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.

Infraspecific variation is recorded by the recognition of subspecies, varieties, formae and cultivars. These taxa dif-fer 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. Α 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 condi-tions alter, one ecotype may be better able to survive than another. Variation thus becomes very important in conser-vation. 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 bot-anists 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 bv 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: *Semitæ 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 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 accidently, 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. Rudolphi Aponogetonaeae 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 Berdcht. & 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 Grav 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 Pvrolaceae *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) Menvanthaceae 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 Griseliniaceae 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, Honckenva peploides, Lathvrus 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. mariti*mum* 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 involucral bracts. We thus had to give our plant a new name, subsp. nigri*ceps*, 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. *albonaevis* 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. nemorosus comes into flower in wet places in August and September and is a large and handsome plant. When numbers of var. nemorosus 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. nemorosus is the plant most likely to hybridise with S. aquaticus subsp. aquaticus var. aquati*cus*, as it grows in the same habitat and flowers at the same time. Although it reproduces itself from seed we have wondered whether var. nemorosus 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 hav 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 fumitories 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 polygoni*, 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 gamecover 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. jacquinii, 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 vellow, 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 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 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 *Corvlus 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. rhvtidophvllum 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 \times 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 Alpestria 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 vellow 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. leyanum*. 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, Craigiau 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. tormina*lis.* 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 $8-12 \times 11-16$ cm and fruits $10-12 \times 10-12$ mm, and var. *majestica*, with leaves $9-18 \times 5-11$ cm and fruits $11-18 \times 13-16$ 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.