists a large number of species (79), planted in the Silwood arboretum, and wonders why he has seen no



seedlings. Although there are trees apparently planted in some very odd places one rarely does see seedlings. On the other hand the native *B. pendula* and *B. pubescens* are known to take over whole hillsides.

Perhaps our most important finding is that *B. celtiberica* is almost certainly native in Wales and that it hybridises with both *B. pendula* and *B. pubescens*. A widely planted tree is the North American *B. populifolia*. When the European *B. pendula* was planted in North America it hybridised with *B. populifolia* (Catling & Spicer, 1988). Now we have these hybrids in Great Britain, but they may not have occurred in the wild. Hybrids or intermediates could have been taken from nurseries and planted together with the species *B. populifolia* that has been here for a long time. J. F. M. Dovaston evidently had it growing in his grounds at Westfelton, Shropshire, as early as the 1840s, when William Leighton (1841, p. 477) named it *B. alba* var. *salax*. We have a Leighton specimen in CGE. *B. populifolia* is widespread in new woods and along streets and country roads and is even implanted in old hedgerows in Cambridgeshire. Arthur Chater has it also in Cardiganshire. Any large-leaved *B. pendula* with more than 30 small and large teeth on one side of the leaf should be studied carefully.

A whole range of other species from all over the northern hemisphere, from Asia as well as North America, may be planted anywhere. Arthur Chater has found *B. kamtschatica* (*B. japonica* auct.) in what he thought was a native birch wood. We do not know whether the long series of species across Asia has intermediate populations which reproduce themselves, or whether such intermediates are hybrids created in nurseries, but they do exist.

### **Corylus**

As a boy at Bassingbourn in Cambridgeshire during the Second World War, when sweets were scarce, P. D. S. used to look for hazel nuts in the village hedgerows. There were three kinds – that with the nut clearly showing at the base of the involucre, which the locals called the Cob; that with the involucre extending just beyond the slightly longer nut, which was called the Filbert; and that with the involucre twice as long as the nut, which was called the nut with the long husk. When we looked at them for this flora we called them *Corylus avellana* forma *avellana*, *C. avellana* forma *schizochlamys* and *C. balcana*. In recent years the Woodland Trust had added the Kent Cob, *C. avellana* forma *grandis*, in new woods.

When Christopher Taylor and Susan Oosthausen started work on the landscape history of the area and asked me about the trees and shrubs which grew there, everything fell into place. Lord Tiptoft, who lived in Castle Manor over 500 years ago, had taken many of his ideas from Italy and probably obtained nuts from there also. *Corylus balcana*, which is possibly native in the Balkans and northern Italy, had lined one side of the old drive to his manor. In the 1940s they were very large shrubs, some four or five metres across, that had probably been regularly coppiced. The area was levelled in the 1950s, but some of the shrubs still occurred in the area. One interesting point remains.

P. D. S. was to find some *Corylus balcana* by the side of a natural stream in Shedbury Lane at Bassingbourn. This mystery was solved when the daughter of the adjacent house said that her father had obtained them from the drive to Castle Manor. *C. avellana* forma *avellana*, our native nut, in Bassingbourn grows almost entirely by the natural watercourses. A purplish-leaved form of *C. balcana* is widely grown in gardens. All this shows that understanding the ecology and distribution of plants may be better achieved by studying the history of an area rather than dots on a map! To add to this complexity there is a gradual transition between *C. avellana* forma *avellana* in western Europe to *C. pontica* in southern Russia, with all the plants, including intermediates, breeding true. To this has been added much artificial hybridisation and selection. The plants appear to be naturally self-pollinated.

### **Swida (Cornus auct.)**

*Swida australis*, from the Black Sea and Caspian Sea area, is the first look-alike plant we recognised at Histon Wood in Cambridgeshire, and it is one of the easiest to distinguish. It is a more handsome plant than our native *S. sanguinea* and is easily recognised by the adpressed, medifixed hairs on the undersurface of the leaf, while *S. sanguinea* has them ascending and basifixed. Intermediates occur, but we do not know whether they reproduce themselves or are hybrids. Another species, *S. koenigii*, has the same hairs as *S. sanguinea*, but has much larger leaves. In Bassingbourn, both species have been implanted in a hedge by Spring Lane and the hedge by the track to Well Head; in both cases the native *S. sanguinea* already grew there. The two introductions probably occur throughout Great Britain along motorways, in new woods, in parks and amenity areas and wherever a local conservation body thinks they are helping to conserve the flora.

### **Viburnum**

These shrubs are as common as *Swida* but much more difficult to identify. To start with there are two different native varieties of *V. lantana*. Var. *lantana* is in south-east England and presumably came across the North Sea. Var. *glabratum* is in south-west England and Wales, east to the Isle of Wight; it extends into France and presumably came across the English Channel. It would be interesting to compare the DNA of these two plants. Var. *glabratum* flowers at least three weeks earlier than var. *lantana* and continues to do so when planted in eastern England. *V. lantana* is crossed with *V. rhytidophyllum* in nurseries and both the hybrid and the species are planted in the Cambridgeshire countryside, as is *V. lantana* var. *rugosum*, which may be part of this hybrid complex. *V. veitchii* from central China also occurs. The new Ford Wood at Bassingbourn has a very variable set of this group of plants as well as much *Swida australis*.

*V. sargentii* from China and *V. trilobum* from North America are very near to *V. opulus*. There is also a very distinct plant that we cannot find a name for. All occur in new woods and are implanted in hedgerows in Bassingbourn. Arthur Chater says that *V. trilobum* is frequent by road

verges in Cardiganshire and *V. sargentii* occasional. There are two shrubs of *V. trilobum* at Bassingbourn, which could have been bird-sown. They are about half a mile from the nearest known planted *V. trilobum*. It is not a place where anyone would plant them, but curiously in both places dumped rubbish has been seen.

### *Crataegus*

Hawthorns are probably the main constituents of our hedgerows and woods and many have been there since the last ice age. Whether *Crataegus monogyna* and *C. laevigata* with hybrids have always been there together is not known; there is some suggestion that originally *C. monogyna* was the plant of the lighter soils and *C. laevigata* of the heavier soils. The mix that we get today with many hybrids may be due to an increase in *C. monogyna* or to management techniques in the past. We are in agreement with most of the papers published on this hybrid complex from woods.

Our native *C. monogyna* appears to be subsp. *nordica*. There are two varieties: var. *nordica* with berries 6–9 mm, shining orange-red in colour, and petals tending to overlap, and var. *splendens* Druce with berries 8–11 mm, dull purplish-red in colour, and petals not overlapping. Var. *nordica* is usually the common plant of woods. Var. *splendens* is a hedgerow plant and may not be native. The two different berry sizes were discussed by B. & D. Snow in *Birds and berries* (1988). We can confirm that Fieldfares take the big-berried fruits and leave the small-berried ones. All the woodland *C. laevigata* is subsp. *laevigata*.

Hedgerows have been created since the sixteenth century and in some places much earlier, but probably the largest number were planted between 1750 and 1850. Oliver Rackham writes in *The illustrated history of the countryside* (1994, p. 81): “The Great Enclosures, though not a universal transformation, were a time of more hedging than ever before or since. The hedges planted between 1750 and 1850 – probably about 200,000 miles – were at least equal to all those planted in the previous 500 years. ... A thousand million or more hedging plants were necessary, which founded the fortunes of several Midland nursery firms.” The only disagreement we have with this is that we think that as many trees and shrubs have been planted in the last 30 or 40 years, but by roads, on farmland and in ‘new woods’ and forestry plantations. These hedgerow hawthorns may be identical for miles of hedge, or there may be as many as six different kinds in a short length of hedge.

To study these different kinds of hawthorns you need first to mark the bush you wish to investigate, so that flowers and fruits can be collected from the same bush. To guess which bush you collected flowers from earlier is no good. Bushes look very different when in fruit from when in flower, as we have found from bitter experience. To see the difference in the hawthorns you need to look at the colour of the underside of the leaf, division of lobes, length of petiole, size and hairiness of leaf, stipules, size of flower, overlapping of petals and size and colour of fruit. If part of the hedge comes into flower before the rest it

will almost certainly be a different taxon. Most plants will have one style and belong to the *C. monogyna* aggregate. In addition there are *C. rhipidophylla*, *C. heterophylla* and *C. subheterophylla*, all of which have one style. *C. laevigata* subsp. *laevigata*, with two or three styles, rarely occurs in hedgerows. *C. laevigata* subsp. *palmstruchii* occasionally occurs in hedgerows and is presumably an introduction. *C. laevigata* and *C. monogyna* × *laevigata* also rarely occur in hedgerows, but they can usually be recognised from *C. monogyna* aggr. by at least some flowers having more than one style. Red-flowered plants of many of the taxa are planted along streets and around amenity areas and sometimes in quite remote places. Intermediates between *C. monogyna* and *C. rhipidophylla* (*C. subsphaerica*) and between *C. laevigata* and *C. rhipidophylla* (*C. macrocarpa*) also occur. Recently we have dealt with the black- or blackish-red-berried species. *C. pentagyna* and *C. rubrinervis*, with two to five styles, have been in one hedgerow for at least 30 years. *C. longipes*, with small berries, long pedicels and a characteristic habit, is widely planted in Cambridgeshire. The berries are not eaten by birds and are often still on the bush when it flowers in the following April or even May. It is easier to interpret the hedgerows if you know a locality well. At Bassingbourn the hedgerows in the old fen area contain many native shrubs. On the hills towards Royston, however, originally a heath, where all the hedge plants had to be brought in from elsewhere, there are miles of hedge with each bush exactly like every other bush. Even in a hedgerow which has grown up along a natural watercourse one finds trees and shrubs implanted. Some trees around amenity areas, along streets, in parks and estates and occasionally elsewhere are North American and may be apomictic. Most of the European taxa may be pseudogamous, as each species tends to include triploids and tetraploids as well as diploids.

## APOMICTS AND VEGETATIVE GROWTH

There are three main kinds of apomicts. *Hieracium* has either no pollen or a little sterile pollen, and it is **apogamous**. It cannot therefore cross with any sexual species in the same genus. *Sorbus* has sexual and apomictic species, both of which have good pollen, and is **pseudogamous**. If the pollen from an apomictic plant falls on the stigma of a sexual species the offspring are usually apomictic. A pseudogamous *Sorbus* needs pollen to stimulate the reproductive process, but the male pollen does not have any representation in the offspring, which are exactly like the mother plant (cp. Rich et al., 2010, pp. 3–5). We do not know whether self-pollination will function, but solitary trees in a garden do not seem to produce good seed. Many species in the genus *Ulmus* do not produce good seeds, or if they do germinate the seedlings rarely survive. These species spread by **vegetative growth** and they are very difficult to kill. In woods they sometimes cover large areas. They also spread in hedgerows but may often have been

planted there originally. We have treated them as species and some are very widespread.

### *Hieracium*

The species of this genus consist almost entirely of triploid, apogamous apomicts. Pollen is absent or more or less sterile. If the conditions are right, seeds from one plant can soon become thousands of plants. Only one sexual diploid is known in Great Britain and Ireland, *H. umbellatum*, and even in that case there are some plants that cannot be distinguished morphologically which are apomictic triploids. Most of the species of *Hieracium* that are native are in the west and north and probably arrived in Great Britain and Ireland from across the English Channel, or those in the north from across the North Sea. Most of the plants of the east were probably introduced much later; there is a suggestion that many of them then spread along roads and railway lines. Section *Cerinthoidea* almost certainly came from the south-west and sections *Alpina* and *Alpestris* from across the North Sea. Most of the species spread by Man are in sections *Vulgata* and *Hieracium*.

We grew over 300 clones of *Hieracium* in Cambridge Botanic Garden and discovered that the offspring by seed of any one clone were identical in any one year and at a set time of the year. Some species were identical whatever time of the year they germinated; others were so different between spring and autumn flowering that they looked like different species. We grew the seeds of the autumn-flowering plants and found that they flowered the next autumn, but in the following year we found that they flowered in the spring. We then found out that C. H. Schultz 'Bipontinus' (1805–1867) had done the same experiment well over 100 years before. The section *Alpina* species grown in garden soil tend to grow much larger and have more than one capitulum. David Tennant overcame this by using soil from their native habitat. All the descriptions in this flora are made from plants collected in the field at first flowering. Mary McCallum Webster found hawkweeds in full flower on the north coast of Sutherland at the end of May. P. D. S. could not be away from his full term duties and Cyril West had to be persuaded that the trip was worthwhile. Like most English botanists he thought Scotland not worth a visit until late June or July. To his surprise he saw many species looking the best he had ever seen them. Much, however, depends on the weather and the year. P. D. S. has seen many of the species in the Clova Mountains flowering in mid-June. Raven's Scar in Yorkshire in the 1950s was yellow with hawkweeds, with many thousands of plants. By the 1980s there was not a hawkweed to be seen; you had to look for them in the grykes.

It is wise to study more than a single species of *Hieracium*. Even in apomictic species not every plant is exactly alike, and you will always find aberrant ones. You get a better idea of how the species fit together if you take a group of plants like *H. caledonicum*, *H. veterascens*, *H. subrubicundum*, *H. rubicundiforme*, *H. boswellii* and *H. leyantum*. You will find plants which are not quite a particular species but not distinct enough to describe as a new species. It is not a good idea to take achenes of such a plant,

grow them on and then describe them as a new species. It is better to leave it in the species it is near to until you can find more like it in the field and then decide whether it is worth describing as new. On the other hand it is not good taxonomy to forget about such plants. P. D. S. was lectured on this very subject by Charles Raven, over breakfast, over 50 years ago and has never forgotten it! In evolution the exception may be more important than the rule.

There are some interesting distributions and ecologies of *Hieracium* species. *H. hypochaeroides* is one such case. A very handsome plant with blackish-purple-marbled leaves, it has therefore been collected wherever it has been seen. It is known only from limestone near Tutshill in Gloucestershire, Dyffryn Crawnon in Breconshire, Craigiaw Eglwyseg near Llangollen in Denbighshire, frequently in mid and north-west Yorkshire and the English Lakes, the Burren in Co. Clare and Murlock Bay in Co. Antrim. *Hieracium optimum* is even more difficult to understand. It is very distinct and known from only two remote stations in Argyll. When P. D. S. looked for it his first impression was that the whole cliff was granite and that it was unlikely to be there. However, it had been collected by two famous botanists, E. S. Marshall and J. E. Raven. So P. D. S. started at the far end of the cliff and worked his way along. About half way along there was a large bulge of rock. It was an outcrop of Dalradian schist and was covered with *H. optimum*. The plant grew nowhere else on the whole length of cliff. The reason that the other two botanists had found it was that the easiest way up the cliff was by a small stream, which led straight to the plant. At Dyffryn Crawnon in Breconshire the cliff is part limestone and part sandstone, and *H. hypochaeroides* is restricted to the limestone, *H. sanguineum* to the sandstone. Many botanists have asked P. D. S. why he does not have aggregate species. His answer is that any sort of lumping implies intermediates and misrepresents the ecology. You can have three taxa which retain their characters in cultivation, one of which is intermediate between the other two, and they are not growing together in the wild. Even to put the species into sections tends to make it difficult to draw a line.

Most of the native *Hieracia* occur on cliffs where there are few niches for them to spread. The species of sections *Vulgata* and *Hieracium*, however, which are widespread in the lowlands, often occur on open ground where, because they are apogamous, they can spread rapidly. If it is a building site or road-widening site they can be brought in on construction vehicles. In some places such as the Royston by-pass in Hertfordshire 11 closely allied species occur. Where a large number of species occur on open ground there is a greater chance of aberrant plants surviving and forming new species. Nils Hylander was the first to recognise this when he described a large number of species from Swedish grassland sown with introduced seed. P. D. S. took him to see the Royston plants on one of his visits to Cambridge. Quite a large number of species have very restricted distributions in Great Britain and Ireland; however, many of these also occur in Continental Europe. Others form a large colony in their only locality,

but numbers can fall very quickly if the area becomes heavily sheep-grazed, overgrown or much disturbed.

### *Pilosella*

This is perhaps the most difficult of all genera to study. There are diploid ( $2n = 18$ ) and tetraploid ( $2n = 36$ ) sexual species forming nine and 18 pairs of chromosomes respectively in the pollen mother cell at meiosis. Triploid sterile hybrids ( $2n = 27$ ) occur and survive and spread by stolons. Other polyploids occur, up to  $2n = 63$ , and are mostly apomictic with good pollen. These chromosome types sometimes grow mixed. If pollen from the apomictic plants gets on to the diploid and tetraploid plants' stigmas, the offspring will be apomictic. It is possible that individual flowers in a capitulum can be pollinated from both sexual and apomictic plants, so that seeds from the same capitulum may produce both sexual and apomictic offspring. K. H. Zahn, in his world monograph in Engler's *Das Pflanzenreich* **82(IV.280)**: 1147–1705 (1923), had over 600 subspecies of *P. officinarum* (*Hieracium pilosella*) alone. Such a classification shows no meaningful distribution or ecology. Cyril West and P. D. S. produced a much broader concept of taxa in *Flora Europaea*, and that concept is followed in this flora. When preparing these accounts, we had available 500 voucher specimens of G. & B. Turessons' chromosome counts in the genus, but we could not relate taxa to chromosome numbers. We concluded that, whereas *Hieracium* had reached a state of apomictic completeness, *Pilosella* was still in a state of flux. It was *Pilosella*, not *Hieracium*, which puzzled the great Gregor Mendel.

### *Sorbus*

Great Britain and Ireland have three main sexual diploid ( $2n = 34$ ) species, *S. aucuparia*, *S. aria* and *S. torminalis*. There are at least four apomictic tetraploids ( $2n = 68$ ) near to *S. aria*, which have good pollen and have crossed with the three diploid sexual species to produce a series of apomictic triploids ( $2n = 51$ ). The triploids produce good fruit, but they need pollen stimulation to start the process. It is not known whether their own pollen stimulates or whether they require pollen from another tree. It took P. D. S. nearly 40 years to see most of the species in the field, but Cambridge Botanic Garden had an almost complete set in cultivation, so that much information was readily available for the account in this flora. The recently published account by Rich et al. (2010) contains an enormous amount of information on the genus in the British Isles and clearly describes pseudogamy in the introduction. It has been suggested by Robertson et al. (1991) that the diploids should be in separate genera, in which case the hybrids would have hybrid generic and specific names.

A number of species have been introduced and planted along streets, in waste areas, amenity areas, hedgerows and estates, around sports grounds and even in the corners of fields and along field margins. Five very similar species, *S. austriaca*, *S. hazslinszkyana*, *S. croatica*, *S. intermedia* and *S. mougeotii*, have probably all been recorded as *S. intermedia*, which is regarded as the most common,

but it is not. As well as being native, *S. aucuparia* is widely planted. Var. *hortorum*, which is much planted, is illustrated in *Bot. Mag.* **168**: tab. 123 (1951) as *S. poscharskyana*, which it is not. A tree similar to *S. aucuparia* which comes into flower when *S. aucuparia* is in young fruit is its American counterpart *S. americana*, which is sometimes planted as a street tree or around amenity areas. Two varieties of red-fruited *S. aria*, var. *magnifica*, with leaves  $8\text{--}12 \times 11\text{--}16$  cm and fruits  $10\text{--}12 \times 10\text{--}12$  mm, and var. *majestica*, with leaves  $9\text{--}18 \times 5\text{--}11$  cm and fruits  $11\text{--}18 \times 13\text{--}16$  mm, are widely planted. It is not known whether these varieties of the sexual *S. aria* are sexual or apomictic. Two trees very similar in appearance to these varieties of *S. aria* but with brown fruits are *S. vestita* and *S. thibetica*.

### *Ulmus*

Elms are very tedious to study as the tree has to be visited three if not four times in a year. It has to be carefully marked to ensure that you have the same tree each time. The best time to mark the tree is mid-summer, when, if there is more than one tree, you can select the best and collect mature leaves on short shoots. Flowers are collected early in the year, sometimes as early as January, and fruits a couple of months later. Early in the year is the best time to make notes on bark, angle of branching, shape of crown and buds. During a summer visit sucker leaves should be collected. It is a mistake to think that all large elms have been killed by the ascomycete fungi *Ophiostoma ulmi* (Buisman) Melin & Nannf. (*Ceratocystis ulmi* (Buisman) C. Moreau) and *O. novo-ulmi* Brasier. Dutch Elm Disease is spread by two bark beetles, *Scolytus scolytus* (Fabricius) and *Scolytus multistriatus* (Marsham), but here and there you can still find a mature tree. Also, even when a tree has died, suckers spring up again and often reach a height at which they flower and fruit, by which time the leaves are mature enough for the tree to be named. Some species are so characteristic that they can be recognised along miles of hedgerows.

Most species spread by suckers and their seeds seem only occasionally to germinate. Even when you see a few seedlings they rarely seem to develop into trees. The only elms which reproduce from seed are *Ulmus glabra* and *U. scabra* and a few of their close allies.

There are two opinions about the distribution of elms, one that they have been introduced by Man and the other that they are remnants of native trees. Ronald Melville of Kew thought that the large number of different kinds was brought about by hybridisation and had a complicated formula for working out their origins. Richard Richens believed that they were all brought in by Man from various parts of Europe and were planted in the area in which he settled. Although he always talked about them as separate taxa, he never gave them names. We are quite sure that the only way to study them is to give each a binomial. Some species occur in ancient woods or along natural streams and are almost certainly native. Others occur along hedgerows and in copses, where they may have been introduced by Man. Many more species probably need to be named. Specimens laid out along a long bench with the smallest

leaves at one end and the largest at the other show a gradual series in size but not in total characters. No populations have been seen that include intermediates, which would suggest hybridisation.

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- Many other books and journals were consulted, mainly in the University of Cambridge Department of Plant Sciences, including the N. D. Simpson collection of local floras, and in the Cory Library at the Botanic Garden. Where these references were considered to be important for particular plants, we have cited them under the family or genus concerned.
- The University herbaria at Cambridge, on which the flora is mainly based, are ideal for the study of the British flora for the following reasons:
1. The large British collection contains specimens from most of the main collectors of British plants from 1800 onwards, including sets of published exsiccatae and specimens sent through the Botanical Exchange Clubs. Many of the critical species have been named by experts.
  2. The British collection contains some 50,000 specimens collected by us in the last 50 years. The specimens are accompanied by detailed field notes and photographs and are often of critical species or infraspecific taxa. Often a gathering may consist of more than one sheet, particularly of trees, which may have been visited three or four times.
  3. There is a good collection of Continental European plants with which to compare the British plants.
  4. The world collection contains over 50,000 sheets of John Lindley's herbarium made when he was Secretary of the Royal Horticultural Society, when plants were coming into the country from all parts of the world, and the C. M. Leman collection, named by George Bentham and put together at the same time. These collections are very important as regards the alien species when considered in conjunction with the Botanic Garden, the Herbarium and recent gatherings of alien specimens.
  5. The Botanic Garden herbarium contains a large collection of cultivated plants.
- Thus, the libraries, herbaria, our own field notes and plants grown in the Botanic Garden have enabled us to do most of the work in Cambridge. Over many years books and specimens elsewhere have been consulted.

*Conspectus of families*

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**2. SELAGINELLACEAE**

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**3. ISOETACEAE**

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## Order 6. PAPAVERALES

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