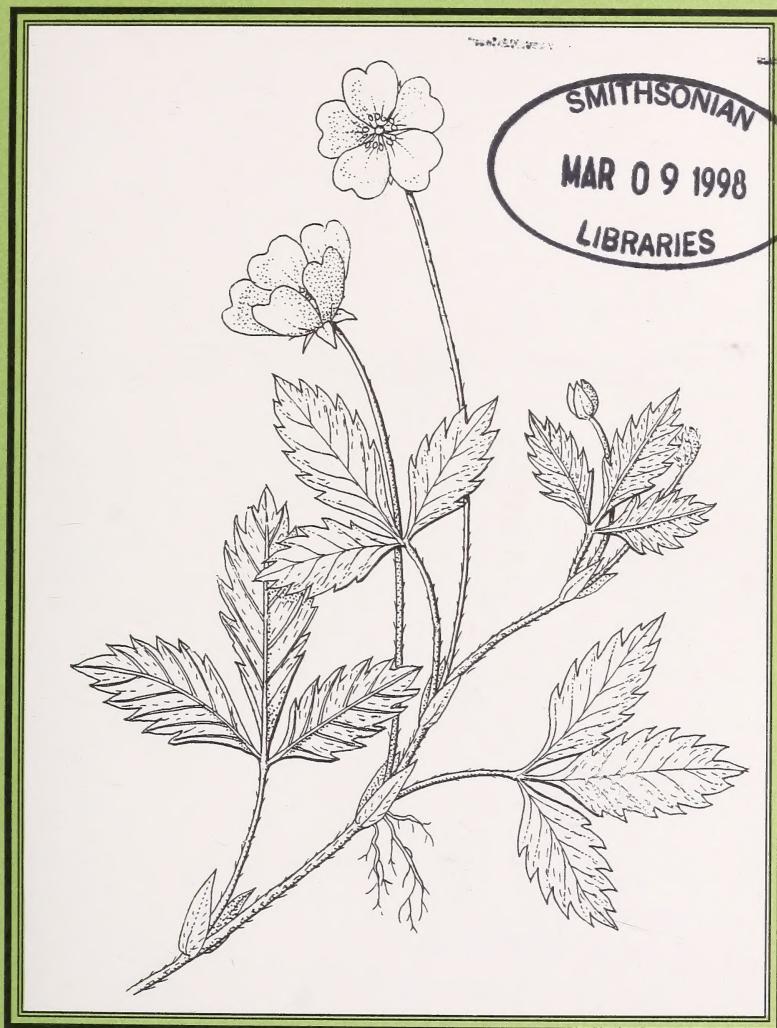


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Rosemary Wise.

The independent gametophytic stage of *Trichomanes speciosum* Willd. (Hymenophyllaceae), the Killarney Fern and its distribution in the British Isles

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ABSTRACT

Uniquely amongst European ferns *Trichomanes speciosum* Willd., the Killarney Fern, has perennial, gemmiferous gametophytes which may grow and persist in the absence of the sporophyte generation. The presence of widespread independent colonies of the gametophyte generation and their habitats is briefly described and their distribution in the British Isles documented. The conservation implications of this unique situation are discussed.

KEYWORDS: gametophyte, sporophyte, pteridophyte, Atlantic cryptogamic community, ecology, conservation biology.

INTRODUCTION

HISTORICAL

Trichomanes speciosum Willd., the Killarney Fern or Bristle Fern has been described as “one of the rarest and most celebrated species in the British flora” (Ratcliffe *et al.* 1993). The species’ great rarity, beauty and image of tropical incongruity have acted to generate a potent mythology, only paralleled by that of some orchids. It is one of a large genus of filmy-ferns showing their greatest diversity in tropical montane rain forests. *Trichomanes speciosum* was originally described from plants collected in the Canary Islands and is restricted now to those and other islands of the Macaronesian archipelago and a few relict sites in Europe. In Britain considerable and understandable secrecy has surrounded the location of this fern, following the wholesale depredation of localities to adorn the drawing rooms of the Victorian upper classes (Allen 1969).

Trichomanes speciosum has a long history of records, a resumé of which is given below. The first ever collection of *T. speciosum* in the British Isles was that by Dr Richard Richardson in 1724 (Ray 1724), by a spring head on Bell Bank, Bingley, Yorkshire, voucher material of which can be seen in the Sloane Herbarium at BM – (H.S. 145, f. 9; H.S. 302, f. 66). Within 50 years its original site had been destroyed and *T. speciosum* was thought to have died out but was refound in the early 1780s (Bolton 1785; Teesdale 1800) and again brought into cultivation. Unfortunately this was probably responsible for the plant’s demise, as from about 1785 *T. speciosum* was not recorded as being seen again and was, once again, considered extinct. The botanical exploration of Ireland in the first years of the 19th century, however, revealed this species to be more widespread and achieving abundance at some sites in the extreme south-west, most notably around the Killarney area of Co. Kerry (v.c. H1–2). This fact is commemorated in its current vernacular name, although to many Victorian botanists it was the “Irish Fern”. Its potential for specialised culture, already developed for plants demanding similar high humidity brought in from New Zealand and elsewhere, was quickly seen, and plants were sold through professional outlets in Britain, and by rural entrepreneurs in Ireland.

As the nineteenth century advanced, the advent of the Wardian case enabled the elite of London to have Killarney ferns in their drawing rooms. Almost from its discovery, *Trichomanes speciosum* was under threat in Britain and Ireland.

Collection and subtle but crucial disturbance to microhabitats through visitation still arguably pose the greatest threats to this species' survival (Wigginton, in press). The necessary caution surrounding the plant's localities has, however, made it difficult to establish losses and gains, as the history of the species within its few sites, e.g. in terms of extent, performance and fertility is, where known, unpublished, or so vaguely identified that its worth is regrettably limited. Even past and present distribution in broader terms is difficult to establish accurately, posing further complications for those seeking to understand the environmental factors acting to limit the species' distribution and explaining its dispersal. This is of increased importance given recent discoveries which have revealed a disparity in the distributional extent and amount of the two phases of the life cycle.

THE GAMETOPHYtic STAGE OF THE LIFE CYCLE

Trichomanes speciosum is unique amongst European ferns in that its gametophytic generation, the sexual or gamete-bearing phase of the life cycle, is not only perennial but produces specialized structures for its vegetative propagation (gemmae), allowing the potential development of extensive stands of this usually overlooked generation. Originally described and illustrated from cultivated material over a century ago (Goebel 1888), the distinctive filamentous gametophyte of this species appears to have been completely overlooked in the field prior to the finds reviewed here.

The fact that fern gametophytes can establish and reproduce themselves independently of the sporophyte has been known for some time, and the, now classic, examples from Eastern U.S.A. of gametophytes of Hymenophyllaceae, and other ferns in the families Grammitidaceae and Vittariaceae that have in some instances spread several hundreds of kilometres beyond the ranges of the sporophyte or persist in their complete absence, have been well-documented (Farrar 1967; Farrar *et al.* 1983). Farrar (1985) has shown that populations of the gametophyte of N. American *Trichomanes boschianum* Sturm, the United States endemic "equivalent" of *T. speciosum*, exist up to 40 km distance from the nearest sporophytes. In addition, a further more widespread and numerous *Trichomanes* taxon, found in the eastern United States and initially thought to be the gametophyte of *T. petersii* A. Gray, has been shown (by comparison of enzymes) to be a new species, *T. intricatum* Farrar, currently known only as its gametophyte generation (Farrar 1992). Preliminary investigation elsewhere suggested independent *Trichomanes* gametophyte populations may be a widespread phenomenon in temperate areas (Rumsey & Sheffield 1996). During a sabbatical visit to the U.K. late in 1989, Farrar discovered gametophytes he recognized to be those of a *Trichomanes* species at two sites in the English Lake District (Rumsey *et al.* 1990). These were compared isozymically with a range of *Trichomanes* species and gave banding patterns identical to, and characteristic of, *T. speciosum* (Rumsey *et al.* 1993; Rumsey 1994). As records increased of this inconspicuous, albeit mostly non-sexual gametophytic stage of a taxon that was rare, and listed as a critically endangered and protected species, its presence posed profound implications for those drafting and enforcing conservation legislation.

The gametophyte has been located within the known sporophytic distribution from Tenerife, Canary Islands; Madeira; the Azores; Algeciras, S. Spain; Asturias, N. Spain (Viane, pers. comm., 1992); Douro Valley, Portugal; Brittany (Jermy & Viane in Ripley 1990; Prelli, pers. comm., 1993); and Apuane Alpes, N. Italy; all sites recorded by A.C.J. and/or F.J.R. unless otherwise stated. However, research has revealed that gametophyte populations extend into continental Europe far beyond the known sporophytic range of the species and closely parallel the known past distribution of *Hymenophyllum tunbrigense* (L.) Sm (cf. Richards & Evans 1972). The gametophyte generation is now known from several areas in central Europe. It is most widespread and relatively abundant in the Wasgau, the southern Pfälzerwald of Germany (C. Stark, pers. comm., 1996) and the adjacent N. Vosges of France (Jérôme *et al.* 1994). It is also reported from the sandstone massif shared by Luxembourg and Germany in the southern Eifel (Rasbach *et al.* 1993, 1995; Bujnoch & Kottke 1994; Reichling & Thorn 1997), and is known to be present as small scattered populations in the Elbsandsteingebirge, straddling eastern Germany and the Czech Republic (Vogel *et al.* 1993), and the Zittauer Gebirge (Jessen, pers. comm., 1997) – its easternmost known locality. It would appear to be thinly scattered in the intervening areas, with records from the northern Black Forest, east of Heidelberg in the Neckar valley, from the Spessart in the Main valley north-west of Würzburg, from

the Wupper valley near Solingen and from the northern Eifel near Monschau (Bennert *et al.* 1994; Kirsch & Bennert 1996).

Over the past six years, an extensive survey by F.J.R. and A.C.J. and local recording by others in the British Isles has shown the gametophyte to be widespread, far beyond the present range of the sporophyte. Many suitable areas remain to be investigated but a summary of the position to early 1997 is presented here with the hope that it will stimulate additional recording.

The wider gametophyte distribution reported here poses many questions, not least of which are: how is the disjunction between the generations perpetuated? (an issue addressed by Rumsey *et al.* 1992; and further discussed in Rumsey & Sheffield (1996)) and, when was the current range achieved and by what means? (the topic of an on-going research project at the Natural History Museum, London).

TRICHOMANES SPECIOSUM IN THE BRITISH ISLES

Crucial to the understanding of the distribution of this species is the elucidation of the ecological differences between the two phases of the life-cycle, an aspect which may play a major role in perpetuating independence of either generation (Rumsey & Sheffield 1996). Much can be inferred from a comparison of the overall distribution of the two generations, the broad extent of which are given in Fig. 1.

The distribution of the sporophyte within Britain has been outlined by Ratcliffe *et al.* (in Wiggin, in press). They report the past presence of 24 separate colonies, in 17 localities, occurring in a total of eleven widely scattered vice-counties. Only 16 colonies in ten localities are known to be extant. In Ireland only ten sites (in six vice-counties), out of the 43 once recorded were reported to be extant by Curtis & McGough (1988). The species is, however, clearly under-recorded, especially in the hill country of Counties Kerry and Cork where Ratcliffe *et al.* (1993) report the presence of 26 of the 30 Irish colonies known to them over the past three decades. The importance of these rare sporophyte colonies as potential sources, by means of spore dispersal, of the wider gametophyte distribution, remains to be resolved and is currently under investigation. The history of the discovery of the sporophyte in various areas of the British Isles is not elaborated further here but is discussed in part by Roberts (1979) and Church (1990).

Since the discovery of the distinctive filamentous gametophyte generation and with growing awareness of its habitat preferences, wider surveys have revealed it to be remarkably widespread, if often extremely localized. We must assume that a combination of a morphology not readily assignable to any one cryptogamic group, coupled with growth in a poorly investigated and often inaccessible environment has resulted in its being overlooked for so long. Given this oversight a brief description of the habitats in which the gametophyte may be found is given below.

MORPHOLOGY OF THE GAMETOPHYTE

The morphology of the gametophyte has been described and illustrated (Rumsey *et al.* 1990; 1993) but is described again here with the hope that a wider audience will come to recognize it.

Trichomanes speciosum gametophytes consist of branched filaments, the individual cells of which are c. 40–55 µm wide and 150–300 µm long, that grow interwoven into tufts or mats with an open, felt-like appearance (Fig. 2). These are of a clear bright glowing green when well hydrated, taking on a somewhat bluish-black metallic cast as the filaments crumple on drying. The gametophyte colonies can vary in overall size, from occurring as scattered filaments among bryophytes, to more or less pure patches covering several square metres to a depth of about one centimetre. The majority of sites, however, support small tufts ranging from thumbnail-sized patches to up to c. 10 cm². The combination of colour, shape and restriction to particular niches within habitats makes field recognition of the gametophyte relatively easy in the majority of cases. The filaments maintain a rigidity, giving a distinctive wool-like resilience, when lightly touched, and by which an experienced worker can identify the colony or mat. They are distinguished from bryophyte protonemata by their larger diameter filaments, the cells of which are without oblique end-walls, and from filamentous green and yellow-green algae by their pale brownish rhizoids and the presence of characteristically-shaped gemmifers, gemmae and gametangia (sex organs), when present. The

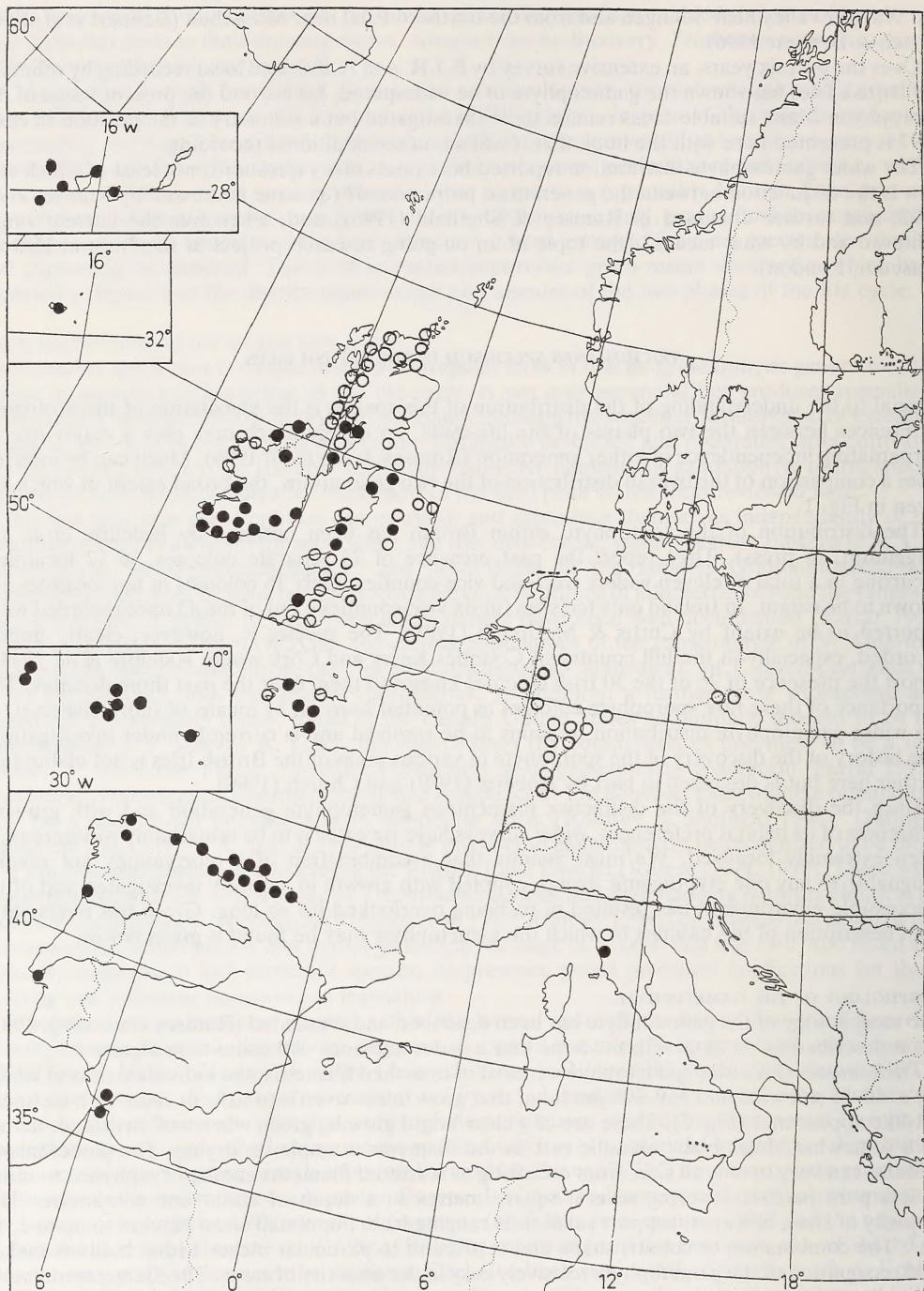


FIGURE 1. World distribution of *Trichomanes speciosum* Willd.: ● both generations; ○ gametophyte only. All known records mapped on the *Atlas florae Europaea* base map (Jalas & Suominen 1972) amended to include the Canary Islands and Madeira. Dots indicate the presence of the species at any time within 50 km squares of the UTM grid map.

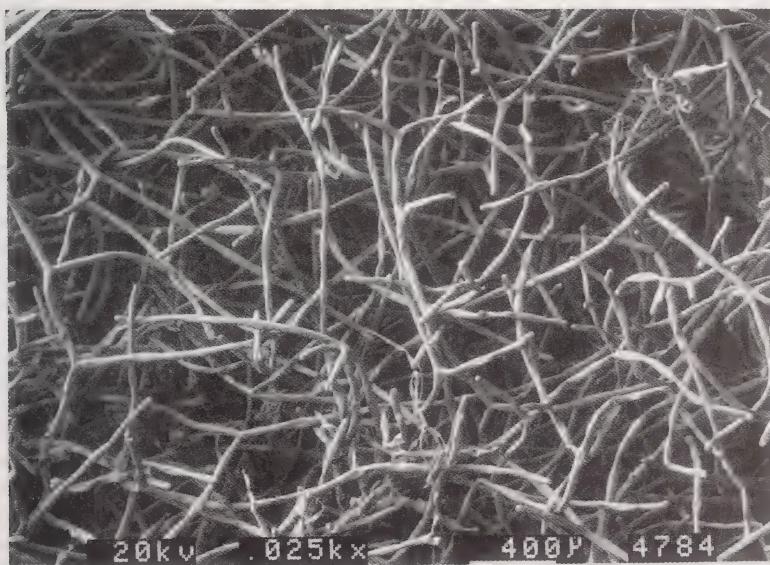


FIGURE 2. Upper. Typical gametophyte habitat under millstone grit boulders at Bell Bank, Yorkshire, 1989. Don Farrar, who first drew attention to the gametophyte in Europe, is holding the torch. (Photograph, A. C. Jermy.) Lower. Scanning electron micrograph of a gametophyte "mat" ($\times 30$). (Micrograph, Natural History Museum.)

most superficially similar algae grow in wet, well illuminated positions, in which *T. speciosum* gametophytes have never been found.

Discrimination from other ferns is straightforward as no other native European fern genera produce filamentous gametophytes. As the gametophytes of all taxa within *Trichomanes* Section *Lacosteopsis* Prantl (= *Vandenboschia* Copeland) are so morphologically similar as to be effectively indistinguishable, certainly in the field, the possibility that one or more "independent gametophyte" taxa (i.e. lacking a known sporophyte) may occur in Europe, as in N. America, must be considered. This is particularly likely to be the case given that the diploid progenitors of the tetraploid *T. speciosum* are unknown. Available molecular evidence would suggest, however, that all material examined to date is of one, admittedly variable, taxon. Confusion following the spread of exotic species is unlikely but cannot entirely be ruled out (e.g. Rumsey *et al.* 1993).

The gametangia are very similar in structure to those of other *Trichomanes* sensu lato (Stokey 1948; Yoroi 1972) and are obviously of a Filicalean form (see Fig. 3). The archegonia are produced on a specialised structure, the archegoniophore which is borne on a short broader filament and is produced just above the substrate, deep in the gametophyte tufts. They are apparently rarely produced, being found in less than 10% of gametophytes collected from the field, and later development in material grown in the laboratory has made no significant difference to this figure. In contrast, the antheridia, which may be found on the same filament, are more readily produced; c. 25% of gametophytes had at least one when collected and following cultivation nearly 75% had produced them (Rumsey & Sheffield 1996). Antheridial dehiscence with functional (i.e. motile) antherozoids has, however, rarely been observed. Thus the potential for gametophyte colonies to generate sporophytes cannot be assumed.

DISTRIBUTION OF THE GAMETOPHYTE IN THE BRITISH ISLES

All gametophyte records have been lodged with the Biological Records Centre, Monks Wood. While details of the gametophyte's distribution remain to be established, especially in Scotland and Ireland, the provisional map (Fig. 4) probably represents an accurate picture of its distribution and general regional abundance. Up to February 1997, gametophytes have been recorded in 38 British vice-counties: 1, 2, 3, 4, 14, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 52, 57, 62, 63, 64, 67, 69, 70, 88, 95, 98, 100, 101, 102, 103, 104, 105, 107, 108 and 109 and in 120 10-km grid squares (hectads). In three of these, both those in v.c. 1 (West Cornwall), and one in v.c. 2 (E. Cornwall) it is present in grottoes and artificial features in gardens, and in two cases closely associated with sporophytes which are assumed to have been deliberately introduced. It is currently recorded from 13 Irish vice-counties: H1, 2, 3, 6, 8, 10, 13, 16, 20, 26, 27, 33, 35 and 22 10-km squares but has not been searched for as exhaustively as in some other places.

Some local botanists have been encouraged by finding both topography and geology in their area suitable for the gametophyte and have quickly come to recognise both its habitat and morphology. We believe that as more become acquainted with the gametophyte, much of the appropriate country where sandstone and the coarser volcanic rocks predominate will be shown to house this stage of the Killarney Fern. It should be noted, however, that although widespread, the gametophytic generation is by no means common. More than 75% of the grid squares mapped contain only single populations, in many cases restricted to a single microtopographical feature. Furthermore, we must stress (and see below) that the species in its entirety is protected under laws in the European Union, the U.K. and the Republic of Ireland. After many years of observation of the sporophyte generation Ratcliffe *et al.* (1993) concluded its distribution "... is puzzling in that it is absent from a great many apparently suitable habitats within its climatic range". The problem is that too little is currently known of the environmental constraints on either generation's growth and survival. The apparently anomalous distribution of this species, as with many other rare "Atlantic" cryptogams which show great individual longevity but very little or no current dispersive ability, can be arguably best explained as the product of rare climatic and stochastic events. Given no, or very limited, ability to recolonize once lost, the occurrence of these species implies a local continuity of site/habitat suitability, where an absence merely suggests that conditions have become unsuitable, if only once in the last few hundred years. It is thus not surprising that attempts to match this species' distribution to climatic factors, often expressed as means, have met with only limited success.

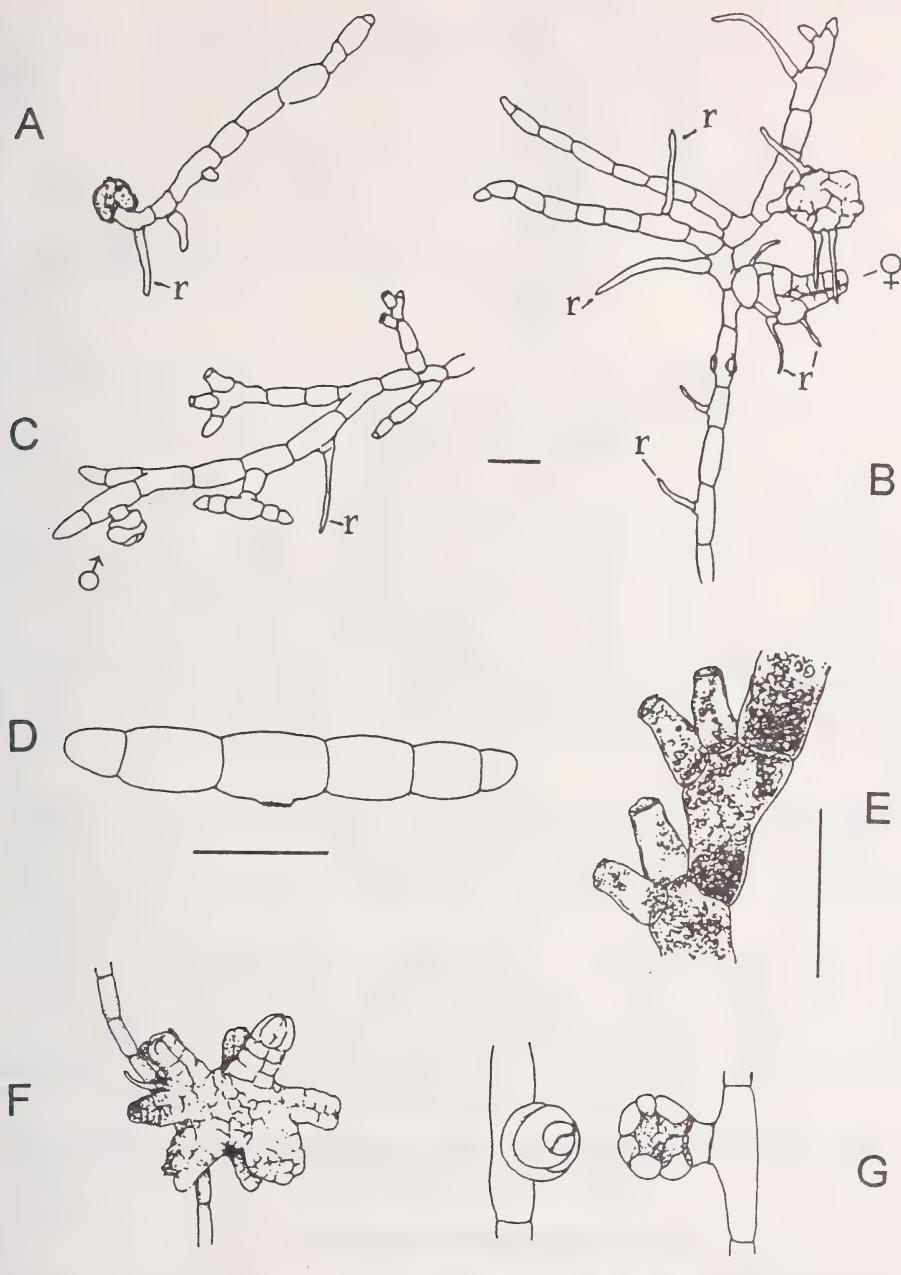


FIGURE 3. *Trichomanes speciosum* gametophytes. A. Germinating spore (r = rhizoid); B. Gametophyte with archegoniophores (♀); C. Gametophyte with antheridium (♂) and gemma; D. Gemma; E. Gemmifers; F. Archegoniophore with archegonia; G. Antheridia. Scale bar = 100 μm .

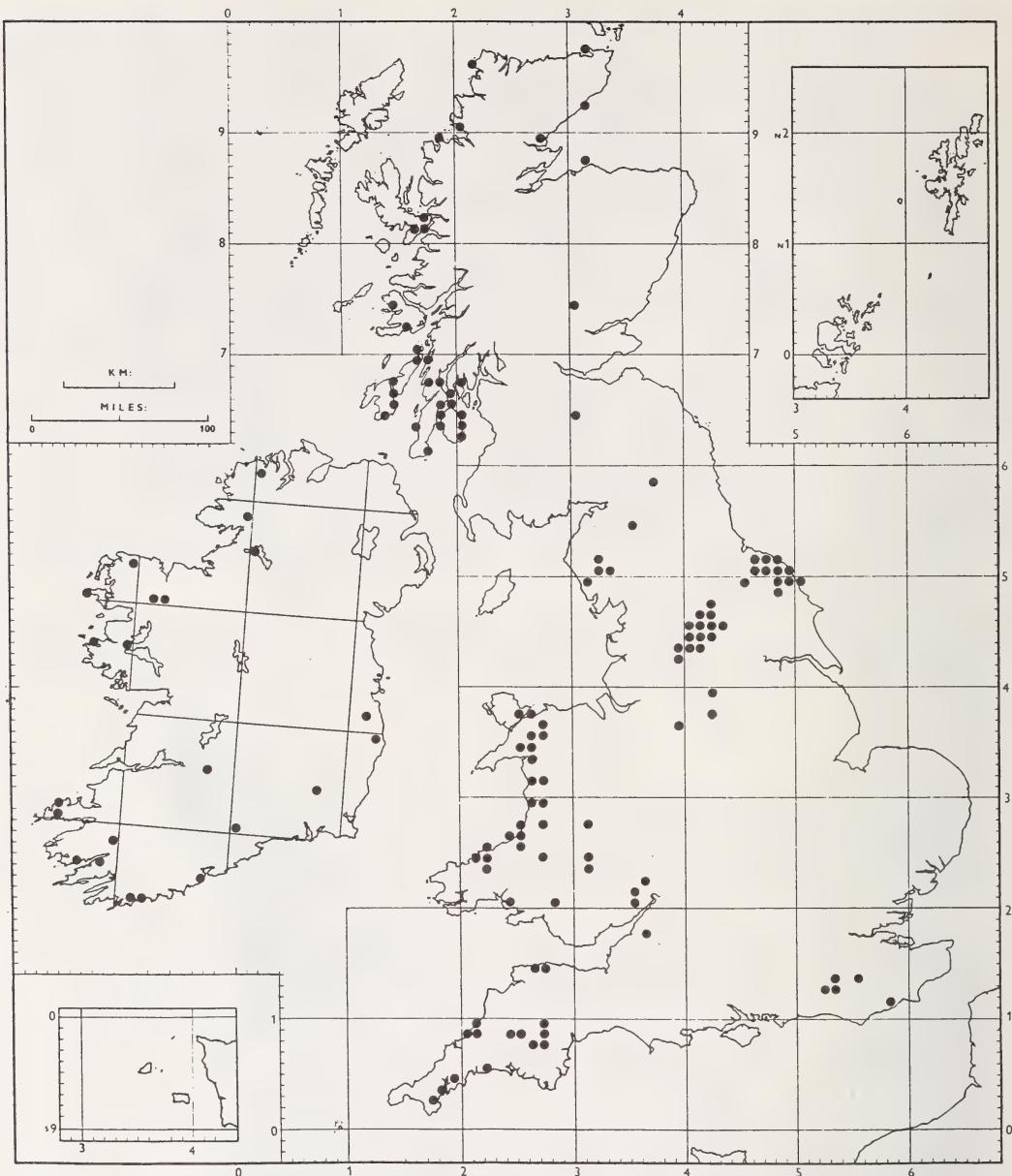


FIGURE 4. Distribution of the *Trichomanes speciosum* Willd. gametophyte generation in the British Isles (1989–1997).

GAMETOPHYTE SITE RECORDS

First records only for each tetrad are listed below. Vice-county names follow Dandy (1969) for those in Britain, and in Ireland they are as adopted by Scannell & Synnott (1987). In order to protect the location of extant sporophyte sites in Ireland we have cited in many cases a hectad reference only and an appropriate broad locality. The figure in square brackets after the hectad reference is the

number of tetrads in which the gametophyte has been recorded when that is more than one; the recorder and date that follows is the first finding in that hectad. The altitude range at which the gametophyte is found in Ireland is similar to that in Britain, being from near sea-level to 300 m on Brandon Mountain but have not been cited in many cases for the above reason. The following abbreviations are used: ADH = A. D. Headley; AH = A. D. Hale; AOC = A. O. Chater; AP = A. M. Paul; ARC = A. R. Church; BM = B. Meatyard; CJ = A. C. Jermy; CP = C. D. Preston; CR = C. J. Raine; DB = D. Batty; DCB = D. C. Bryce; DF = D. R. Farrar; DH = D. M. Henderson; DJ = D. Jones; DP = D. A. Pearman; DR = D. A. Ratcliffe; EC = E. G. Cutter; ES = E. Sheffield; FR = F. J. Rumsey; GS = G. A. Swan; HB = H. H. Birks; IM = I. K. Morgan; JB = H. J. Birks; JH = J. S. Holmes; JM = J. Mitchell; JPW = J. P. Woodman; JV = J. C. Vogel; JW = J. Walls; LF = L. Farrell; LG = L. R. Gander; MD = C. M. Dowlen; MR = M. H. Rickard; NK = N. Kingston; NS = N. F. Stewart; PT = P. Thompson; RC = R. J. Cooke; RF = R. FitzGerald; RM = R. J. Murphy; RN = R. H. Northridge; RS = R. J. Stewart; RW = R. M. Walls; SC = S. P. Chambers; SD = S. R. Davey; S&JG = S. & J. B. Grasse; SM = S. J. Munyard; SR = S. M. Rumsey; TR = T. C. G. Rich; WC = W. Condry.

THE RECORDS

V.c. 1 W. Cornwall

SW/77.27. Glendurgan, 50 m alt., FR, SR & ES, Apr. 1991; SW/80.39. Tregye Wood (private garden), nr Truro, 55 m alt., FR, SR & ES, Apr. 1991; SW/99.46. In old fern grotto, Heligan Gardens, 3 km NW of Mevagissey, 70 m alt., CJ, Sept. 1990.

V.c. 2 E. Cornwall

SX/07.88. St Nectan's Glen, nr Tintagel, 80 m alt., FR, Sept. 1990; SX/07.89. Rocky Valley, nr Tintangel, 20–50 m alt., CJ, Sept. 1990; SX/08.88. St Nectan's Kieve, nr Tintagel, 120 m alt., CJ, Sept. 1990; SX/12.89 & 12.90. Lesnewth stream, 125–165 m alt., FR, SR & ES, Apr. 1991; SX/25.52. In cliff by promenade, West Looe, <3 m alt., NS & RS, June 1994.

V.c. 3 S. Devon

SX/48.80. Blacknor Park, W. side of River Burn, c. 200 m alt., NS, Aug. 1995; SX/50.83. Lydford Gorge, by the White Lady Waterfall, 120 m alt., NS & RS, Oct. 1996; SX/50.84. Lydford Gorge, 150 m alt., FR, Sept. 1990; SX/61.77. Wistman's Wood NNR, 420 m alt., RC, 1995; SX/70.90. Whitewater, W of Great Tree Hotel, c. 170 m alt., NS, Oct. 1996; SX/76.79 & 76.80. Becka falls, nr Manaton, 160 m alt., FR, SR & ES, Apr. 1991.

V.c. 4 N. Devon

SS/66.49. By small waterfall on coast path, nr Hollow Brook, 150 m alt., RC, Mar. 1997; SS/67.48. Woody Bay, 130 m alt., FR, SR & ES, Apr. 1991; SS/70.49. Mother Meldrum's Cave, Valley of Rocks, 200 m alt., FR, SR & ES, Apr. 1991; SS/73.48. Myrtleberry Cleave/Lyn Cleave, Lynmouth, 50 m alt., FR, SR & ES, Apr. 1991; SS/74.48. Watersmeet, 120 m alt., FR, SR & ES, Apr. 1991.

V.c. 14 East Sussex

TQ/29.28. Nr Spicer's Farm, SW of Balcombe, 76 m alt., RC, SD & TR, Mar. 1995; TQ/31.29. Balcombe Mill, crevice above waterfall, c. 50 m alt., RC, SD & TR, Mar. 1995; TQ/33.31. Wakehurst Place, Ardingly, 75 m alt., CJ & MD, Aug. 1993; TQ/35.32. Philpots, West Hoathly, 135 m alt., FR, Mar. 1997; TQ/55.36. Eridge Rocks, Eridge Green S.S.S.I., 76 m alt., RC, Feb. 1997; TQ/83.10. Ecclesbourne Glen, nr Hastings, 70 m alt., SM, Feb. 1993; TQ/85.11. Fairlight Glen, c. 7 km E Hastings, 76 m alt., CJ, JV, MG & RC, Nov. 1992.

V.c. 34 W. Gloucs.

ST/62.76. R. Frome valley, E. Bristol, 30 m alt., C & MK, Mar. 1997; SO/5412. Rodge Wood nr Staunton, 230–260 m alt., FR, MG, AP, MR & JV, Feb. 1997.

V.c. 35 Mons.

SO/52.03 & 52.04. Cleddon Shoots Reserve, Cleddon, 185–200 m alt., FR, MG, AP & JV, Feb. 1997.

V.c. 36 Herefs.

SO/61.23. Penyand Park, Ross-on-Wye, 150–160 m alt., FR & MR, Feb. 1997.

V.c. 39 Staffs.

SJ/98.65. Lud's Church, 2 km NE of Swythamley Hall, 320 m alt., EC, FR & ES, Jan. 1991.

V.c. 41 Glam.

SN/82.01. Melincourt, Glamorgan W.L.T. Reserve, at waterfall, c. 75 m alt., RC, 1993.

V.c. 42 Brecks.

SO/12.38. Brechfa Common, nr Llyswen, 300 m. alt., CJ, Apr. 1990.

V.c. 43 Rads.

SO/11.42 & 12.43. Cwm Bach Howie gorge, 12 km W Hay-on-Wye, c. 200 m alt., RC, 1993; SO/1.7. Lawn Brook, Beacon Hill, 135 m alt., CJ, Apr. 1990.

V.c. 44 Carm's.

SN/44.07. Cwm Clydach, 50 m alt., IM, May 1991.

V.c. 45 Pembs.

SN/24.37. Cwm Cych, nr Cenarth, IM, May 1991; SN/26.35. Cwm Cych, nr Cenarth, 40 m alt., AOC, Apr. 1991.

V.c. 46 Cards.

SN/19.43. N of Coedmor mansion, Teifi estuary, 25 m alt., AOC, Mar. 1994; SN/19.44. Just S of Cwm Du, Coedmor, Teifi estuary, 20 m alt., AOC, Apr. 1991; SN/22.46. By Nant Arberth N of Point Rhyd-Arberth, 40 m alt., AOC & LG, May 1995; SN/29.52. NW of Llanborth, Penbryn, 15 m alt., AOC, Mar. 1994; SN/43.60. SW of Panteryrod, Afon Drywi valley, 50 m alt., AOC, Jan. 1996; SN/49.62 & 50.62. By Afon Arth, nr Monachty-back, 75–80 m alt., AOC, APF, Apr. 1991; SN/56.68. NNE of Plas Howell, Nant Rhydrosser, 115 m alt., AOC, Feb. 1992; SN/56.70. E of Pencwmisaf, Wyre valley, 65 m alt., AOC, July 1994; SN/59.59 & 59.60. Coed Gwenfrrwd, nr Llangeitho, 120 m alt., AOC, APF & DCB, Apr. 1991; SN/66.92 & 67.91. Coed Cwm Clettwr, nr Tre'r-ddol, 60–110 m alt., AOC & CJ, Apr. 1991; SN/69.94. S side of Cwm Einion, ESE of Ty'n-y-garth, 80 m alt., AOC, Nov. 1993; SN/69.96. By Afon Melindwr in garden of Llwyncelyn, Eglwys-fach, 15 m alt., AOC, Feb. 1994; SN/70.94. By Afon Einion, S of Dol-goch, Cwm Einion, 200 m alt., AOC, Nov. 1993; SN/71.97. Llynfnant valley, W end of scree, just east of Allt-ddu, 40 m alt., AOC, CJ, Apr. 1991; SN/73.72. Below road bridge WNW of Pontrhyd-y-groes, 150 m alt., AOC, July 1994; SN/73.77. Coed Rheidal NNR, E of waterfall, Derwen, WNW of Devil's Bridge, 160 m alt., AOC & CJ, Apr. 1991; SN/73.96. By Nant Cefn-coch, Llynfnant, 110 m alt., AOC, SC & AH, Feb. 1994; SN/73.97. Llynfnant Valley, east of Allt-ddu, 110 m alt., FR, Jan. 1991; SN/74.77. W side of Mynach Falls, Devil's Bridge, 120 m alt., AOC & JPW, Feb. 1995; SN/74.78. Coed Rheidal NNR, NW of Erwbarfau, 150–180 m alt., AOC, CJ, FR & CR, Feb. 1992; SN/76.48. Craig Ddu, Doethie, 320 m alt., AOC, Sept. 1992; SN/76.73. Below Mariamne's Garden, Hafod, 190 m alt., AOC, Dec. 1993.

V.c. 47 Monts.

SH/77.10. Below Lwydiath Hall, Afon Dulas, 130 m alt., CJ, FR, WC, S & JG, Apr. 1992.

V.c. 48 Merioneth

SH/62.38. Y Garth, 30 m alt., FR, 1996; SH/63.13. Afron Morfa, SW of Arthog, side of stream gorge, c. 90 m alt., RC, July 1993; SH/63.37. Coed Caerwych, 105 m alt., FR, Jan. 1991; SH/66.18. Bontddu, 40 m alt., FR, Jan. 1991; SH/65.39 & 66.38. Ceunant Llennyrch, nr Maentwrog, 30–90 m alt., DF & FR, Nov. 1989; SH/69.41. Ceunant Cynfal, nr Maentwrog, 60 m alt., CJ & FR, Apr. 1992; SH/72.11. Cader Idris. Nant Cader and scree on south side of Llyn Cau, 210 m alt., CJ, FR, WC, S & JG, Apr. 1992; SH/75.18. Torrent walk, 130 m alt., CJ, FR, WC, S & JG, Apr. 1992; SH/79.10. Nr Aberllefenni, in F.C. woodland, 205 m alt., CJ, FR, WC, S & JG, Apr. 1992.

V.c. 49 Caerns.

SH/55.47. Cwm Llefrith, Moel Hebog and adjacent Moel yr Ogof, 410–500 m alt., FR, Mar. 1990; SH/63.51. Clogwyn y Barcut, 150 m alt., ADH, Jan. 1992; SH/66.70 & 66.71. Aber Falls NNR, 120–200 m alt., RC, 1991; SH/72.57. Coed Bryn Engan, 190 m alt., ADH, Apr. 1990; SH/76.68. Conway Valley, west of Tal y bont, at Caer-illlin-ford, on the tributary Afon Dylin, 155 m alt., CJ & FR, Apr. 1991; SH/77.66. Coed Dolgarrog N.N.R., along Afon Ddu, 120 m alt., RC, 1992.

V.c. 52 Anglesey

SH/55.73. Cadnant Dingle S.S.S.I., 1 km S of Llandegfan, 75 m alt., RC, 1991.

V.c. 57 Derby's

SK/24.76 & 25.77. Froggatt Edge, c. 1 km NE of the village of Froggatt, 250–270 m alt., FR & ADH, Jan. 1990.

V.c. 62 N.E. Yorks

SE/58.98. Tripsdale, 260 m alt., KT, Oct. 1996; SE/81.91. Newton Dale, Newton-on-Rawcliffe,

120 m alt., KT, Mar. 1997; SE/83.84. Hyggitt's Scar, nr Pickering, 180 m alt., KT, Feb. 1997; SE/94.97. Castlebeck Wood S.S.S.I., Harwood Dale, 100 m alt., K.T., Apr. 1996; SE/94.98. Bloody Beck S.S.S.I., 120 m alt., KT, Apr. 1996; SE/99.98. Hayburn Beck, 4 km N of Cloughton, 0–90 m alt., KT, Aug. 1995; SE/99.99. Beast Cliff, 9 km N of Scarborough, 90 m alt., KT, Oct. 1995; NZ/64.13. Wileycat Beck, nr Charlton, 220 m alt., KT, Feb. 1997; NZ/64.14. Wileycat Wood, nr Charlton, 160 m alt., KT, Feb. 1997; NZ/65.03. Wood Dale, Waites Moor, 250 m alt., KT, Mar. 1997; NZ/70.03 & 71.04. Great Fryup Dale, 330–350 m alt., KT, Mar. 1997; NZ/70.14. Mill Beck Woods, Moorsholm, 130 m alt., KT, Nov. 1996; NZ/70.17. Mains Wood, Loftus, 65 m alt., CJ, FR, & KT, Feb. 1996; NZ/71.18. Whitecliffe Wood, Loftus, c. 40 m alt., CJ, FR & KT, Feb 1996; NZ/71.02 & 72.02. Woodhead, Great Fryup Dale, 300 m alt., KT, Sept. 1996; NZ/72.06 & 73.06. Danby Crag Wood, 160–220 m alt., KT, Oct. 1995; NZ/72.17. Wauple Wood, nr Liverton, 140 m alt., KT, Dec. 1996; NZ/73.01, 74.01 & 74.02. Glaisdale Head Crag, 280 m alt., KT, Oct. 1996; NZ/74.14. Upper Roxby Woods, 140 m alt., KT, Feb. 1997; NZ/75.07. Crunkly Gill, Leatholme, 120 m alt., KT, Oct. 1996; NZ/75.16. Lower Roxby Woods, 90 m alt., KT, Feb 1997; NZ/77.05. Glaisdale Wood, 80 m alt., KT, Oct. 1995; NZ/77.08. Stonegate Gill, nr Leatholme, 130 m alt., KT, Nov., 1995; NZ/78.04. West Arnecliffe Woods, nr Egton Bridge, 100–170 m alt., KT, Nov 1994; NZ/79.03. Park Hole Wood, nr Egton Bridge, 120–150 m alt., KT, May 1996; NZ/79.05. Limber Hill Wood, nr Egton Bridge, 90 m alt., KT, Oct. 1996; NZ/80.04. Below Blue Beck Cottage, Egton bridge, 60–100 m alt., KT, Nov. 1996; NZ/81.00. Scar Wood S.S.S.I., nr Goathland, 100–120 m alt., KT, Mar. 1996; NZ/81.02. Combs Wood, nr Beck Hole, 130–160 m alt., KT, Mar. 1996; NZ/81.04. Spring Wood, nr Grosmont, 130 m alt., KT, Mar. 1996; NZ/81.06. Hunter Hill, nr Grosmont, 90 m alt., KT, Nov. 1996; NZ/81.13. High Dale nr Mickelby, 120 m alt., KT, Nov. 1996; NZ/82.01. Carr Wood and Mallyan Spout, nr Goathland, 80–90 m alt., ADH, Sept. 1993; NZ/80.12. Thomason Foss, nr Beck Hole, 110 m alt., MD, Aug 1994; NZ/82.04. Crag Cliff Wood, nr Grosmont, 70–90 m alt., KT, Mar. 1996; NZ/83.04. Lythe Beck, nr Grosmont, 50–150 m alt., KT, Nov. 1996; NZ/83.11 & 84.11. Mulgrave Woods around Biggersdale Hole waterfall, 80 m alt., KT, June 1995; NZ/85.11. Mulgrave Woods, nr Sandsend, 90 m alt., KT, Jan. 1997; NZ/86.11. Dunsley Woods, nr Sandsend, 50 m alt., KT, Nov. 1996; NZ/88.03. Nr Falling Foss, S of Littlebeck, 110 m alt., KT, Apr. 1995; NZ/88.04. Nr Littlebeck, 90 m alt., KT, Dec. 1996; NZ/92.03. Oak Wood, nr Fylingthorpe, 100 m alt., KT, Dec. 1996; NZ/90.07 & 91.07. Rigg Mill Wood, nr Hawkser, 90 m alt., KT, Dec. 1996; NZ/90.08. Cock Mill Wood, nr Ruswarp, 30 m alt., KT, July 1995; NZ/95.01. Howdale Wood, nr Stoup Brow, 130 m alt., KT, Dec. 1996; TA/00.96. Hayburn Wyke, 2 km N of Cloughton, 5–90 m alt., FR, SR & ADH, Jan. 1992; TA/00.99. Beast Cliff, 9 km N of Scarborough, 90 m alt., KT, Oct. 1995.

V.c. 63 S. W. Yorks.

SD/96.26. Jumble Hole Clough, c. 240 m alt., ADH, Sept. 1991; SD/97.26 & 98.26. Callis Wood, SW of Hebden Bridge, 130–200 m alt., DF, CJ & FR, Nov. 1989; SD/97.25. Dill Scouts Wood/ Colden Clough, nr Hebden Bridge, c. 170 m alt., DF, CJ & FR, Nov. 1989; SD/97.29. Greenwood Lee, 220 m alt., FR & ADH, Mar. 1990; SD/97.30. Hardcastle Crags, 200–225 m alt., ADH, Sept. 1991; SK/23.96. Spout Brow/Bull Clough, 250 m alt., FR, Aug. 1990; SK/23.97. Valley between Ewden Lodge Farm and Cottage Farm, 260 m alt., FR, Aug. 1990; SK/24.96. Ewden Beck, 240 m. alt., ADH, Dec. 1989; SK/24.93. Agden Beck, 220 m alt., ADH, June 1990; SE/07.36. Harden Beck, 170 m alt., MG, FR, ES & JV, Feb. 1993; SE/10.38. Bell Bank, Bingley, on either side of A65 (previously B6429), 100–140 m alt., DF, CJ, FR, Nov. 1989.

V.c. 64 Mid-W. Yorks.

SE/06.56. Strid Woods, Wharfedale, 2 km N of Bolton Abbey, 115–120 m alt., FR & ADH, Mar. 1990; SE/07.56. Valley of Desolation, Hudson Gill Beck, 2 km N of Bolton Abbey, 180 m alt., FR & SR, July 1990; SE/09.46 & 09.47. Hebers Gill, 1.5 km SW of Ilkley, 185–235 m alt., FR & ADH, Dec. 1989; SE/10.47. Panorama Wood, 1.5 km SW of Ilkley, 200 m alt., FR & ADH, Dec. 1989; SE/12.50. West Moore and March Gill, 180–190 m alt., ADH, FR & SR, Mar. 1991; SE/15.63 & 15.64. Ravensgill, Bewerley, 180–240 m alt., FR & ADH, Jan. 1990; SE/20.63. Braisty Woods, nr Summerbridge, 235 m alt., FR & ADH, Sept. 1993; SE/20.64. Brimham Rocks, 270 m alt., ADH, 1996; SE/22.44. Danefield Wood, Otley, 170 m alt., FR, Sept. 1993; SE/23.77. Hackfall, 1 km NE of Grewelthorpe on SW side of River Ure, 130 m alt., FR & ADH, Jan. 1990; SE/27.54. Cardale Woodland, nr Harrogate, 108–115 m alt., FR & ADH, Sept. 1993; SE/35.53. Plumpton Rocks, 45 m alt., FR & ADH, Nov. 1996.

V.c. 67 S. Northumb.

NY/73.83. Roughside Moor, Cragshield Hope, 10 km W of Bellingham, 245 m alt., CJ & GS, July, 1995.

V.c. 69 Westmorland

SD/17.99. Stanley Force, 0.5 km SW of Eskdale, c. 100 m alt., DF, Oct. 1989; NY/36.06. Rydal Beck 1 km N of Rydal, 130 m alt., DF, CJ & FR, Nov. 1989; NY/36.07. Rydal Beck, 165 m alt., FR, Jan. 1991.

V.c. 70 Cumberland

NY/21.01. Hardknott Gill, 150 m alt., ADH, Dec. 1991; NY/26.18. Watendlath Beck, above and below Lodore Falls; c. 80–100 m alt. DF, Oct. 1989; NY/50.49. Eden Brows/Froddle Crook, 45–60 m alt., ADH, Nov. 1995.

V.c. 88 Mid Perth

NO/00.41. The Hermitage, Dunkeld, c. 100 m alt., FR, July 1995.

V.c. 95 Moray

NJ/18.71. Covesea, on raised beach 5 km W of Lossiemouth, 20 m alt., CJ & JV, July 1992.

V.c. 98 Main Argyll

NR/96.66. Kilbride Bay, Loch Fyne, 1 km N of Ardlamont Point, 5 m alt., CJ, July 1991; NS/00.77. Loch Riddon, N of Tignabruaich, c. 120 m alt., DR & JM, Apr. 1996.

V.c. 100 Clyde Is.

NR/86.40. Arran, Imachar Point, 25 m alt., FR, Oct. 1993; NR/86.41. Arran, N. of Imachar, 15 m alt., ARC, Aug. 1996; NR/88.31. Arran, shoreline just north of King's Cave, c. 5 m alt., FR & SR, Sept. 1996; NR/89.35. Arran, Machrie Bay, 20 m alt., FR, Oct. 1993; NR/90.48. Arran, S of Catacol Bay, 10 m alt., ARC, Sept. 1994; NR/93.51. Arran, Lochranza, 5 m alt., RC, May 1997; NR/94.52. Arran, Lochranza, Fairy Glen, 90–120 m alt., ARC & CJ, June 1991; NR/95.52. Arran, just east of An Scriodan, 85 m alt., FR, Sept. 1996; NR/96.51. Arran, Picture (Ossian's) cave and woodland 1 km SE of Cock of Arran, 25–35 m alt., FR & ARC, Oct. 1993; NS/01.37. Arran, Brodick Castle grounds, 20 m alt., ARC, Feb. 1994; NS/01.44. Arran, Sannox Bay, 25 m alt., FR & ARC, Oct. 1993; NS/01.46. Arran, North Sannox, rocks by sea, c. 6 m alt., CJ, June 1991; NS/02.39. Arran, S of Pirates Cove restaurant, c. 10 m alt., FR & ARC, Oct. 1993; NS/02.40. Arran, S of Rubha Salach, c. 10 m alt., FR & ARC, Oct. 1993; NS/03.29. Arran, Lamlash Bay, below Gortonallister, 7–40 m alt., FR, Oct. 1993; NS/03.35. Arran, Brodick-Corriegills Point, 10–35 alt., FR & ARC, Oct. 1993.

V.c. 101 Kintyre

NR/66.32. Bellochantuy, 20 m alt., FR & SR, Sept. 1996; NR/73.19. Glenramskill, 25 m alt., FR & SR, Sept. 1996; NR/74.76. Between Eilean na Bruachain and St Columba's Cave, 30 m alt., FR & SR, Sept. 1996; NR/76.15. Shoreline N of mouth of Balnabraid Glen, 5 m alt., FR & SR, Sept. 1996; NR/76.77. Roadside at Caolisport, 15 m alt., FR & SR, Sept. 1996; NR/81.37. Port Righ, Carradale, 15 m alt., FR & SR, Sept. 1996; NR/85.76. Artilligan Wood, 30 m alt., FR & SR, Sept. 1996; NR/85.78. Just N of Nead an Fhitich, 30 m alt., FR & SR, Sept. 1996; NR/86.55. E bank of Allt a Bhuie, Claonaig, 10 m alt., FR & SR, Sept. 1996; NR/91.60–91.62. Skipness to Rubha Grianain, 0–25 m alt., CJ & DB, July 1991.

V.c. 102 S. Ebudes

NR/37.45. Islay, Srón Dubh, between Laphroaig and Port Ellen, 20 m alt., FR & SR, Sept. 1996; NR/41.73. Islay, Bunnahabhain, <5 m alt., FR & SR, Sept. 1996; NR/44.67. Jura, raised beach cliff, 1.5 km S of Feolin Ferry, 20 m alt., FR & SR, Sept. 1996; NR/44.72. Jura, raised beach beyond Inver Cottage, 15 m alt., FR & SR, Sept. 1996; NR/46.53. Islay, Claggain Bay, 5 m alt., FR & SR, Sept. 1996; NR/46.76. Jura, coast S of Loch na Sgrioba, c. 3 m alt., LF & CP, June 1991; NR/48.63. Jura, below Jura House, Brosdale, in sea caves, c. 3 m alt., CJ & LF, June 1991; NR/67.99. Jura, Beinn nan Capull, in cave by shore, 2–5 m alt., CJ, June 1991; NR/70.98. Jura, woodland above Kinuachdrachd Harbour, 30 m alt., FR & SR, Sept. 1996; NM/67.00. Jura, cave on Uirigh Ghlas, 75 m alt., CJ, June 1991.

V.c. 103 Mid Ebudes

NM/43.42. Isle of Mull, in crevices along shore, 3 km N of Ulva Ferry, 12 m alt., CJ, JH & BM, Sept 1995; NM/55.21. Isle of Mull, Carraig Mhór, 1 km E of Carsaig, 3–5 m alt., CJ, JH & BM, Sept. 1995.

V.c. 104 N. Ebudes

NG/61.11. Skye, Toskavaig, c. 100 m alt., HB & JB, July 1992; NG/73.15. Skye, Isleornsay, on Sound of Sleat, nr Rubha Guail, 10 m alt., CJ & RC, Aug. 1991; NG/78.19. Skye, between Dunan Ruadh and Port Aslaiq, c. 10 m alt., HB & JB, July 1992; NG/76.24. Mudelach, Sron an Tairbh, 75 m alt., HB & JB, July 1992.

V.c. 105 W. Ross

NG/81.90. In cave once used as a church, S of Cove, nr Gairloch, 2 m alt., CJ & DH, July 1992; NC/07.03. Allt nan Coisiche, on western slopes of Ben More Coigach, about 0.5 km ENE of Culnacraig, 120 m alt., CJ & DP, July 1993.

V.c. 107 E. Sutherland

NH/76.98. Loch Fleet, on the NE facing cliffs of Creag an Armalaidh, 1 km NW of The Mound (Causeway), 12 m alt., CJ & RW, Aug. 1993.

V.c. 108 W. Sutherland

NC/18.61. On coast NW of Kinlochbervie, 1 km S of Rubh'an Fhir Leithe, 20 m alt., CJ & RW, Aug. 1993.

V.c. 109 Caithness

ND/18.73. W side of Dunnet Head, S of Dunnet Hill, nr Chapel Geo and W of old chapel, 175 m alt., JW & RW, Aug. 1993; ND/19.76. Dunnet Head, N of Burifa Hill on coast by Shira Geo, 8 m alt., JW & RW, Aug. 1993; ND/11.22. On steep banks of Langwell Water, at Berriedale, 17 m alt., CJ & RW, Aug. 1993.

V.c. H1 S. Kerry

Q/4.1. Brandon Mtn, FR & ADH, May 1993; Q/4.0. Brandon Mtn, RC, Aug. 1994; V/6.6. Cloonaghlin Lough, NE of Waterville, FR, May 1993; V/8.6. Cloonea Lough area, RC, July 1992; V/9.8. Killarney, RC, July 1992.

V.c. H2 N. Kerry

V/9.8. [4] Killarney area, FR & ADH, May 1993.

V.c. H3 W. Cork

W/1.3. Skibbereen, RF, Apr. 1994; W/2.3. Leap, NK, Feb. 1995; W/7.5. Hungry Hill, NS, Oct. 1993.

V.c. H6 Co. Waterford

S/0.0. Lismore, MD, July 1993.

V.c. H8 Co. Limerick

R/7.5 [2]. Slievefelim mountains area, FR & ADH, May 1993.

V.c. H10 N. Tipperary

R/7.5. Slievefelim mountains area, FR & ADH, May 1993.

V.c. H13 Co. Carlow

S/7.4 [2]. Tinnahinch, FR & ADH, May, 1993.

V.c. H16 W. Galway

L/67.62. NE slopes of Tully Mtn, 150 m alt., CJ, Aug. 1994.

V.c. H20 Co. Wicklow

O/19.12. Powerscourt Waterfall, 190 m alt., FR & PT, Sept. 1992; T/23.99. Devil's Glen, c. 180 m alt., NK, Feb. 1995.

V.c. H26 E. Mayo

G/20.04. Pontoon, NE of Castlebar, 70 m alt., MD, July 1993.

V.c. H27 W. Mayo

F/55.04. Achill Is., Croaghaun, 180 m alt., CJ, Aug. 1994; F/99.35. Benmore, 230 m alt., CJ, Aug. 1994; G/10.06. Nephin, 210 m alt., CJ, Aug. 1994; G/15.01. Shanvoley, 80 m alt., CJ, Aug. 1994; L/67.62. Tully Mtn, Letterfrack, 120 m alt., CJ, Aug. 1994; L/92.65. N slopes Devil's Mother, 130 m alt., CJ, Aug. 1994.

V.c. H33 Fermanagh

H/03.55. Lough Navar Forest, 280 m alt., NS, Feb. 1993; H/05.55. E. of Lough Navar, c. 200 m alt., RN, Jan. 1994; H/06.53. Derryvahon, at E end of cliff, c. 175 m alt., RN, Mar. 1996; H/07.54. Correl Glen, nr Derrygonnelly, about 50 m below bridge, 237m alt., NS, Feb. 1993; H/08.54. Correl Glen, lower end, 180 m alt., RN, May 1994.

V.c. H35 W. Donegal

G/0.2. Glenveagh, NS, Sept. 1993; G/9.8. Ardnamona Woods, MD, July 1993.

THE HABITAT OF THE GAMETOPHYTE

The microsites inhabited by gametophytes are usually under deep rock overhangs, in undercut areas at cliffbases, in sea caves, by streamsides, in recesses amongst boulders in small natural caverns and crevices, all relatively humid, but not wet (Fig. 2). Some sites appear particularly dry but there may be a retention of moisture by the rock strata sufficient to retain a high humidity. In some "dry" sites *Trichomanes speciosum* grows on soft rock or hard glacial debris which facilitates the movement of moisture through capillary action. As with many "Atlantic" cryptogams, the majority of sites have shaded, NE aspects (Ratcliffe 1968), although at higher altitudes (>270 m) the proportion of sites facing into sun, i.e. SW, rises significantly (see Fig. 5), perhaps to offset decreases in ambient temperature, or length of growing season. The gametophyte thus occurs in areas of low light intensity, most measured values being $<1\mu\text{Em}^2\text{s}^{-1}$, which represents 1% or less of the ambient light level exterior to the occupied site. The gametophyte has the ability to photosynthesize at very low irradiances, maintaining a positive carbon balance in an environment too dark for photosynthesis to occur in other terrestrial ferns for which reliable measurements have been reported (Rumsey *et al.* 1996), which allows the exploitation of a stable, competition-free, climatically moderated environment and must be considered responsible for the species' survival in much of northern and continental Europe.

Occupied sites show remarkably little variation in diurnal and annual temperature and humidity (Rumsey 1994). The latter is obviously of crucial importance as the species is absent from habitats where there is considerable movement of air, e.g. amongst block scree and tumbled boulders in stream beds, where other filmy-ferns thrive. Most sites are near geological transitions where differential weathering provides suitable undercut areas, waterfalls and steep-sided valleys, where temperatures remain moderated and humidity high. A wide range of acidic to neutral rock substrates are occupied (andesites, gneiss, basaltic lavas, granite, schists, sandstones, mudstones, greywackes, slates, grits and conglomerates), although slow growth rates and assumed poor dispersal means that rapidly eroding substrata, such as shales, are not generally suitable. Absence from limestone may be more the result of physical rather than chemical factors, especially given the weakly basicolous nature of the sporophyte, and also the fact that the gametophyte is found on weathered basalt. Porous substrates such as millstone grits and sandstones in general support more extensive gametophytic growth than non-porous, e.g. slates and schists, even in less macroclimatically suitable areas, such as Yorkshire. In these more continental areas the plant is almost always closely associated with spring lines and sub-surface moisture, which may permeate the porous rocks to provide a moderated humidity in the drier months. Desiccation is as liable to occur in the winter months, when lack of woodland canopies and herbaceous cover allows greater air movement into microsites, as in the warmer summer months when precipitation is reduced.

The majority of sites occur in woodland; those in open situations are predominantly coastal or rarely in hyper-oceanic montane areas, extending to c. 500 m on Moel yr Ogof. This latter habitat is more frequently occupied in the wetter, winter-warm, west of Ireland, as is true too, of the sporophyte (Ratcliffe *et al.* 1993). The woodland sites occupied have a long history but many have obviously been extensively felled at some stage in the past judging from the paucity of Atlantic bryophyte species (Edwards 1986). The extremely sheltered habitats of the gametophyte have, we suggest, allowed its survival through clear-felling episodes which have resulted in the loss of less "oceanic" but more photophilic species. A similar explanation may be advanced to account for the presence of the liverwort *Jubula hutchinsiae* (Hooker) Dum., a regular associate of *Trichomanes speciosum*, in otherwise bryophytically depauperate localities.

The species intimately associated with the gametophyte generation consist of a limited range of common, shade-tolerant calcifuge bryophytes, (cf. Ratcliffe *et al.* 1993, for sporophyte associations) of which the most regularly present are *Isopterygium elegans* (Brid.) Lindb. and *Calypogeia arguta* Nees & Mont., with *Tetraphis pellucida* Hedw. an important associate in gritstone sites. Whilst seldom growing intermixed, preferring constantly damp rock surfaces, *Tetradontium brownianum* (Dicks.) Schwaegr. is a useful site indicator of suitable undercut areas. The presence of a range of the Atlantic species recognised by Ratcliffe (1968) within the more continental areas of central and eastern Britain indicate that a search for the gametophyte may well be rewarded, given the presence of suitable niches. The requirement for suitable habitats cannot be overemphasized; climatically suitable sites supporting very rich Atlantic assemblages, e.g. Coed Ganlywd, Merioneth, do not

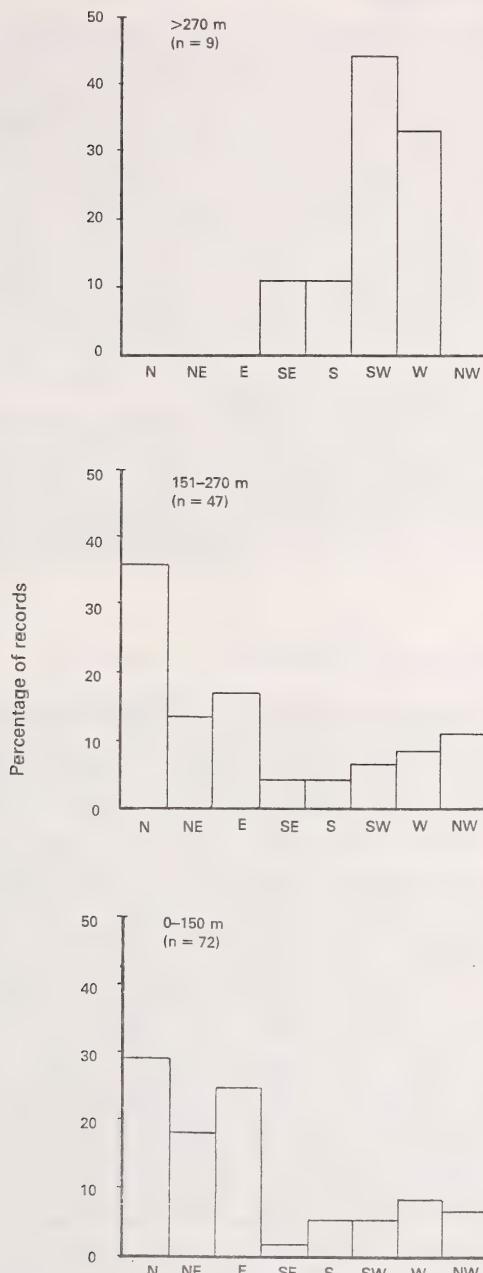


FIGURE 5. Gametophyte of *Trichomanes speciosum* microsite aspect at three different altitudes. Aspects have been simplified to the nearest of eight cardinal points; bar height is proportional to the number of records of that aspect in that particular altitudinal class.

support gametophytes, presumably as the bedding plane orientation has not allowed the development of undercut areas above the stream. On the other hand the gametophyte survives in climatically ameliorated pockets in marginal sites supporting a very impoverished Atlantic flora on the Yorkshire grits and Scottish sea cliffs.

The gametophyte is almost entirely absent in the British Isles from artificial habitats such as tunnels, quarries and mine adits, etc., even where closely adjacent to occupied natural sites. It has been reported to us as present in an adit, at Carr Wood, Goathland, N. Yorks (K. Trewren, pers. comm., 1995), and the only site seen by the authors is an adit, perhaps of Roman age, at Watersmeet, N. Devon. This suggests that successful dispersal and establishment, whether by spores or gametophyte gemmae is, within the British Isles, of very infrequent occurrence, at least under the conditions which have prevailed in historical time. The restriction of the sporophytic stage to an artificial habitat (well shafts) in Brittany (Louis-Arsene 1953a-c; McClintock 1963) would appear to be something of a paradox. It is significant that of all the known sites were of wells of considerable age, the species being absent from apparently similar but younger well sites. Was long-distance spore dispersal and colonization briefly possible under particular climatic conditions in the mediaeval period? Successful spore dispersal and colonization is obviously still occurring within Macaronesia, as evidenced by the species' presence on lava fields of known age on Terceira and Pico in the Azores, levada edging on Madeira, and on many road and trackside dry-stone walls on Flores, Azores, where the species achieves its greatest abundance.

One of the greatest paradoxes of this species and other "Atlantic" cryptograms, is in explaining how species which show little or no current dispersal over much of their range managed to reach the mid-Atlantic and effectively colonize these volcanic islands some 1000 km or more from the nearest landmass on the western fringe of Europe. Consideration of the climatic factors which may currently distinguish the Azorean region from elsewhere and which may have prevailed more widely in the past, would seem to offer the best opportunity for explaining the conditions necessary for dispersal to occur.

IMPLICATIONS FOR CONSERVATION AND THE LAW

Few would argue against the stringent legal protection of a species attractive to and vulnerable from collectors, especially if known as very few scattered and effectively isolated individuals, as is true of the Killarney Fern. This rarity and vulnerability is reflected throughout the species' range on the European mainland and its occurrence in Macaronesia is becoming increasingly threatened by changes in agricultural practices and laurel forest clearance (A.C.J. and F.J.R., unpublished observations). Accordingly, *Trichomanes speciosum* (which must be interpreted as both generations) has received special attention and is afforded legal protection throughout under the Berne Convention on the Conservation of European Wildlife and Natural Habitats (Appendix I) and is covered by the Directive of the Council of European Communities on the Conservation of Natural Habitats and of Wild Fauna and Flora 1992 (Annexes II and IV). This latter document requires Member States to preserve habitats, a laudable intention which obviously requires as a prerequisite accurate delimitation and documentation of the species' distribution. In Britain it is thus protected under Schedule 4 of the *Conservation (Natural Habitats, etc.) Regulations*, 1994 and Schedule 8 of the *Wildlife and Countryside Act*, 1981; in Northern Ireland, the species is protected under the *Conservation (Natural Habitats, etc.) Regulations (N.I.)*, 1995 and Pt. 1 of Schedule 8 of the *Wildlife (N.I.) Order*, 1985. In the Republic of Ireland the fern is protected under the *Flora Protection Order*, 1987, made under Section 21 of the *Wildlife Act*, 1976. In all cases these laws prohibit (except under licence) the picking, uprooting or otherwise taking, purchasing or selling the plants, or wilfully altering, damaging, destroying or interfering with the habitat of the species so protected.

The discovery of the distinctive, persistent populations of the gametophyte has resulted in a unique problem. The sheer abundance of sites both in the British Isles and in continental Europe precludes their effective protection as demanded by law. We thus run the risk under the current situation that legal protection may be considered inappropriate or unworkable. One solution may be effectively to ignore the gametophyte generation and redraft legislation to render the sporophyte alone as protected. Any such decision must primarily consider the role of the gametophyte in the production of new sporophyte plants. If the generations are isolated by failure to reproduce sexually

and very limited fertility respectively (Sheffield 1994), then the gametophyte might be considered as effectively a discrete organism and treated accordingly. Ratcliffe *et al.* (1993) in an in-depth discussion on the ecology and conservation of the Killarney Fern observed that no new sporophyte colonies had formed in Britain and Ireland, close to existing colonies known to them, over the past 30 years.

Recent study reveals the situation may be less bleak, with juvenile sporophytes seen in four Scottish, five English and two Welsh sites over the period 1990–1996. Of these, however, more than half have been at sites which already support sporophytes. In addition juveniles have shown high rates of mortality, all being lost from at least one site in this brief period (Rumsey *et al.* 1991). The incidence of sporophyte production throughout the species' range has a definite geographical bias, strongly suggesting climatic factors such as winter warmth are of importance (Rumsey & Sheffield 1996). If so, slight macroclimatic change may have a profound effect on rates of sporophytic recruitment and therefore anything which jeopardized the gametophyte's survival should be avoided. Gametophytes are perhaps vulnerable to disturbance by collection, the long term effects of which are unclear. However, given the growth form and totipotency of small fragments, collection is unlikely to cause the species' extinction at a site, but regrowth and recolonization is a slow process. Small bare areas left when material was collected under licence in 1989 could still be identified five years later!

The gametophyte is distinctive and does not need to be gathered for identification, nor is it obvious to, or easily damaged by, casual observers. It is also unlikely to be lost as a result of habitat destruction in the majority of its sites. If a responsible policy of non-collection by enthusiasts (the raising of sporophytes from gametophyte material is not a realistic option for amateur growers) and an ongoing monitoring programme to detect novel sporophytes can be maintained, then legal protection might sensibly be restricted to the sporophyte alone. Until such time, both generations have full legal protection as stated above.

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The use of B.S.B.I. Monitoring Scheme data to predict nationally scarce species in Britain

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ABSTRACT

It has recently been argued that the results of the B.S.B.I. Monitoring Scheme, a sample survey, can be used to identify species which may be nationally scarce in Britain. The practical usefulness of this method for estimating the frequency of uncommon species is discussed and shown to be limited by the large confidence limits associated with small sample sizes. The frequency estimates based on Monitoring Scheme data are tested for scarce species and for species in the Potamogetonaceae and Ruppiaceae, and are shown to under-estimate the distribution of many species. The revision of the list of nationally scarce species should await the results of the Atlas 2000 project, a geographically comprehensive project which will collate records collected over a longer time-span.

KEYWORDS: plant surveys, mapping, rare species.

INTRODUCTION

In Britain, nationally rare species are currently defined as those present in 1–15 10-km squares (Perring & Farrell 1983) and nationally scarce species are defined as those in 16–100 10-km squares. We recently contributed to a review of the distribution of nationally scarce species (Stewart *et al.* 1994). The species selected for review were those on an existing list of scarce species (Nature Conservancy Council 1989), corrected and modified in the light of later information. This list is in turn based on the distribution maps in the *Atlas of the British flora* (Perring & Walters 1962), the last geographically comprehensive survey of the British vascular flora.

In a recent paper, Rich (1997) has argued that the results of the B.S.B.I. Monitoring Scheme rather than those presented in the *Atlas of the British flora* should have been used to select the potentially scarce species. In the B.S.B.I. Monitoring Scheme, a sample of 1 in 9 of the British 10-km squares (or “hectads”) were surveyed in two years’ fieldwork (1987–88). Rich (1997) dismisses as incorrect the suggestion of Stewart *et al.* (1994) that this survey was not designed to detect trends in relatively uncommon species, arguing that “the sample survey as designed should have detected trends in all species, though clearly not as sensitively as a more detailed study, and less accurately for relatively uncommon species”. He asserts that the results of the scheme “could have been related to Britain as a whole using standard statistical methods to provide a more up-to-date, rigorous selection of species to be investigated”. Rich suggests that as the Monitoring Scheme sampled approximately 1 in 9 10-km squares, the total number of squares in which a species occurs can be

estimated by multiplying the number of squares in which it was recorded in the Monitoring Scheme by approximately nine. To be precise,

$$N = \frac{M \times 2860}{317} \pm 1.96 \times 2860 \times \sqrt{\frac{1}{317} \times \frac{M}{317} \times \left(1 - \frac{M}{317}\right)}$$

where N is the number of 10-km squares containing the species expected nationally $\pm 95\%$ confidence limits, M is the number of 10-km squares recorded in the Monitoring Scheme, 317 is the total number of 10-km squares covered by the Monitoring Scheme and 2860 is the number of 10-km squares in Britain. (The formula cited above is the one used by Rich, although it is cited incorrectly in his paper.)

In this paper, we examine the limitations of Rich's method as a predictive tool for rarer species. We then test the accuracy with which this method predicts the distribution of scarce plant species and of another group for which data have recently become available, the Potamogetonaceae and Ruppiaceae.

RICH'S METHOD APPLIED TO UNCOMMON SPECIES

Stewart *et al.* (1994) suggest that the results of the Monitoring Scheme should not be used to provide data on relatively uncommon species; Rich (1997) disagrees. The difference between the two points of view is almost certainly semantic rather than a real difference of opinion. Rich (1997) argues that the results will detect trends in the distribution of all species, but less accurately for the relatively uncommon species. We maintain that there comes a point where the accuracy is sufficiently low that one has to conclude that the method is not working, rather than working less accurately. There are, for example, 16 of the 253 nationally scarce species listed by Stewart *et al.* (1994) and an additional 145 out of some 310 rare species included in the *Red data book* (Perring & Farrell 1983) which were not recorded in any of the 10-km squares recorded for the B.S.B.I. Monitoring Scheme in 1987–88. It would be difficult to argue that the Monitoring Scheme has provided much useful data on these species.

If a species is recorded in a few Monitoring Scheme squares, the prediction of the number of squares in which it occurs nationally is necessarily accompanied by large confidence limits. This severely limits the practical usefulness of Rich's method for uncommon species. Even a species recorded in ten Monitoring Scheme 10-km squares is predicted as occurring in 90 ± 55 squares nationally, i.e. between 35 and 145 squares. This spans the range between species which are manifestly scarce to those which are much too frequent to qualify. Rich (1997) lists as potentially scarce all those species where the *minimum* prediction falls below 100 squares, as long as these are not known from other evidence to be more frequent. Only eight of the 65 species listed by Rich (1997) have a *maximum* predicted national distribution below 100 squares (*Barbarea stricta*, *Callitricha brutia*, *Equisetum hyemale*, *Juncus ranarius*, *Monotropa hypopitys*, *Salicornia fragilis*, *Utricularia australis* and *U. ochroleuca*). Six species (*Calystegia soldanella*, *Eryngium maritimum*, *Glaucium flavum*, *Silene acaulis*, *Spartina anglica* and *Vaccinium uliginosum*) which are listed as potentially scarce are estimated as occurring nationally in the range 96–246 squares. As Rich (1997) states, it is unlikely that many of the species will qualify as scarce.

TESTS OF RICH'S METHOD

SCARCE SPECIES

We have compared the predicted distribution of the potentially scarce species included in *Scarce plants in Britain* (Stewart *et al.* 1994) with the known distribution of the species as reported in that book. The Monitoring Scheme results correctly predict the distribution of 231 species (72%) using Rich's methods, over-estimate the distribution of one species (<1%) and under-estimate the distribution of 91 species (28%).

There were 62 species considered by Stewart *et al.* (1994) which turned out to be present in more than 100 10-km squares, and were therefore too frequent to be considered as nationally scarce. The results of the Monitoring Scheme predict that 59 of these (95%) might be scarce, i.e. the minimum

prediction of these species is fewer than 100 10-km squares, and that twelve (19%) will be scarce, i.e. the maximum prediction for these species is fewer than 100 squares. (These 62 species are omitted from Rich's paper as they were already known not to be scarce.) These results suggest a tendency of the Monitoring Scheme results to under-estimate the national distribution of species.

POTAMOGETONACEAE AND RUPPIACEAE

The accuracy of the predictions made by Rich's (1997) method can be tested against another recently published dataset. In an account of the Potamogetonaceae and Ruppiaceae, Preston (1995) presented updated distributional data for the British taxa. The 24 species and the three commonest hybrids in these families are considered here. In compiling the distributional data, attempts were made to collect as many reliable records as possible for 18 species and the three hybrids, e.g. by contacting B.S.B.I. vice-county recorders. These are subsequently described as the well-recorded taxa (although they may not be well-recorded by the standards of other, more popular groups). The vice-county recorders were not contacted for records of six of the commoner species, and the 10-km square distribution of these species may therefore be underestimated. These six species are described here as the under-recorded taxa.

The number of squares in which the well-recorded and under-recorded taxa have been recorded in the period from 1970 onwards is compared in Table 1 to the figures predicted from the Monitoring Scheme results. The Monitoring Scheme data are derived from Rich & Woodruff (1990) and the expected national totals calculated using the equation cited above.

The results in Table 1 show that four of the 21 well-recorded taxa were not recorded at all in the Monitoring Scheme. The predicted number of squares falls below the recorded number for 15 of the remaining 17 taxa. For seven taxa, the recorded number is greater than the range predicted by the Monitoring Scheme results, based on the 95% confidence limits. If one assumes that there was no significant decrease in these taxa between 1970 and 1988, the results of this test also suggest that the Monitoring Scheme data tends to underestimate the national frequency of species. The Monitoring Scheme prediction exceeds the known 10-km square distribution for two of the under-recorded taxa, and it is almost certainly a more accurate estimate of their frequency. The estimate is below the recorded total for one under-recorded species, even though the recorded total is believed to be too low.

POSSIBLE REASONS FOR UNDER-ESTIMATION USING RICH'S METHOD

The results discussed above suggest that the Monitoring Scheme results consistently underestimate the distribution of species. Rich (1997) implicitly assumes that the results of the Monitoring Scheme provide an adequate list of the species in the 10-km squares surveyed. There are two reasons to suggest that this assumption may not be justified:

1. There were two aspects to the botanical recording for the Monitoring Scheme. Recorders were asked to record the flora of three tetrads (2×2 km squares) within each 10-km square. They were also asked to record the species in the rest of the square. Our personal experience in recording for the Monitoring Scheme suggests that in areas where there were many botanists, both the specified tetrads and the rest of the squares were well recorded. However, in areas where there were few resident botanists, or which had to be recorded by visitors, the tetrads tended to be visited but the recording of the rest of the square was sometimes inadequate. This suggestion is supported by Rich & Woodruff's (1990) analysis of the Monitoring Scheme database and by the data plotted in Fig. 1, which show that for a minority of 10-km squares almost all the records received came from the designated tetrads. The results of the Monitoring Scheme 10-km square survey are therefore likely to underestimate the number of 10-km squares in which a species occurs nationally. This does not preclude the use of tetrad rather than 10-km data to assess the national frequency of species.

2. Some species are likely to be under-recorded in a survey limited to two field seasons. These include species which are difficult to detect in the field or to identify once found. Botanists with a particular interest in such difficult or critical species are much more likely to record them than those who do not have such specialised knowledge. The knowledge of such species is therefore likely to grow gradually as specialists in a county or country cover the area. In order to test whether species were under-recorded, we have examined the extent to which each nationally scarce species was

TABLE 1. COMPARISON OF NATIONAL FREQUENCY PREDICTED FROM MONITORING SCHEME DATA WITH OBSERVED VALUES FOR MEMBERS OF THE POTAMOGETONACEAE AND RUPPIACEAE

Species	No. of 10-km squares recorded in Monitoring Scheme	Predicted number of squares nationally $\pm 95\%$ confidence limits	No. of squares recorded nationally (Preston 1995)	Monitoring scheme prediction as percentage of observed value
Well-recorded taxa†				
<i>Greenlandia densa</i>	21	189 \pm 78	211	90
<i>Potamogeton acutifolius</i>	0	0	11	0
<i>P. alpinus</i>	15	135 \pm 67	236	57
<i>P. berchtoldii</i>	57	514 \pm 121	522	98
<i>P. coloratus</i>	7	63 \pm 46	71	89
<i>P. compressus</i>	0	0	30	0
<i>P. epihydrus</i>	0	0	1	0
<i>P. filiformis</i>	6	54 \pm 43	94	57
<i>P. friesianus</i>	4	36 \pm 35	110	33
<i>P. gramineus</i>	18	162 \pm 73	227	71
<i>P. lucens</i>	16	144 \pm 69	231	62
<i>P. \times nitens</i>	3	27 \pm 31	108	25
<i>P. nodosus</i>	1	9 \pm 18	8	113
<i>P. obtusifolius</i>	13	117 \pm 62	225	52
<i>P. praelongus</i>	5	45 \pm 39	110	41
<i>P. pusillus</i>	31	280 \pm 94	319	88
<i>P. rutilus</i>	0	0	12	0
<i>P. \times salicifolius</i>	1	9 \pm 17	21	43
<i>P. trichoides</i>	8	72 \pm 49	83	87
<i>P. \times zizii</i>	3	27 \pm 31	37	73
<i>Ruppia cirrhosa</i>	2	18 \pm 25	47	38
Under-recorded taxa†				
<i>Potamogeton crispus</i>	91	821 \pm 142	733	112
<i>P. natans</i>	184	1660 \pm 155	1018	163
<i>P. pectinatus</i>	68	614 \pm 129	657	93
<i>P. perfoliatus</i>	49	442 \pm 114	524	84
<i>P. polygonifolius</i>	154	1389 \pm 157	695	200
<i>Ruppia maritima</i>	7	63 \pm 46	126	50

† See text for explanation.

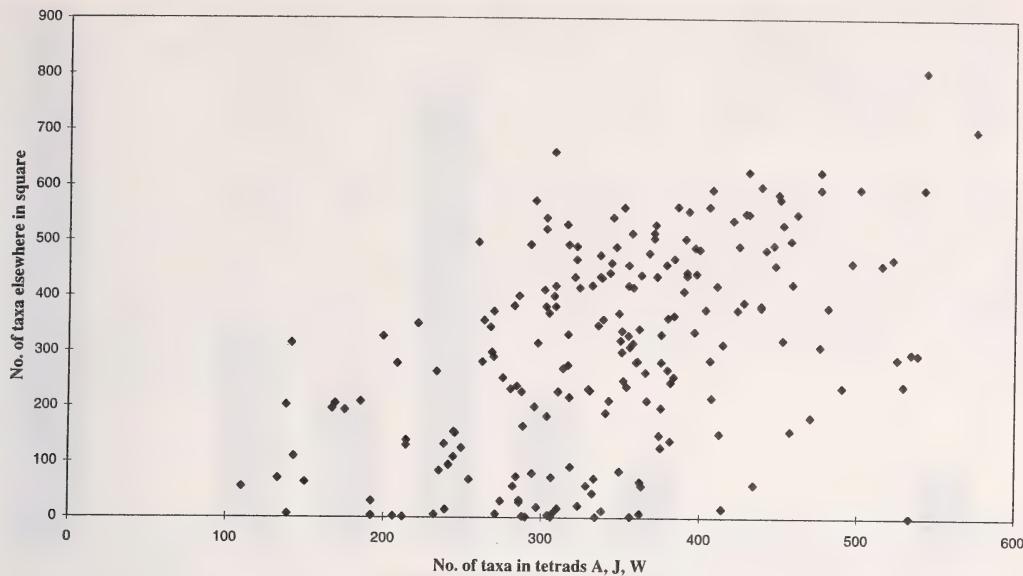


FIGURE 1. The total number of taxa recorded in tetrads A, J and W for each British 10-km square covered by the B.S.B.I. Monitoring Scheme, plotted against the number of additional taxa recorded during the Scheme elsewhere in that 10-km square. Squares which lack records from tetrads A, J or W were excluded from the analysis: the excluded squares are coastal squares without land in one or more of these tetrads or unrecorded inland squares.

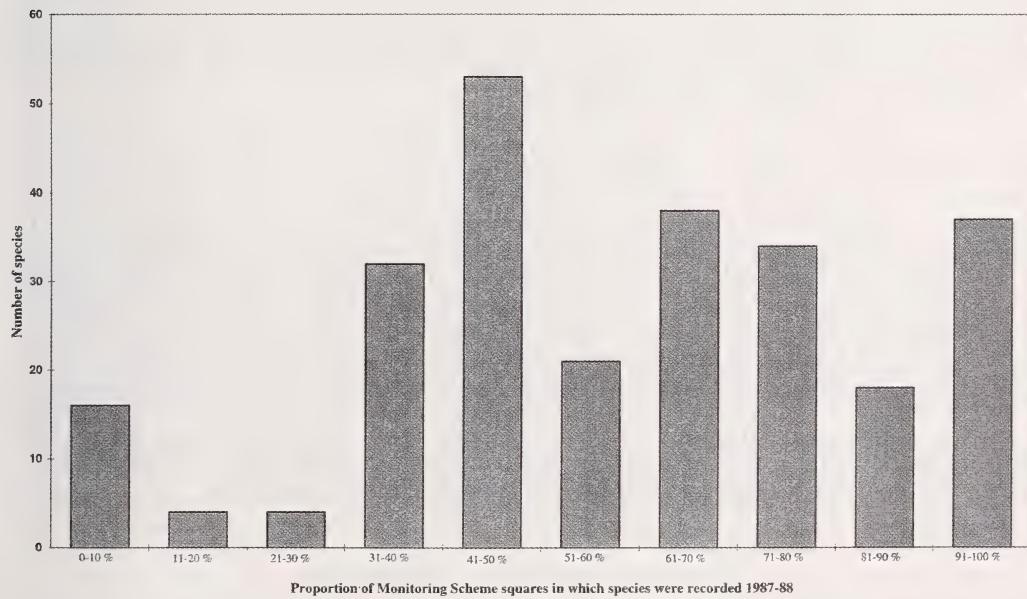


FIGURE 2. The number of 10-km squares in which nationally scarce species were recorded during the B.S.B.I. Monitoring Scheme (1987-88), expressed as a percentage of the total number of Monitoring Scheme squares in which they were recorded between 1970 and 1995. The number of species (vertical axis) falling in successive 10% bands is plotted.

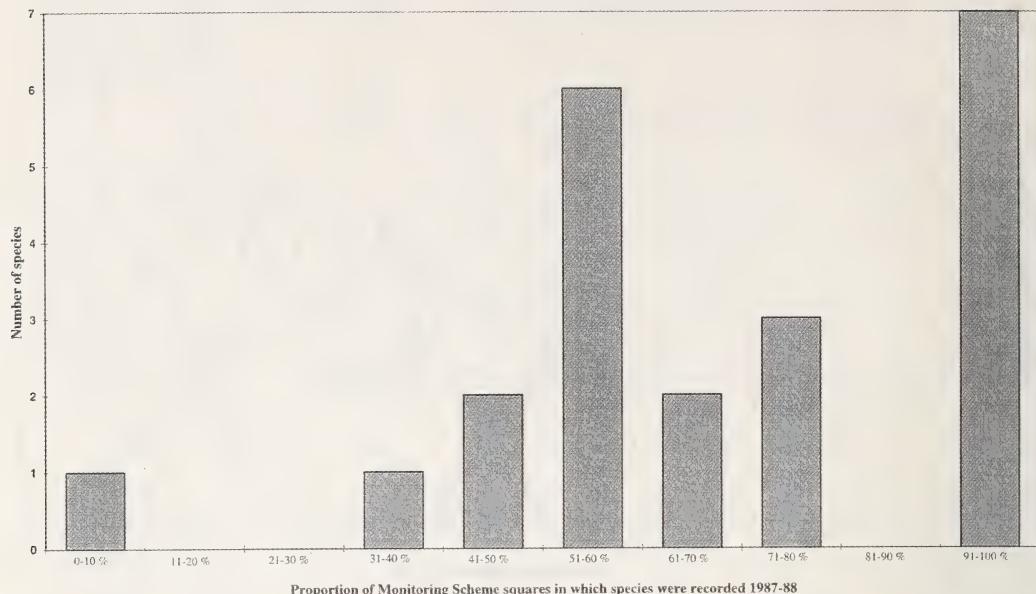


FIGURE 3. The number of 10-km squares in which *Groenlandia* and *Potamogeton* species were recorded during the B.S.B.I. Monitoring Scheme (1987-88), expressed as a percentage of the total number of Monitoring Scheme squares in which they were recorded between 1970 and 1995. The number of species (vertical axis) falling in successive 10% bands is plotted.

recorded in 1987-88 in those 10-km squares covered by the Monitoring Scheme in which it is known (from Monitoring Scheme and other records) to have been present in the period 1970-1995. The results of this analysis (Fig. 2) show that there was a wide range in the efficiency with which Monitoring Scheme recorders detected scarce species. The same analysis for *Groenlandia* and *Potamogeton* species provides similar results (Fig. 3).

It will be noted that many of the potentially scarce species listed by Rich (1997) are easily overlooked, difficult to identify or taxonomically critical, and are just the sort of species which are likely to be under-recorded in a "snapshot" survey or, in some cases, in any survey involving non-specialists. The species with a predicted number of 10-km squares below 100 include recently recognised segregates of *Juncus bufonius* (*J. foliosus*, *J. ranarius*) and *Utricularia intermedia* (*U. ochroleuca*, a plant not well understood even now by British botanists), species in the critical genera *Callitrichie* (*C. brutia*) and *Salicornia* (*S. dolichostachya*, *S. europaea*, *S. fragilis*), rather inconspicuous plants such as *Bromus lepidus* and *Epipactis purpurata*, and species which show variation in flowering behaviour from year-to-year (*Utricularia australis* and *U. vulgaris* sens. strict.). Five of the eight species with a maximum predicted square total below 100 are included in this group. The case of the *Utricularia* species is particularly difficult, as flowering material can be identified easily but is rarely encountered; both species usually reproduce vegetatively. Even if a detailed survey reveals records from fewer than 100 squares, it is arguable that the species should not be regarded as scarce as there are post-1970 records of vegetative material from 242 10-km squares (Preston & Croft 1997), and these plants must be referable to one or other of the two segregates.

TREATMENT OF DOUBTFULLY NATIVE SPECIES

Rich (1997) describes as "welcome and objective" the fact that *Briza minor* and *Poa palustris* are excluded as aliens from the list of scarce species. In this Stewart *et al.* (1994) followed Stace (1991). However, Rich (1997) lists *Barbarea stricta* as a potentially scarce species, as he himself (Rich 1987) regards it as probably native although Stace (1991) describes it as probably introduced. In the

controversial subject of native status there are numerous individual opinions, and the only practical course open to us as editors of *Scarce plants in Britain* was to follow a standard source. All botanists will, if given a chance, argue for the inclusion of some taxa and oppose the inclusion of others. Thus, one of us (D.A.P.) strongly favoured the inclusion of *Briza minor* as a native and another (C.D.P.) would have excluded *Erodium moschatum* as an alien, but we both agreed to set aside our personal opinions and follow Stace (1991).

In *Scarce plants in Britain* our explanation for including *Brassica oleracea* as a scarce species is inadequate; we are therefore to blame for the fact that it has been misunderstood by Rich (1997). Stace (1991) regards this species as possibly native and we therefore include it as a scarce species. We accept that it is impossible in many instances to distinguish native from alien colonies, but as there are fewer than 100 10-km square records for all the established coastal colonies, native and alien, we list the species as scarce. The confusion arises as the author of the *Brassica oleracea* account (Richards 1994) considers that the species is introduced. Following our arguments would not result in the inclusion in the lists of rare or scarce species of taxa which are accepted as introductions in all their British localities.

TREATMENT OF ARABLE WEEDS

The particular and in some ways insuperable difficulties of dealing with arable weeds are discussed in *Scarce plants in Britain* (Stewart *et al.* 1994, p. 473). These difficulties have been highlighted by the publication, also in 1994, of a booklet by Wilson & Sootherton (1994). Whereas we published records of *Ranunculus arvensis* from 221 10-km squares from 1970 onwards and over 100 from 1980 onwards, Wilson & Sootherton believe that there may be as few as six viable populations left. Similarly they describe *Scandix pecten-veneris* as probably occurring now in fewer than 25 10-km squares, although there are records from 85 squares from 1980 onwards and 131 squares from 1970 onwards. In evaluating the status of these rapidly declining species we decided to alter the criterion for inclusion of scarce species and take records from 1980 onwards, rather than use the 1970 date employed for the other species. This decision was made on purely pragmatic grounds. We accept Rich's (1997) view that it is inconsistent and subjective, but we believe that where circumstances differ, uniformity of treatment is not necessarily desirable. Retention of the normal 1970 cut-off date for these species, as Rich (1997) recommends, appears to us to be an unrealistic option.

CONCLUSIONS

We do not dissent from Rich's (1997) view that the list of scarce species in Stewart *et al.* (1994) is provisional; all such lists inevitably are. We ourselves stated that there must be a strong possibility that the list would require revision in the light of current work on rare species (Stewart *et al.* 1994, p. 18) and that other formerly commoner species may now qualify as scarce (Stewart *et al.* 1994, p. 12). However, it would be a more efficient use of resources to await the results of the Atlas 2000 project (Pearman & Preston 1996), which will provide up-to-date geographically comprehensive data on the distribution of the British flora, rather than investigate the particular species listed by Rich in isolation.

We also agree with Rich (1997) that it might be preferable to define rare and scarce species as a percentage of the British flora rather than in absolute terms, although this would require a co-ordinated look at both rare and scarce species. It will probably be desirable to assess the distribution of both rare and scarce species in a more small-scale unit than the 10-km square (Pearman 1997).

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Relationship between species richness and rarity in Welsh aquatic floras

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ABSTRACT

Comparison of the biodiversity of sites, such as potential nature reserves, often has to use incomplete data. In such cases rules of thumb, such as a positive correlation between species richness and the presence of rarities, could allow more rational decisions to be made. Such a relationship is tested in two Welsh aquatic data sets. This analysis supports the general positive relationship between species richness and rarity; however in a lake data set no correlation was found between the species richness or number of rarities when the emergent and submersed plant communities were compared; i.e. a site which was good for emergent plants was often not a good site for submersed plants and vice versa. It is suggested that the species richness/rarity rule only applies to tightly constrained, homogenous data sets.

KEYWORDS: nature reserves, biodiversity, botanical surveys, *Pilularia globulifera*.

INTRODUCTION

The preservation of biodiversity is a major aim of applied ecology (Wilson 1992). One of the approaches to this is to construct networks of nature reserves, though serious questions have been raised about this as a long term strategy in the light of continuing environmental change, both natural and anthropogenic (Hunter *et al.* 1988; Huntley 1994). Biodiversity is composed of a variety of measures such as species richness (number of species at a site), species abundance (population size of species of a site) and habitat diversity (Hambler & Speight 1995). In comparing sites, for example in selecting nature reserves, often the main data available are species lists for the better studied taxa (e.g. vascular plants, birds or butterflies). This raises a number of important questions. For example, does species richness of a well studied taxon such as vascular plants positively correlate with species richness of less well studied groups such as beetles (Wilkinson & Slater 1995)? Does species richness in a group correlate with the occurrence of rare species of that group at a site? Selecting sites on the basis of a high species richness could be a mistake if important rare species are found in species poor sites which would not receive protection were such a criterion used (Hambler & Speight 1995).

Such questions can only be successfully addressed in an empirical manner, by investigating the relationships between the occurrence of different taxa, species richness and rarity at a variety of sites. As a contribution to such a research agenda this paper examines the relationship between species richness and rarity in two aquatic flora data sets from Wales, U.K.

THE DATA SETS

Two published data sets on Welsh aquatic floras were used.

1. A set of 36 shallow and often ephemeral upland ponds from mid Wales, ranging in altitude from 320–500 m (Slater *et al.* 1991). These ponds are of particular conservation interest as around half of them contain the aquatic fern *Pilularia globulifera*. This fern is endemic to Europe and threatened throughout most of its range due to loss of habitat through drainage. These mid Wales ponds are one of its strongholds and of international importance (Woods 1993). One site, Park Farm, which

TABLE 1. SPECIES FROM SEDDON (1972) LISTED AS IN NEED OF SPECIAL PROTECTION IN THE WELSH WATER AUTHORITY AREA BY PALMER & NEWBOLD (1983)

Submersed and floating species	Emergent species
<i>Apium inundatum</i>	<i>Baldellia ranunculoides</i>
<i>Ceratophyllum demersum</i>	<i>Butomus umbellatus</i>
<i>Elatine hexandra</i>	<i>Carex acuta</i>
<i>Isoetes echinospora</i>	<i>C. acutiformis</i>
<i>I. lacustris</i>	<i>C. elata</i>
<i>Lemna trisulca</i>	<i>C. lasiocarpa</i>
<i>Lobelia dortmanna</i>	<i>C. riparia</i>
<i>Luronium natans</i>	<i>C. vesicaria</i>
<i>Myriophyllum spicatum</i>	<i>Cladium mariscus</i>
<i>Potamogeton alpinus</i>	<i>Eleocharis acicularis</i>
<i>P. crispus</i>	<i>Hippuris vulgaris</i>
<i>P. gramineus</i>	<i>Oenanthe fistulosa</i>
<i>P. lucens</i>	<i>Ranunculus lingua</i>
<i>P. obtusifolius</i>	<i>Schoenoplectus lacustris</i>
<i>P. perfoliatus</i>	<i>S. tabernaemontani</i>
<i>P. pusillus</i>	<i>Typha angustifolia</i>
<i>Ranunculus circinatus</i>	<i>Veronica anagallis-aquatica</i>
<i>R. trichophyllum</i>	
<i>Sparganium angustifolium</i>	
<i>S. natans</i>	
<i>Subularia aquatica</i>	
<i>Eleogiton fluvians</i>	
<i>Callitrichia hermaphroditica</i>	
<i>C. obtusangula</i>	

Nomenclature follows Stace (1991).

appears in the data set of Slater *et al.* (1991) has been omitted from this analysis as it is a lower, more species rich site in improved farmland and so is atypical of the rest of the data set.

2. A data set of plants from Welsh lakes including both upland and lowland sites (Seddon 1972). This data set is comprised of two subsets: i. submersed and floating aquatic plants from 70 Welsh lakes; and ii. emergent plants from 72 Welsh lakes.

Rare species are those having low abundance and/or small ranges, and this raises the question of how low or how small? This is often affected by factors such as the area under study or the purpose for which the list is being constructed. A single objective definition of rarity which can be applied in all studies of all taxa is unrealistic. This is illustrated by the wide range of definitions of rarity which have been used in the past (reviewed by Gaston 1994).

In this study a rare species is defined as any species listed as "in need of special protection in the Welsh Water Authority area" by Palmer & Newbold (1993). This is an inclusive list containing some quite widespread and locally common species which were however considered to be possibly declining and in need of protection. In the upland pond data set there were two species "in need of special protection", *Pilularia globulifera* and *Apium inundatum*. The lake data set contained a longer list of such species which are listed in Table 1. In the following analysis species richness refers to the total number of species at a site and rarity refers to the number of species listed as "in need of special protection" found at a given site.

RESULTS AND DISCUSSION

The correlations between species richness and rarity for each of the data sets are shown in Table 2. In each case there is a positive correlation significant at $p<0.001$, although the correlation coefficients range from 0.500 to 0.722. A number of previous studies on a variety of taxa have found rare species to be positively correlated with species richness (Gaston 1994). For example, Wheeler

TABLE 2. RELATIONSHIP BETWEEN SPECIES RICHNESS AND RARITY IN WELSH AQUATIC FLORAS

Data set	Reference	No. sites	Total no. spp.	Total no. rare spp.	r_s
Upland pools, Mid Wales	Slater <i>et al.</i> (1991)	36	66	2	0.722
Welsh lakes (all plants)	Seddon (1972)	54	91	41	0.500
Welsh lakes submersed plants	Seddon (1972)	70	41	24	0.536
Welsh lakes emergent plants	Seddon (1972)	72	50	17	0.631

Note: all correlations significant at $p < 0.001$.

(1988) found a highly significant ($p < 0.001$) positive relationship between number of rare species and total species richness for British fen vegetation. In the present study the strength of the correlation varies between data sets. The highest correlation ($r_s = 0.722$) is for the upland pond data set where there are only two rare species, *Pilularia globulifera* and *Apium inundatum*, which are significantly associated ($\chi^2 = 13.38$, $p < 0.01$, $n = 36$) in the data set though it included some sites with *Pilularia* but no *Apium* and some with *Apium* but no *Pilularia*. In this case selecting species rich sites would be an effective way of selecting sites with rarities.

The Welsh lake data set is of particular interest. Although there is a significant correlation between species richness and rarity for total species (i.e. all lakes where Seddon (1972) lists data on both submerged and emergent plants), if the submerged and emergent data subsets are compared (Tables 2 & 3 of Seddon 1972) then no significant correlations are found (correlation between submerged and emergent species richness $r_s = 0.144$, not significant at $p = 0.05$, $n = 54$; correlation between number of rare submerged and number of rare emergent species $r_s = 0.029$, not significant at $p = 0.05$, $n = 54$). Therefore good sites for emergent plants tend not to be good sites for submerged plants. This is true whether a "good site" is selected on the basis of species richness or by the presence of rare species. This suggests that correlations between species richness and rarity may be community specific, with a whole lake being too large a unit for analysis as it contains a number of very different communities (e.g. emergent and submerged). This requires investigation by further studies as it is important for comparing sites of nature conservation importance. It is of interest that for the upland pond data set Wilkinson & Slater (1995) found a positive correlation between plant species richness and a measure of general invertebrate species richness but no correlation between water beetle species richness and plant or general invertebrate species richness. This suggests that different taxa as well as different communities can show different patterns of species richness, so that a good site for water beetles may not be a good site for aquatic plants.

These results suggest that caution is required in the make up of data sets when extrapolated from species richness data to rarity richness. For example the relationship between plant species richness and rarity in British fens identified by Wheeler (1988) means that selecting the most species rich sites would also select the sites with the most rarities. However if the exercise were repeated for all British mires then selecting by species richness would miss many rarities as most of the sites selected would be fens as these tend to be more species rich than ombrotrophic mires (Wheeler 1993), so rare ombrotrophic species would be missed. This underlines the suggestion in the data presented above that the species richness/rarity rule is only likely to work for tightly constrained, homogenous data sets. Such heuristic rules, tested on the relatively well known British flora, could be of great use in areas where the flora is less well known, such as tropical forests, which are thought to contain some 40% of the world's flora, sometimes with over 300 species/ha⁻¹ (Archibald 1995).

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The current status of *Rumex rupestris* Le Gall (Polygonaceae) in England and Wales, and threats to its survival and genetic diversity

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ABSTRACT

All U.K. sites from which *Rumex rupestris* Le Gall, a dock endemic to N.W. Europe, had previously been recorded, and which could be identified from herbarium specimens and Flora records, were surveyed. The objectives were to obtain up-to-date information on the distribution of this apparently declining species, the size of its extant populations and the suitability of previously occupied sites for re-introduction under the Species Recovery Programme. The amount of genetic variation, and its distribution within and between populations was measured using isozyme electrophoresis. Although a relatively large amount of the total variation found is held within individual populations, there is evidence of some isolation of populations by distance. Results also support the expectation that larger populations hold more genetic diversity. Possible threats to the survival of populations and to variation within the species are discussed.

KEYWORDS: Shore Dock, distribution, isozymes, gene flow.

INTRODUCTION

Rumex rupestris Le Gall (Shore Dock) (Polygonaceae) is a rare and threatened European endemic growing in scattered populations along the coasts of Galicia, western France, the Channel Isles, south-west England and south Wales, with an outlying (possibly introduced) population on Anglesey. It grows above high water mark where there is a supply of fresh water. Some populations occur in wet crevices in the lower parts of cliffs, where fresh water discharges on to the upper parts of beaches or slumped head material. Others are found in seepage zones at the base of cliffs or in small pools on wave cut platforms. Less frequently, plants also grow along the margins of streams or ponds in dune slacks. Population size is usually small, frequently with fewer than ten individuals, growing as scattered individuals or small clumps. Throughout its range it appears to be vulnerable to the same set of threats: habitat instability, human activity and small population size. The objective of the present study, sponsored by English Nature under the Species Recovery Programme, was to determine the current status of the species in Britain and the Channel Islands, assess the magnitude of the different risks and develop proposals for its reintroduction into some of its former sites. This paper reports the results of the first two of these activities.

METHODS

Floras and herbaria were consulted in order to determine the locations of all past and present populations of *R. rupestris* in England and Wales, and the dates when last records were made. In late summer 1994 all known extant sites in Devon and Cornwall, based on data in King (1989) and information from local botanists, were visited and counts made of plants present (McDonnell 1995). Species associated with colonies of *R. rupestris* were also recorded. Similar counts were made of populations in the Isles of Scilly by R. Parslow (Parslow & Colston 1994). Q. Kay and A. Jones provided information on the present status of the species in Wales. In summer 1995 most of the mainland sites were revisited together with all sites in Cornwall, Devon and Dorset for which old records had been found in order to determine whether any plants were still present (Daniels, McDonnell & Moy 1996). Comparisons were also made with sites visited the previous summer, in order to assess suitability for re-introduction, bearing in mind the known or predicted ecological requirements of the species and practical considerations. Such information, together with site history, where this was known, was also used to suggest possible reasons for loss of individual populations and to select sites for re-introduction.

In 1994, small seed samples were collected from all populations visited. A sub-sample of these seeds was used to grow plants for examination of electrophoretic variation in leaf material. Enzyme extracts were prepared in 0.1M Tris buffer containing 10% glycerol, 1% ascorbic acid and 0.1% mercaptoethanol. The natural acidity of the leaf tissue obviated the need for pH correction of the buffer to pH 7.0 using HCl. The resulting slurry was centrifuged at 1400 rpm for 3 minutes and the supernatant was stored at -73°C until used for electrophoresis. Electrophoresis was performed in a BioRad Protean II chamber using 1 mm thick polyacrylamide gels. The 13% separating gel was prepared in a 0.4M Tris-HCl buffer (pH 8.8) and a 7% stacking gel in a 0.1 Tris-HCl buffer (pH 6.8). Gels were run for 7 hours at a constant 250V using a 0.072M glycine-0.005MTris electrode buffer (pH 8.5). Gels were stained for eight different enzyme systems using the protocols of Raybould *et al.* (1991).

RESULTS

STATUS AND DISTRIBUTION

The distribution of extant (in 1989–1995) and former sites in England and Wales is shown in Fig. 1. Subsequent to this survey, a new site was found in Glamorgan, south Wales (Kay 1996). Table 1 gives the number of plants present in each of the surveyed sites in Devon and Cornwall in 1989 (data from King 1989), 1994 and 1995, together with 1994 and 1996 data for the Isles of Scilly (Parslow & Colston 1994; Parslow 1996) and 1996 data from Glamorgan (Kay 1996). Some difficulty was experienced in assessing absolute numbers because of possible confusion of vegetative plants with non-fruiting specimens of *Rumex crispus*, especially in its coastal variant, subsp. *littoreus* (J. Hardy) Akeroyd. Because of this, reliable comparisons of population size can only be made using counts of fruiting plants.

Sites at which the plants had been recorded formerly but were not found in 1994 are listed in Table 2, together with the dates of last records. In some cases the actual locations are ill-defined because of lack of clarity in recording the precise location of a Flora entry or a herbarium specimen. In a few cases it has been assumed that two records with different names have referred to the same populations, especially where one of them has been as vague as "near Plymouth". Whilst some locations appear several times, with the species being noted by more than one recorder, others are represented by single records only.

GENETIC VARIATION

Pot-grown plants at Furzebrook showed a wide range of variation in height, differences in leaf characters and divergence in inflorescence structure. In particular, nine robust plants with leaves standing out widely from the stems and wavy leaf margins (five from seed collected at Rame and four from seed collected at Westcombe) developed tall flowering shoots in which the branches formed acute angles with the main axes and the flowers were arranged in closely-set whorls. In addition, the fertile fruits produced had distinct wings. These plants so closely resembled *R. crispus*

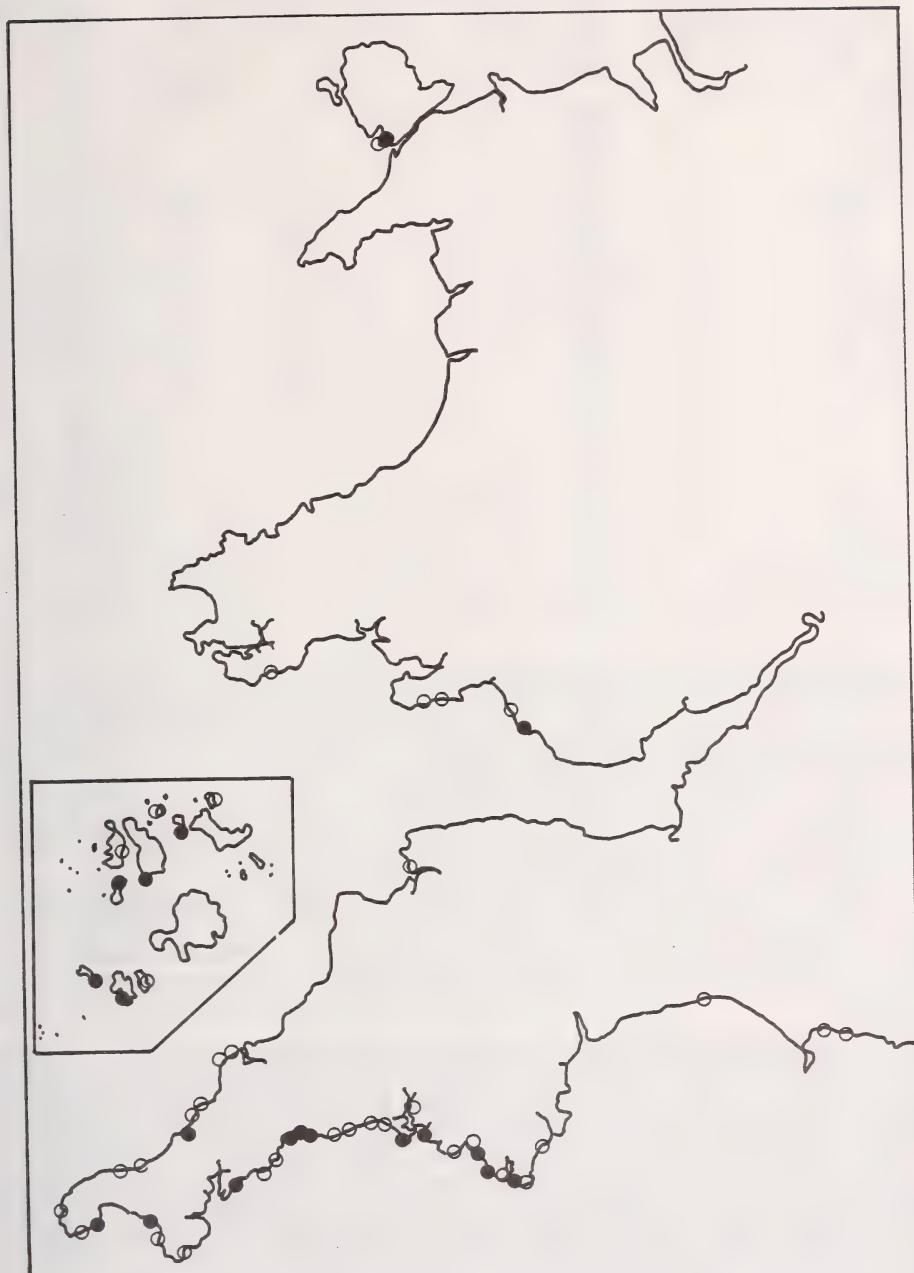


FIGURE 1. Distribution of extant (closed circles) and historical (open circles) populations of *Rumex rupestris* in mainland Britain, Anglesey and the Isles of Scilly.

TABLE 1. NUMBER OF PLANTS OF *RUMEX RUPESTRIS* (IN FRUIT AND IN TOTAL) AT DIFFERENT LOCATIONS IN ENGLAND IN 1989, 1994, 1995 AND 1996

A zero indicates that no plants were observed: a dash indicates that no observations were made.

Site	1989		1994		1995		1996	
	+ fruit	total						
Cornwall								
Penhale	-	>50	33	>33	-	>50	>70	>70
Lamorna	-	-	2	3	2	3	-	-
Gunwalloe	-	>50	7	7	0	2	-	-
Pendower	-	18	9	9	9	9	-	-
Pencarrow	-	-	3	>3	7	7	-	-
Llantivet Bay 1	-	2	2	4	1	4	-	-
Llantivet Bay 2	-	-	-	-	7	7	-	-
Rame	-	69	24	36	31	35	-	-
Devon								
Wembury	-	-	-	-	1	1	1	1
Westcombe	2	4	2	2	-	-	-	-
Soar Mill	5	6	13	>13	3	8	-	-
Rickham	-	19	0	0	0	0	-	-
Venericks	-	9	5	13	10	12	-	-
Isle of Scilly								
Tean	-	-	19	72	-	-	19	97
Tresco	-	-	33	33	-	-	52	60
Samson	-	-	40	40	-	-	90	124
Annet	-	-	6	6	-	-	51	51
St Agnes	-	-	14	14	-	-	18	18
Wales								
Newborough	-	-	-	c 25	-	-	-	-
Glamorgan	-	-	-	-	-	-	21	>21

that it appears most likely that in the field specimens of *R. crispus* subsp. *littoreus* were sampled rather than *R. crispus*, despite conviction at the time that all seed came from shore dock plants. A second group of plants grown from seed collected at Church Cove had spreading, leafy, inflorescences and comparatively long petioles and were, undoubtedly, *R. conglomeratus* Murray. Field survey in 1995 confirmed that all plants at this site were *R. conglomeratus*. Several individuals showed characteristics which were intermediate between *R. conglomeratus* plants and more typical *R. rupestris* in the cultivation trial. This suggests that either the range of variation is continuous between the two species or that some of the plants were of hybrid origin.

Of the eight enzyme systems tested, five produced only monomorphic banding patterns and only three (esterase, malate dehydrogenase and phosphoglucu-isomerase) showed polymorphism. Even in these cases, band interpretation in terms of alleles at different loci was difficult and different band combinations were recognised only as different phenotypes. Because of this, variation at the species and population levels was calculated using the Shannon Diversity Index (King & Schaal 1989) rather than F-statistics.

Each of the phenotypes for each of the systems where polymorphism was found were combined to give a set of overall phenotypes (e.g. AAA represents a phenotype showing banding patterns recognised as phenotype A for each of the systems whilst AAB represents a combined phenotype with a different PGI banding pattern). The proportions of each of these combined phenotypes were used to calculate dissimilarity indices. Calculations of overall diversity (H_{sp}), the mean diversity within populations (mean of H_{pop}) and the contributions of within-population and among-population to overall diversity were made at three different scales. Taking all populations as distinct, independent, units, 55% of the total variation was contained within populations and 45% was attributable to differences among populations. This implies that, although there are differences among the isolated populations of *R. rupestris* in south-west England, each still retains much of the total variability found within the species in England. The maintenance of diversity may result from gene flow between populations (either through pollen transfer or seed dispersal) and if this is the

TABLE 2. FORMER SITES OF *RUMEX RUPESTRIS* IN ENGLAND AND WALES
English sites with asterisk are those where there is only a single record.

Site	Grid square	Last record
Cornwall		
Harlyn Bay	SW/8.7	1900*
(Trevose Head &	SW/8.7	1963)
(Constantine Bay		1951)
East Pentire	SW/7.6	
Fistral	SW/7.6	1912
Newquay	SW/8.6	
Gravel Hill mine, Cubert	SW/7.5	1903*
Godrevy Point	SW/5.4	1951*
Lelant	SW/5.3	1909*
Sennen Green	SW/3.2	1870's*
Boscawen Cliff	SW/4.2	1900*
Poltesco	SW/7.1	1870's
Hemmick Beach	SW/9.4	1905*
Vault Beach	SX/0.4	1900*
Looe	SX/2.5	1917*
Downderry	SX/3.5	1875*
Portwrinkle	SX/3.5	1875*
Tregantle	SX/3.5	1875*
Devon		
Wadham	SX/5.4	1875*
Pamflete	SX/4.5	1876*
Little Seacombe	SX/7.3	1989
Gammon Head	SX/7.3	before 1939
Slapton Ley	SX/8.4	1977*
Braunton Burrows	SS/4.3	1955
Dorset		
Lyme Regis	SY/3.9	1923*
West Bay	SY/4.9	1949*
Ringstead Bay	SY/7.8	1985
Durdle Door	SY/8.8	1985
Poole	SZ/0.9	1900*
Glamorgan		
Three-cliffs Bay	SS/5.8	1985
Pennard Burrows	SS/5.8	1910
Kenfig Burrows	SS/7.8	1948
Dunraven Bay	SS/8.7	1934
Methyr Mawr	SS/8.7	1954
Pembrokeshire		
Lydstep Haven	SS/0.9	1957

case we would expect the highest rates of gene flow to be between neighbouring populations and the lowest between the most distant populations (isolation by distance). Gene flow could not be implied directly from our results because of our inability to define alleles and our resulting reliance on calculation of dissimilarity from phenotypic data only. Pairwise calculations were made to determine the relative amount of variation found within pooled pairs and between them. The results were then compared with geographical distance (log transformed to allow for the wide range of distances used) between the population pairs. A significant positive relationship was found between geographical distance and the amount of dissimilarity shown by the population pairs ($b = -2.98 \times 10^{-2}$; $p(b>0) = 0.035$). The further apart the populations were, the more dissimilar they were. Separating Scilly Isles populations from those on the mainland and performing partial regressions on the results to allow for the fact that populations within each of the two regions are closer to each other than populations in different regions showed highly significant distance and region effects. In other words, the effect of distance between populations (after removing effects due to their

presence in different regions) on their dissimilarity was highly significant ($b = 5.77 \times 10^{-2}$; $p (b > 0) = 0.0014$). Dissimilarity between regions (Scilly Isles and mainland), once distance effects had been removed, was also significant ($b = 4.41 \times 10^{-2}$; $p (b > 0) = 0.0056$).

Although individual populations do hold much of the variation, we might expect that the amount would be reduced as population size decreases so that dispersed, small, populations would be susceptible to gradual loss of genetic variation. A regression of diversity on population size did show a positive relationship ($r^2 = 34.3\%$) so confirming this expectation.

DISCUSSION

The fact that the list of extant sites is shorter than that for former sites suggests a sharp decline in distribution of the species. In some cases the reasons for loss of *Rumex rupestris* from particular sites are quite clear. Drastic habitat modification caused by sea wall construction and cliff consolidation are known to have been instrumental in the decline of *R. rupestris* from sites such as Gunwalloe and may have been major factors in eliminating the plants from sites such as Lelant, Hemmick Beach and Slapton. Elsewhere, erosion, especially under the influence of severe storms, may have been responsible for colony destruction, as appears to have been the case at Ringstead Bay. Plant community development (especially the growth of a closed sward of coarse grasses and herbs) may also have been a contributory factor to the loss of *R. rupestris* from sites such as that at Constantine Bay.

The occasional occurrence of a single plant, or a few, isolated, individuals in sites from which they subsequently disappear may indicate that many populations are inherently ephemeral. Conditions for successful germination and seedling establishment may occur only occasionally, with those plants which do become established surviving for one or several years depending on site stability. At the same time, the appearance of plants in new locations from time-to-time does suggest that either seed banking and subsequent exposure, or seed dispersal, is effective and that seeds do occasionally arrive at suitable germination sites. Such a dynamic situation is not uncommon among species (including *Rumex* spp.) which do bank seed and require re-exposure before they can germinate successfully (Kendrick & Heeringa 1986; Voesenek *et al.* 1992). However, the unstable coastal habitats in which *R. rupestris* grows do not appear conducive to the retention of a persistent seed bank and so the potential for recolonisation will depend on a supply of seed from neighbouring populations reaching suitable germination and establishment sites. Given suitable sites we know from practical experience that seedling establishment is possible. However, as individual populations are extirpated or as conditions lead to the progressive loss of suitable germination or establishment sites, the capacity for replenishment is decreased.

In a species which, with a few exceptions, appears to occur predominantly as small, isolated, populations, there are clearly risks associated with that small population size. Individuals become relatively more important as significant components of the population and the risks of loss of genetic diversity are increased. Isolation will also limit gene flow between individuals in different populations, unless there are effective mechanisms for pollen or seed dispersal, and so reduce the capacity to replace lost variation.

The existence of a high level of genetic diversity within populations and within groups of populations suggests that isolation may not be complete and that each population is a random selection of genes present in a wider gene pool. As the distance between populations, or groups of populations, increases, the possibilities for gene exchange are decreased and local patterns of variation become established. This is shown in particular when the Scilly Isles populations are compared with those on the mainland. When introducing or reintroducing the species to locations it may be more effective to use seed from more than one population in the region of the new site in order to obtain a more complete sample of the variation present in that region. Seed collected from a single (especially a small, single) population may represent only a small part of the variation available in the vicinity of the establishment site.

These results are only preliminary and more work is required: firstly, to develop systems for measuring genetic variation which can be interpreted more accurately in terms of allelic variation; secondly, to determine differences between plants in south-west England and other parts of the species' range; and thirdly, to ascertain whether the high levels of variation found at a local scale are

related to gene flow between individual populations at a local scale or to introgression of genes, for example, from the closely related *R. conglomeratus*.

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The distribution and status of *Corynephorus canescens* (L.) P. Beauv. (Poaceae) in Britain and the Channel Islands with particular reference to its conservation

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ABSTRACT

Corynephorus canescens (L.) P. Beauv. is considered to be a scarce plant in Britain. A description of the plant and its habitat are outlined with a brief account of each site. The local problems in the maintenance of the population at the inland site at Wangford in the W. Suffolk Breckland (v.c. 26) are discussed with accounts of conservation treatments.

KEYWORDS: conservation, sand accretion, *Carex arenaria*, pH range, vegetative spread.

INTRODUCTION

Corynephorus canescens (L.) P. Beauv. (Poaceae) is considered to be a scarce plant (i.e. it occurs in 16–100 10-km squares) in Britain (Trist 1994). This paper is concerned with providing a description of the species and an up-date on its distribution including comments on its habitat, population maintenance and conservation measures.

DESCRIPTION

A densely tufted glaucous perennial of variable life span, 5–30 cm high with fibrous roots. Culms mostly erect, 2–5 noded below the middle. Leaf sheaths inflated, light purple; ligules acute, 2–4 mm; blades numerous, glabrous, stiff, setaceous, inrolled, (1.5)–4–12 cm × 0.3–0.5 mm. Panicles narrow, open at flowering, later becoming dense, 0.8–7 cm × 0.5–1.5 cm, pale green or purple; branches short; pedicels 1–3 mm long. Spikelets lanceolate, compressed, 2-flowered, 2.5–4 mm long, breaking up at maturity below the lemma. Glumes narrow, lanceolate, acuminate, equal or almost so, light purple, membranous, slightly scabrid on the keel, with narrow white tips and margins. Lemmas enclosed by the glumes, 1.5–2 mm long, ovate, with a basal tuft of minute hairs and awned at the base. The awn has two parts, in the middle is a ring of hairs, the lower half is orange–brown and twisted when dry, the apex is club-shaped and is mainly enclosed by the glumes but 0.5–0.8 mm of the length is visible. Paleas about as long as the lemmas. Anthers 1.0–1.5 mm long, mostly deep violet. Chromosome no. 2n = 14.

FIELD RECOGNITION

On close approach, a *C. canescens* colony is seen to consist of small single tufted plants with no grouping or display of a sward. In early July plants can be seen 30 to 40 m distant when the panicles are spreading at anthesis and the colony is a mass of silver and pale pink colour. The stiff pointed leaf blades which form a dense cluster are a bright metallic green with the sheaths a pink-purple colour. In the autumn the tufts die back to a grey colour and the young green leaves grow from a bud

low on the culm which is hidden under the growing plant. A diagnostic feature is the shape and division of the awn.

HABITAT

Nomenclature for vascular plants follows Stace (1997) and for mosses, Smith (1978). *C. canescens* is found on tidal beaches, on fixed and mobile dunes and sometimes on coastal sandy turf: it is also known on isolated inland sandy heaths and dunes. It is essentially a plant of open conditions where wind can move and promote sand accretion around the plants. An internode low on the stem responds with vegetative elongation following partial covering by sand. It does not spread vegetatively and the new elongation only forms a replacement plant. Individual clumps of plants in the Breckland sites are rare outside the immediate area of a colony, as few plants are derived from seed. Its position on the coastal sands is often within 100 m of the tide and well within reach of salt spray and we may assume it has a fair salt tolerance.

Marshall (1967) reported that the habitats range from base poor soils to calcareous dunes within a pH range of 4.0–8.3 and also recorded that it is a plant of substrata which are extremely low in mineral nutrients. At Hedderwick, E. Lothian, v.c. 82, numerous samples were taken at ten stations at a depth of 6–105 cm on beach sand with a high proportion of shells. The pH ranged from 6.0–8.7, with one exceptional pH 9.08 and an outlier off the shells of pH 5.18. At Toigal, Westerness, v.c. 97, an equally high pH 8.3 was taken from a shell dune, which also demonstrated very low mineral nutrients with available phosphorus at 4 mg/l, potassium 9 mg/l and magnesium 7 mg/l. At Wangford, W. Suffolk, v.c. 26, the dunes are of coarse brown very acid sand, with a pH 4.6. The sand is mainly of quartz, stained with iron with a very small fraction of hematite black grains and no organic matter.

In various areas *Corynephorus canescens* is accompanied by a number of different taxa but the number of constant species per site is generally small. *Carex arenaria* is present at most sites and *Ammophila arenaria* is generally present at maritime sites.

CONSERVATION

The study site at Wangford Glebe is 2–5 km from Brandon in the W. Suffolk Breckland and is an S.S.S.I. owned by the Suffolk Wildlife Trust. *Corynephorus canescens* occupies a small fixed dune of 7 × 9 m which in 1995 was c. 80 per cent bare sand and invaded by *Carex arenaria* on all sides. *Agrostis vinealis* is its main constant species with a little *Polytrichum piliferum* occurring with *Cladonia* spp. It has recently been noticed that the annual disturbance caused by sand spreading is having the effect of reducing the *Cladonia*.

This site was found by M. G. Rutherford and myself in January 1970 (Trist 1971) and at that time it was thought to be extinct in Breckland. This find was then the only known inland site of *Corynephorus canescens* in Britain. Hind (1889) notes that Druce and Bolton King recorded *C. canescens* in July 1883 "between Lakenheath and Wangford". Druce also collected specimens from the same site in August 1883 (OXF). This site clearly refers to the part of Lakenheath Warren now occupied as Lakenheath Airfield, where several large colonies of *C. canescens* survive.

Wright (1668) recorded severe sand storms in Breckland, which may have caused the large blow-out on Wangford Glebe. Sand storms still occur on arable land in Breckland and can do severe damage to recent seeding and pile up sizeable ridges of sand, but the storms are probably not so fierce as in the past. The taming of the wind has considerable significance in relation to the present conservation management of *C. canescens*. Some 70 years ago, the area from Lakenheath to Brandon was a vast open sandy heath with few trees and subject to frequent wind erosion. Large conifer plantings by the Forestry Commission in the 1920s have grown into mature trees and halted the distances over which erosion takes place, although it can still occur on the Wangford dunes which represent the last of the sites of active erosion in Breckland. This increasing wind protection has halted sand erosion around the Wangford colony of *C. canescens*. So active erosion is being effected by the Trust with annual rotovations in certain areas of the reserve. This colony is above a line of underground spring water which runs from a known site in the forest on the east of the reserve and follows its northern boundary to discharge eventually into the Wangford drain. This latter is over 3 m deep and in July 1992 was dry. The source of this water is probably

being diminished by a deep bore pump within 1·5 km of this site. As proof of its line, there were two very small colonies of *Juncus squarrosum* and a dozen or more plants of *Juncus effusus* which thrived in a water fed zone over an iron pan within the blow-out area and near the northern boundary of the reserve. An area some 250 m away in the centre of the reserve had up to 15 old tussocks of *Carex paniculata* and a bed of *Calamagrostis canescens*; these plants were no longer found after c. 1984. This loss of moisture is an additional factor in the conservation of the *Corynephorus canescens* site as it is encouraging the invasion of *Pteridium aquilinum*, *Deschampsia flexuosa* and *Carex arenaria*, all of which are increasing in the area of the *C. canescens*. The one-time open habitat requires management or it will be invaded to the exclusion of *C. canescens*. When the colony of *C. canescens* was first found in 1970, 231 plants were recorded. No detailed recording took place in the following years, but observations between 1972 and 1974 showed the population had apparently declined to about 150 plants. In the autumn of 1975 a count revealed that the population was reduced to 112 plants. It had been a dry summer and a few seedling plants were noted. A few of the dried up plants were showing young vegetative growth (Trist 1980). At this time, there was no sand movement by wind in the area of the *C. canescens* colony.

Marshall (1967) had noted that *C. canescens* is found in disturbed or open sandy places where up to 10 cm per year of accretion takes place: and while the adult plant cannot withstand complete burial, it responds to partial burial by vegetative elongation. Accordingly, in the autumn of 1975, artificial sand accretion was introduced by cutting a wide trench at the foot of the *Corynephorus canescens* sand bank to aid wind disturbance of sand. In addition, a good covering of sand was spread over the colony. This was repeated in the autumn of each year up to 1978. In Trist (1980) the report showed a count of 422 plants which I now consider inaccurate. The 232 yearling plants would be accurate but, "a further 190 flowering tufts, many of which were developing new vegetative shoots" should be disregarded. The total count should have been assessed at about 250 plants.

The management of the colony has both changed and lapsed. Between 1978 and 1992 no sand was applied to the plants and no counts were made until 6 February 1992 when 226 plants were recorded. The area was sanded on 7 March 1992. The next count was made on 17 June 1993 and showed 254 plants. Sand was again applied on 19 November 1993 and a count taken on 7 September 1994 revealed 265 plants. Later I did not feel satisfied that this was an accurate record, as at the time I recalled there were some plants in the process of dying back which were not showing the tuft of new leaves at the stem node. On 3 November 1994, a further count gave a total of 304 plants. The summer of 1995 was hot and dry and on 29 November 1995, a count of 142 plants also proved an inaccurate record, as there was an unusual number of seedling plants of *C. canescens* and other grasses which could not be separated at the young stage. Recording in September 1996 gave 303 mainly small plants with only one seed head.

Rabbits may play a small part in the conservation of *C. canescens*. They will eat young shoots of *Carex arenaria* but as long as other food is available, their attention to *C. canescens* is confined to biting off a few inflorescences which matters little as the loss of potential seed is probably of little account. At Wangford, propagation of the species is mainly by vegetative elongation. Since this colony was found in 1970, we have always had rabbits in residence. In 1995 there were two active burrows, the occupants of which contributed to sand disturbance.

The conservation of *C. canescens* is complicated. Some problems may be resolved while the solutions to others are impracticable and some not possible. The inland sites are subject to changes of their immediate surroundings by agriculture and other land uses. I agree with Marshall's (1967) conclusion that "many of the present day European communities of *Corynephorus canescens* owe their existence to human interference". This comment aptly applies to past and present events at Hedderwick, Lossiemouth, Kessingland and Lakenheath, which are recorded below. The coastal sites are at all times open to the threat of gales and tidal erosion.

SITE DESCRIPTIONS

THE COASTAL SITES

Suffolk has three coastal sites. These are considerably smaller in area and in population than those of Norfolk. At Minsmere Haven the area of 40 × 3 m is a restored site c. 230 m from the foot of

Minsmere cliffs. The former site on dunes near the base of the cliffs was destroyed in the sea floods of 1953. This new colony comprises 250 plants on the landward side of a sand bank between the boundary ditch of the R.S.P.B. reserve and the beach shingle ridge. The site is still within danger of a high tide. In 1992 the colony had no constant species.

At Kessingland our plant is sparsely spread out over beach sand and has to tolerate the summer activity of an adjacent holiday camp. *Catapodium marinum*, *Phleum arenarium* and *Vulpia bromoides* are scattered associates.

The site on the beach near Benacre Broad is spread over c. 0.16 ha. This colony flourishes in spite of considerable tidal approach as the land by the east coast inclines. In the past 30 years some gale force tides have crossed the beach to the land.

The Norfolk coastal sites are extensive, on tidal beaches and on hinterland dunes. Their total population of *C. canescens* would number many thousands. From Great Yarmouth dunes where this grass is abundant, north up the coast to Caister-on-Sea, the line of plants is almost continuous on the beaches for nearly 3 km. Just beyond the Caister lifeboat station, *C. canescens* colonises narrower dunes within the Caister golf course for a distance of c. 200 m. Our plants again occur to the south of Winterton-on-Sea where they also colonise hinterland dunes in comparative shelter where *Ammophila arenaria* and *Carex arenaria* are abundant. It is here that the dispersal of *C. canescens* is noticeable and which appears to indicate moisture competition with the above two species. From Winterton our plants continue north-east to Horsey Common and then abruptly stop. They reappear at Blakeney where there is a scattered population from west to east over to Blakeney Point, a distance of c. 800 m where our plant is frequent on grey dunes. There was a colony on the beach at The Hood, Blakeney which has a long and difficult approach over shingle. There are no recent records.

The constant species of the various sites north of Great Yarmouth up to Blakeney are fairly similar. *Jasione montana*, *Hypochaeris radicata* and *Rumex acetosella* are frequent and often with *Festuca arenaria*. Beyond the Caister lifeboat station the dunes are smaller and *Jasione montana* is replaced by *Campanula rotundifolia*. At Holme-next-the-Sea our plant occupies a small open dune on a slope surrounded by *Ammophila arenaria*. Some *Corynephorus canescens* is seen at the base of the slope within reach of high tides as indicated by *Glaux maritima* and *Silene uniflora*. The colony has a population of c. 300–400 plants.

All of the Norfolk sites are much exposed to wind erosion and several stretches of *Corynephorus canescens* between Great Yarmouth and Caister are occasionally subject to tidal wash. A large percentage of the colonies are remote and difficult of access.

The Ainsdale site on the S. Lancashire coast is on private ground on the boundary of the Ainsdale and Southport golf links and is a recent find of c. 1980. Its position partly within the golf course makes it locally safe. It is 1.5 km from high water on the coast and has a railway line and another golf links between it and the sea. Two former sites of *Corynephorus canescens*, at Formby, 6 km south of Ainsdale, have been lost by erosion, but at Ainsdale, accretion is now active and rabbits are contributing to the sand accretion requirements of *Corynephorus canescens*. Here the site is c. 100 × 4 m where our grass is dominant on two fixed dunes and has only *Hypochaeris radicata* and *Ornithopus perpusillus* as constant species. It is described by Savidge *et al.* (1963) as native. They record that there were formerly two sites between Formby and Freshfield in 1930, of which one became extinct in 1937 and the other was subsequently tidally eroded.

The site at Hedderwick near Dunbar is a recent discovery of 1986 by Anna Younger and is considered an introduction. The area is a raised beach of blown sand with a fairly high proportion of shells which is reflected in the soil analysis. The site has been subject to much disturbance in the recent past from sand extraction to use as a tank training ground. The plants were found in two dune bays which were surveyed in 1995 and found to have at least 275 clumps in the main bay of c. 5 m diameter and 35 clumps in the other bay of 1 m diameter. The site is enclosed by *Pteridium aquilinum* with some *Ammophila arenaria* colonising the east end. If the advances of these taxa can be held in check, the site is probably safeguarded. The constant species at Hedderwick are different as here we find *Arenaria serpyllifolia*, *Erodium cicutarium*, *Sedum acre* and *Thymus polytrichus*. One area is being colonised with a low mossy turf of *Brachythecium* sp., *Tortula* spp. and including a *Peltigera* sp.

At Lossiemouth, Morayshire is another introduced site, which is in a disused gravel pit, where 2000 plus plants occupy an area of c. 20 × 14 m. The plants are on a steep bank with *Pilosella*

officinarum and *Hypochaeris radicata*. Another colony by a caravan site has a similar number of plants but spread over a wider area; those on sandy heath have *Erica cinerea*, *Calluna vulgaris* and *Lotus corniculatus* as companion species.

The single plant of *Corynephorus canescens* found at Toigal by Morar, West Inverness-shire (Trist 1992) was on low dunes of highly mobile white sand on the shore of the tidal R. Morar. It was outnumbered by its constant species which included a single plant each of *Aira praecox*, *Rumex acetosella* subsp. *acetosella* and *Carex arenaria*. A few paces away was a small dune with a solitary plant of *Calluna vulgaris*. This was once a thriving colony which may have been introduced to this site. It was first found by F. Townsend in 1895 and now only a single plant bears witness.

The Jersey, Channel Islands, sites are all found in the south-west of the island on coastal dunes and where some of the colonies are extensive and would experience salt spray from high tide. The dunes at St Ouen are relatively flat compared with those of Les Quennevais which attain a little height where the sands are deep and are the largest systems on the island. These latter calcareous dunes of broken down shells are remarkably rich in species which include *Bupleurum fruticosum*, *Hornungia petraea*, *Rosa pimpinellifolia* and *Viola kitaibeliana* with large colonies of *Corynephorus canescens*. On the dunes at Les Quennevais and L'Ouaisné, *Lagurus ovatus* and *Poa bulbosa* are frequent.

THE INLAND SITES

One of the *Corynephorus canescens* sites in W. Suffolk is on Lakenheath Airfield where there are two stations. One is extensive and spread over an area of c. 0.4 ha which overlaps the parishes of Lakenheath and Wangford. The other, in the parish of Lakenheath, is c. 0.2 ha. The former has a population exceeding 5000 plants and the latter c. 500 plants. The site was formerly part of Lakenheath and Wangford Warrens which lie to the west of the A1065 road. It had been sheep grazed from early medieval times to 1942 when it was requisitioned by the Ministry of Defence. It was also an extensive rabbit warren for 700 years and there is some evidence of former cultivation (Crompton 1975). This western part of Lakenheath Warren was occupied by a series of dunes up to 1 km in width in the 1930s, with some dunes up to 6 m in height (Watt 1936). Following requisition, the dunes were destroyed and the entire area bulldozed flat and prepared for an airfield. The *C. canescens* recorded here is a relict of the find by Druce (1883, OXF) and the rediscovery by Crompton (1980). These airfield sites are mown twice monthly in the season and, in spite of this record of disturbance, a number of species survive. The large area contains *Agrostis vinealis*, *Crepis capillaris*, *Campanula rotundifolia*, *Galium verum* and *Silene otites*, while the smaller areas contribute *Coronopus squamatus*, *Festuca ovina* subsp. *hirtula* and a large colony of *Thymus serpyllum*.

The other site in W. Suffolk is also in the adjoining parish of Wangford. It lies 2 km north-east of the Airfield sites and 60 years ago would have been part of the huge dune system on the warren. This site is fully described under conservation at Wangford Glebe.

At Kinver Edge, which lies south-west of Kinver, Staffordshire, there are two sites of *C. canescens* which are c. 170 m apart and separated by an area of gorse, scrub oak and birch. The soil is a pebbly red sandstone with pH 6.7 which lies over Triassic Bunter Pebble Beds. The plants were found on a gentle slope of open semi-stable sand at 130 m. The constant species include seven mosses and three lichens with 24 higher plants which include *Calluna vulgaris*, *Deschampsia cespitosa*, *Erica cinerea*, *Luzula campestris* and *Teucrium scorodonia*. The site has been the property of the National Trust since 1917 and is c. 80 ha in extent. Although it is near to dwellings there is no encroaching urbanisation. The conservation of these two sites is related to passing walkers who are probably mainly responsible for sand compaction and so preventing accretion about the *C. canescens*. The population of c. 500 plants has remained fairly constant since 1977. The site is warded and protective action is taken.

The Worcester sites consist of five colonies separated along the Severn Valley Railway, south of Devil's Spittleful where three of the sites are on the track side with two small colonies and a third site reported in 1991 to have an "abundant colony". Devil's Spittleful is under the care of the local District Council as a Nature Reserve. Two other sites are found on the embankment where, in 1989, a field meeting recorded "several plants", and a "large local area" reported in 1995. Another is located on Burlish Top which is c. 500 m south of the railway, where it was reported "locally

common" in 1989. The sites are within an extensive area of sand covering an area 2×2 km and provide sandy tracks, heath and embankment habitats. The *C. canescens* plants spread along the rail track have originated from the adjacent sandy heath.

It seems clear that these several small locations of *C. canescens* represent a relict of a one-time large open area of sand which over time has become fragmented and buried under the neighbouring towns. *Silene conica*, which is now largely confined to East Anglia, has survived on Hartlebury Common since its discovery in 1900 and this site is within a few kms of the Devil's Spittleful *C. canescens* locations. *Teesdalia nudicaulis* is still frequent, but *Rosa pimpinellifolia* and *Erodium maritimum* found on these sites in recent years are now extinct. Our plant is carefully monitored by the vice-county recorder.

To give some interpretation of the present day inland and coastal habitats of *C. canescens*, we may consider the maritime sand habitats of the grass *Elytrigia repens* subsp. *arenosa*, which has a defined north-western European distribution which includes the east and south coasts of Britain (Trist 1995); it also occurs on heathland and sandy arable land in the Mainz area of Germany. On this extensive inland sand area many of the local taxa are also common to the sands of the W. Suffolk Breckland; both contain *C. canescens* and more than 20 other grasses (Hecker 1987). With the exception of those sites which are known or believed to be introductions, we may regard the W. Suffolk, Staffordshire and Worcestershire sites as relict areas which have resisted erosion.

THE DISTRIBUTION OF *C. CANESCENS* IN BRITAIN AND THE CHANNEL ISLANDS

E. Suffolk, v.c. 25. Dune at rear of beach, Minsmere Haven, TM/479.674, 18 July 1992, P. J. O. Trist; beach near Benacre Broad, TM/534.841, July 1995, P. Lawson and Y. Leonard; the shore, Kessingland Beach, TM/535.857, 7 June 1991, P. J. O. Trist.

W. Suffolk, v.c. 26. Fixed dunes, Wangford Glebe, Brandon, TL/757.843, 15 July 1994, P. J. O. Trist; heathland west of main entrance to Lakenheath Airfield, TL/745.809 and adjacent to runway, south of Wangford Farm buildings, TL/748.827–749.828, 18 July 1995, Y. Leonard and P. J. O. Trist.

E. Norfolk, v.c. 27. Coastal dunes, North Denes, Gt Yarmouth, TG/533.090 and uninterrupted on dunes north to the Lifeboat station, Caister-on-Sea, TG/528.118 and continuing north and through the Caister golf course to TG/527.122, 5 September 1995, A. Bull; mobile dunes, Winterton-on-Sea, TG/502.190, 10 September 1992, P. J. O. Trist; north to Warren Farm, north-east of Horsey Corner, TG/460.247, 5 September 1995, A. Bull; grey dunes, Blakeney Point, TG/000.465–008.465, 4 September 1994, A. Bull.

W. Norfolk, v.c. 28. Coastal dunes, Holme next the Sea, TF/705.445, 13 June 1995, G. Beckett and P. J. O. Trist.

Worc., v.c. 37. Severn Valley Railway track adjacent to Devil's Spittleful, south-east of Wyre Forest, near Kidderminster: a. railway track side, Wribbenhall Junction, SO/798.749, 6 August 1991, R. Maskew and W. A. Thompson; b. railway trackside, SO/809.745–810.745, 6 August 1991, W. A. Thompson; c. railway embankment, SO/805.746, 30 July 1989, Worcs. Flora meeting; d. railway track side, SO/826.750, 29 June 1995, R. Maskew and W. A. Thompson; e. railway embankment, SO/832.752, 29 June 1995, R. Maskew and W. A. Thompson; sandy heath on Burlish Top, south-east of Droppingwells Farm, south-west of Kidderminster, SO/810.739–811.741, 30 July 1989, Worcs. Flora meeting.

Staffs., v.c. 39. Sandy track side, Kinver Edge, south-west of Stourbridge, SO/834.827–834.825, October 1995, B. R. Fowler.

S. Lancs., v.c. 59. On sand boundary with Ainsdale and Southport golf links, SD/318.127, 28 June 1994, V. Gordon.

E. Lothian, v.c. 82. Sandy turf by the estuary at Hedderwick Hill Plantation, John Muir Country Park, west of Dunbar, NT/642.789, 3 September 1995, H. Jackson and A. Silverside.

Moray, v.c. 95. Disused gravel pit, south of Lossiemouth, NJ/231.694, 24 July 1992, J. Edelsten and D. Law; caravan site on coast east of Lossiemouth, NJ/239.699, 24 July 1992, J. Edlesten and D. Law.

Westerness, v.c. 97. Mobile dunes, Toigal by the estuary of the R. Morar, near Arisaig, NM/674.922, 24 July 1991, A. Slack, E. Norman and P. J. O. Trist.

Channel Isles, v.c. 113. Jersey, coast dunes, Ouaisné, St Brelades Bay; coast dunes, La Pulente, St Ouen's Bay; coast dunes, La Carrière, St Ouen's Bay; higher interior dunes, Les Quennevais. All sites reported June 1995, J. Banks.

GENERAL DISTRIBUTION

Britain to S. Baltic and to S. Portugal, N. Italy and across to Central Ukraine, local in the eastern part of its range.

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Hybrids of *Epilobium brunnescens* (Cockayne) Raven & Engelhorn (Onagraceae) and their occurrence in the British Isles

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ABSTRACT

Data are presented on the occurrence of five new hybrids of *Epilobium brunnescens* (Cockayne) Raven & Engelhorn (Onagraceae) growing wild in the British Isles. Descriptions are given of *E. brunnescens* × *ciliatum*, *E. brunnescens* × *lanceolatum*, *E. brunnescens* × *montanum*, *E. brunnescens* × *obscurum* and *E. brunnescens* × *palustre*. These are named respectively as *Epilobium* × *brunnatum* Kitchener & McKean hybr. nov., *E.* × *cornubicense* Kitchener & McKean hybr. nov., *E.* × *confusilobum* Kitchener & McKean hybr. nov., *E.* × *obscurescens* Kitchener & McKean hybr. nov. and *E.* × *chateri* Kitchener & McKean hybr. nov. Records of *E. brunnescens* × *ciliatum* and *E. brunnescens* × *montanum* in the British Isles are re-evaluated.

KEYWORDS: hybridization, willowherbs, New Zealand.

INTRODUCTION

Epilobium brunnescens (Cockayne) Raven & Engelhorn (New Zealand Willowherb) (Onagraceae) has long been naturalized in the British Isles. It was first recorded in 1904 at Craigmillar, Edinburgh, as a garden weed (Fraser 1905). It has been suggested that *E. brunnescens* was probably introduced into Britain for planting in rock gardens where it may have become a rampant weed. It was also brought in with wrappings and soil attached to other New Zealand plants. Its gradual spread accelerated from the 1930s (Davey 1953, 1961) and it now has a substantial presence in those parts of the British Isles whose high rainfall and humidity approximate best to its New Zealand habitats, where it is “especially common on shingly riverbeds in areas of high rainfall” (Webb *et al.* 1988). Its corresponding habitats in the British Isles are in the west and north or in upland areas: moist open areas, on gravel, gritty or stony soils, streamsides, ditches, paths, scree, damp stone walls and banks. Outside Britain, Ireland and its native home, *E. brunnescens* is also reported from Norway as a rarity and mainly as a garden weed. Although originally reported there in 1931 (Davy 1961) it has not become invasive as in Britain and Ireland. Although *Epilobium ciliatum*, *E. montanum*, *E. obscurum* and *E. parviflorum* (but not *E. lanceolatum* or *E. palustre*) have been, or are, found in New Zealand, only *E. ciliatum* has, as yet, been reported as having hybridized in the wild there with *E. brunnescens* (Raven & Raven 1976). The nomenclature used here follows that of Stace (1991) and Kent (1992).

ARTIFICIAL HYBRIDIZATION

Some data are available as to the synthesizing of hybrids between *E. brunnescens* and *Epilobium* species present in Britain. Brockie (1966) succeeded in crossing *E. brunnescens* (sub nomine *E. pedunculare*) with *E. ciliatum* (sub nomine *E. erectum*). From the progeny, an *F*₂ generation was raised. Brockie (1970) also reports an attempt by V. Thakur in the 1960s to cross *E. brunnescens*

(sub nomine *E. nerterioides*) with *E. montanum* in both directions, but with failure to set seed. It should not be assumed that this is evidence of a significant barrier against cross-fertilization, for it is not clear that enough attempts were made to effect good fertilization. Raven (1972) considered the failure of good seed set reported by Thakur and Brockie (1970) and concluded that there was no evidence for failure of good set as a barrier to hybridization between Australasian species of *Epilobium*. He also considered that there was no definite evidence for the operation of such a barrier between any two species of sect. *Epilobium* from anywhere in the world, with the possible exception of short styled small flowered species being incompatible with long styled large flowered species.

THE IRISH RECORDS

Northern Ireland accounts for the first records of *E. brunnescens* hybrids in the British Isles, but these have been the source of considerable confusion. Scannell & Synnott (1987) mention *E. brunnescens* × *ciliatum* and *E. brunnescens* × *montanum* as being present in v.c. H39. The former record is elaborated by Hackney (1992), who refers to *E. brunnescens* × *ciliatum* as being "abundant with both parents". The latter record relates to the specimen which resulted in "*E. brunnescens* × ?*E. montanum*" (sic) being credited to the flora of the British Isles by Stace (1991).

We have examined the relevant specimens (**BEL**) and it appears to us that the specimen determined as *E. brunnescens* × *ciliatum* is *E. brunnescens* × *obscurum*, together with a number of other plants (E) from the same location; the specimen determined as *E. brunnescens* × *montanum* is probably *E. brunnescens* × *ciliatum*.

All these records related to finds at the spoil tips of a quarry at Magheramorne, near the shore of Larne Lough in Co. Antrim (v.c. H39). A series of hybrid specimens were collected by D. Ledsham in 1980, and these now form three sheets held at E. Although sent for identification in 1981, they were unfortunately mislaid until 1994, when they were identified by one of us (D.R.M.) as *E. brunnescens* × *obscurum*, this being confirmed by T. D. Pennington.

Two subsequent collections were made from the same locality. The first, in 1981, was made by D. Ledsham and D. Getty, tentatively identified by C. A. Stace as *E. brunnescens* × *montanum* and so confirmed by P. H. Raven in 1982 (specimen held at **BEL**). An unqualified determination by Raven must carry considerable weight of authority, but this is difficult material. The flowers of such a cross may be expected to bear "confused" stigmas, i.e. almost clavate, but with traces of lobing (resulting from crosses between parents with four-lobed and clavate stigmas). The absence of these is not conclusive, because stigma-shape may vary on the same plant, but examination in 1996 of the most developed flower on this material (H8544) showed a clavate stigma. This suggests either *E. obscum* or *E. ciliatum* as the other parent; the latter is more likely on the basis of stem and capsule hair characters.

Further evidence lies in the fact that *E. montanum* was altogether absent from the site, whereas *E. ciliatum* was frequent (fide D. Getty; P. Hackney, pers. comm., 1993). On the strength of this, *E. brunnescens* × *ciliatum* is given in the current local Flora (Hackney 1992), instead of *E. brunnescens* × *montanum*. The two different determinations of the same single specimen, however, have resulted in both hybrid taxa being recorded in Scannell & Synnott (1987).

The second collection (**BEL**) was made in 1983 by R. Piper and was, following the redetermination of the 1981 collection, tentatively determined by Getty and Hackney as *E. brunnescens* × *ciliatum*. The very limited presence of glandular hairs in the upper parts, however, points to this material being *E. brunnescens* × *obscum*, as with the bulk of the specimens from this site.

A further Irish discovery of *E. brunnescens* × *obscum* was made by J. McNeill (det. D.R.M.) in 1992. This is represented by a fragmentary specimen at E, part of a stem curving from a prostrate to semi-erect position. It was found in the Glenelly valley in the Sperrin mountains in Co. Tyrone (v.c. H36) in the company of *E. brunnescens*, *E. obscum*, *E. montanum* and *E. palustre*.

THE BRITISH RECORDS

E. brunnescens × *ciliatum* was first recorded in Britain during 1995, in v.cc. 1, 2 and 44. In June 1995, A. O. Chater (pers. comm., 1995) noted about 100 plants on a gravelly and stony quarry slope

near Llansawel, Carms. (v.c. 44), three specimens from this population being confirmed as such by T. D. Pennington.

In July 1995, about 20 plants were located by D. T. Holyoak (pers. comm., 1995) on mine waste at Wheal Maid, near United Downs, West Cornwall (v.c. 1). A further plant was found by R. J. Murphy (pers. comm., 1995) and H. Meredith at the end of that month on china clay gravels at a disused tip at Goonamarris near Nanpean, East Cornwall (v.c. 2).

The United Downs locality was re-investigated by D. T. Holyoak (pers. comm., 1996) in July 1996, and while *E. brunnescens* × *ciliatum* was present in its usual small, red, semi-prostrate form, there were two near-erect plants, much larger and well branched. These are discussed in the comparison below. In the same month, he discovered six more specimens of this hybrid on mine spoil at Wheal Busy, West Cornwall (v.c. 1) – these have not been examined by us. Also in July 1996 one of us (G.D.K.) found six further plants, again on china clay gravels: three south of Burngullow Common, and the other three at Carclaze Downs pit, both locations being near St Austell, East Cornwall (v.c. 2).

E. brunnescens × *lanceolatum* was first discovered by D. T. Holyoak in July 1995 as a single small plant in the same United Downs location, being also in the company of *E. brunnescens*, *E. ciliatum*, *E. hirsutum*, *E. lanceolatum*, *E. montanum*, *E. obscurum*, *E. parviflorum*, *E. ciliatum* × *montanum* and *E. ciliatum* × *parviflorum*. The presence of *E. lanceolatum*, and hence its potential as a parent, was not recognised until the next year and so, unfortunately, this record was mistakenly published by one of us (Kitchener 1996) as *E. brunnescens* × *montanum*. The southern distribution of *E. lanceolatum* in Britain renders it unlikely that *E. brunnescens* × *lanceolatum* would be found other than in Cornwall, Devon or South Wales. A further specimen was located by D. T. Holyoak in July 1996, again at United Downs, West Cornwall (v.c. 1).

E. brunnescens × *montanum*, discounting the supposed Irish records mentioned above, was first found in the British Isles in July 1996 by one of us (G.D.K.) with R. J. Murphy and M. & A. Atkinson, growing on imported granite aggregate and rubble at Clicker quarry near Liskeard, East Cornwall (v.c. 2).

E. brunnescens × *obscurum* was first recorded in Britain in East Cornwall (v.c. 2), again from Clicker quarry, where R. J. Murphy discovered it on the occasion, and with the people, mentioned above (M. Atkinson having observed potential *E. brunnescens* hybrids there in the previous year). Also in July 1996 in v.c. 2, one of us (G.D.K.) found three plants on china clay gravels: two at Carclaze Downs pit, and a further one in a china clay pit north east of Stenalees.

E. brunnescens × *palustre* was first recorded in the British Isles by A. O. Chater in August 1995, growing on damp acidic shaley soil by a forestry road in a conifer forest near Hardro, Llyn Brianne, Cards. (v.c. 46). *E. palustre* was growing nearby, and the specimen has been confirmed by T. D. Pennington.

DESCRIPTIONS OF TAXA

Material from all the collections listed above has been examined by us in the compilation of the following descriptions unless otherwise stated.

Epilobium × *brunnatum* Kitchener & McKean, hybr. nov.

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. ciliatum* Raf.) (Fig. 1)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. ciliatum* Raf., characteribus inter parentes variantibus; planta semi-prostrata, stigmatibus clavatis, seminibus praecipue sterilibus, eorum pagina plerumque tuberculato-costata, et in ovario pilis numerosis glandulis praeditis, aliquot pilorum ad pedicellum subtentum extensorum.

Herb with prostrate leafy runners, with stems much branched, curving up to an erect position, 8–20(–30) cm high and little branched above, except in cultivation, when growth habit is more erect and branched. Stems with two lines of short crisped hairs, descending from the nodes, and beginning between a pair of petioles and descending to the next node; the hairs become generally scattered on the stem upper parts and may be absent near the base. Leaves mainly opposite but largely alternate in the upper parts, green on younger growth, especially the upper surface; sessile or with petioles not exceeding 1.5 mm; cauline leaves (0.5–)0.8–1.2(–2.3) × (0.3–)0.4–0.6(–1.1) cm, average ratio of

length to breadth 1:0·4–0·5; ovate-lanceolate to elliptic with a few obscure teeth, glabrous except for marginal pubescence; leaves on runners similar, but tending to more elliptic shape. Sepals lanceolate, 2·5–3·0 × 0·7–1·2 mm, bearing crisped and glandular hairs. Flowers very pale pink, rarely darker c. 9 mm diameter, with petals 5–6 mm long. Four long stamens projecting to or just below top of stigma, their anthers being 0·55–0·85 mm long; four short stamens extending as far as stigma base. Ovary 0·7–1·8 cm, covered with dense patent glandular and crisped eglandular hairs, the glandular hairs extending to, but comparatively infrequent on, the pedicels. Stigma entire, clavate, 1·2–1·9 mm; style longer than stigma, erect, white, 1·3–2·8 mm. Capsules 1·2–3·0 cm long, with hairs as for ovary, sometimes twisted and shrivelled, mostly sterile, containing shrunken abortive seeds 0·34–0·47 mm long; also contained are a few larger seeds, either malformed (0·6–0·7 mm) or fully formed and fertile (0·8–0·9 mm) with rows of tubercles, often with the surface texture tending towards the ridged rows of *E. ciliatum*. The larger seeds may bear a short neck or appendage at the point of attachment of the coma.

HOLOTYPUS: West Cornwall, v.c. 1, Wheal Maid, near United Downs, grid reference SW/745.420, on mine waste, alt. 100 m, 5 July 1995, *D. T. Holyoak* (**E**).

A wild population of this hybrid was seen by P. H. and T. E. Raven in 1969 or 1970 in New Zealand at the Whangaehu River, and they also note a collection from Canterbury, New Zealand in 1919 which is probably the same hybrid (Raven & Raven 1976).

***Epilobium × cornubiense* Kitchener & McKean, hybr. nov.**

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. lanceolatum* Sebast. & Mauri)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. lanceolatum* Sebast. & Mauri, characteribus inter parentes variantibus; planta semi-prostrata stigmata lobis confusis ferens, caulis pilis crispatis brevibus uniformiter obtectis, et floribus in colore ut minimum aliquot spectri colorum *E. lanceolati* exhibentibus.

Herb with stems curving up to erect position, 6·5–25 cm high, little branched above except for larger stems, and with a fairly uniform covering of short crisped hairs. Leaves opposite, largely alternate on inflorescence, reddish, sessile or with petioles not exceeding 1 mm; caudine leaves 0·5–1·1(–1·5) × 0·7(–0·9) cm, average ratio of length to breadth 1:0·57–0·63; basal leaves crowded; leaves ovate to broadly elliptic with a few obscure teeth, glabrous except for marginal pubescence and a few hairs on the underside midrib. Sepals lanceolate, 2·8–3·5 × 1·9–1·4 mm, bearing short crisped and patent glandular hairs. Flowers white, pale pink or very pale pink, and the colour may vary on the same plant, but not on the same flower; with petals c. 5 mm. Four long stamens extending to, or just below stigma, their anthers being c. 0·6 × 0·35 mm; four short stamens well below stigma. Ovary 1·2–1·9 cm, covered with many short crisped hairs and some patent glandular ones, a few of the latter descending to the pedicels; hair coverage of pedicels less dense than that of upper stem (in contrast to *E. × brunnatum*). Stigmas variable, with confused partial lobing 0·8–1·0 mm; style 3·5–4 mm. Capsule 2·2–3·1 cm, mostly sterile, containing shrunken abortive seeds 0·35–0·5 mm long, their surface with rows of platelets, sometimes reticulate; seeds occasionally fully formed, cylindrical, 0·65–0·95 mm with rows of tubercles.

HOLOTYPUS: West Cornwall, v.c. 1, Wheal Maid, near United Downs, grid reference SW/745.420, on mine waste, alt. 100 m, 12 July 1995, *D. T. Holyoak* (**E**).

***Epilobium × confusilobum* Kitchener & McKean, hybr. nov.**

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. montanum* L.)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. montanum* L., characteribus inter parentes variantibus; planta semi-prostrata, stigmata lobis confusis ferens, caulis pilis crispatis brevibus uniformiter obtectis, et floribus coloris pallide purpureorosei.

Herb with stems branched at ground level, creeping at first, and then curving up to erect position, 5–10 cm high, scarcely branched above, and with a fairly uniform covering of short crisped hairs, diminishing in upper parts, and with occasional glandular hairs. Leaves opposite, largely alternate on inflorescence, pubescent petioles not exceeding 1(–1·5) mm; caudine leaves 0·5–1·0 × 0·25–0·5 cm, average ratio of length to breadth 1:0·45; basal leaves crowded; leaves ovate to broadly elliptic with a few obscure teeth; short crisped hairs on underside midrib and veins, with a light scattering elsewhere beneath, pubescent on margins; upper leaf surface varying from pubescent (especially on young growth) to glabrescent. Sepals lanceolate, 1·45–2·90 × 0·73–1·02 mm, with a scattering of

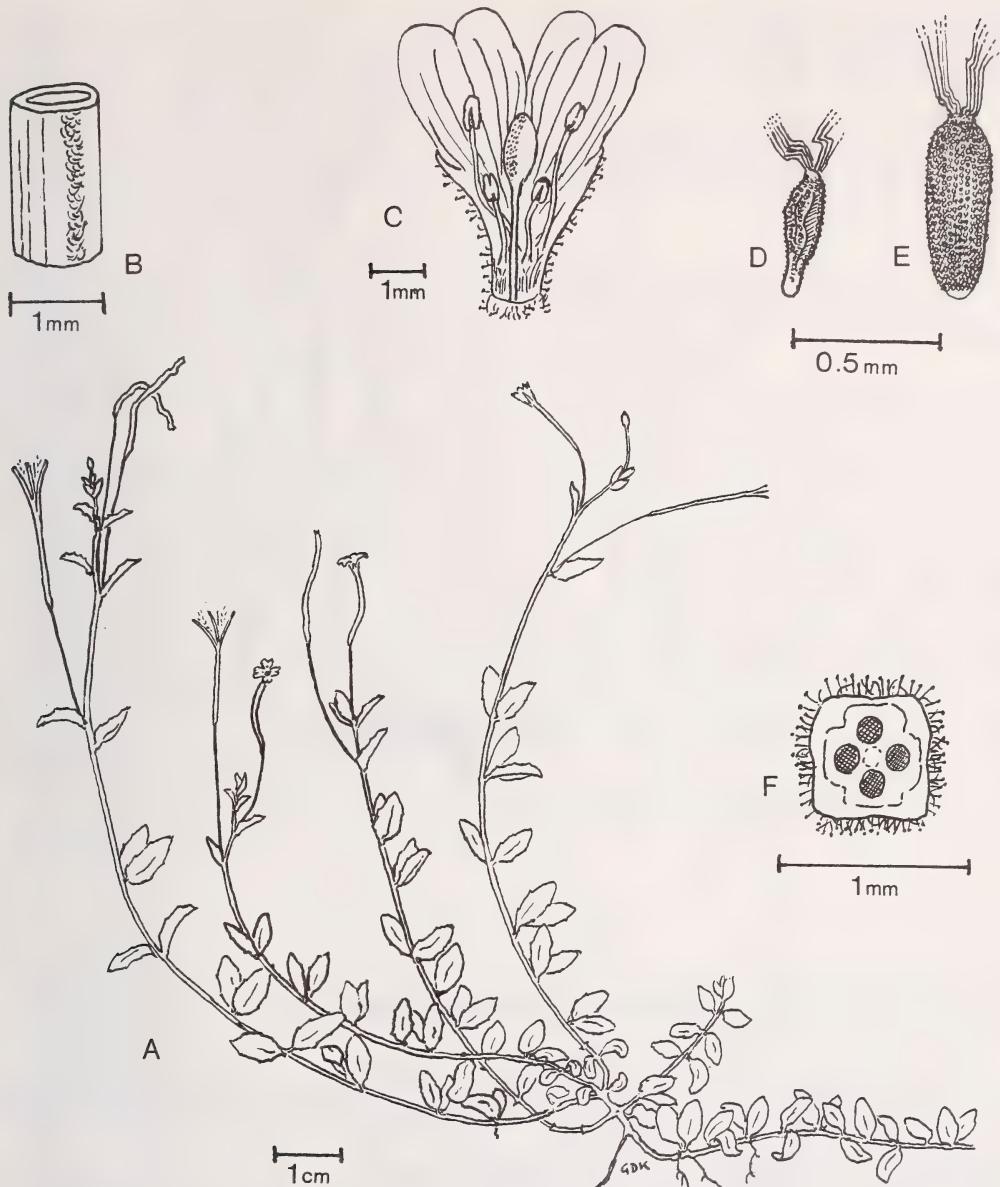


FIGURE 1. *Epilobium × brunnatum*. A. plant; B. mid-stem; C. flower (half cut away); D. sterile seed; E. fertile seed; F. transverse section of ovary.

glandular hairs. Flowers pale purplish pink, with petals c. 3.5 mm. Four long stamens projecting to top of stigma, their anthers being 0.4–0.5 × 0.3–0.35 mm; four short stamens extending to the mid-level or base of stigma. Ovary 0.7–1.25 cm, with lines of dense short glandular hairs, these hairs being scattered down the pedicel also. Stigma with confused partial lobing; style longer than the stigma. Capsule 1.6–2.6 cm, containing shrunken abortive seeds 0.35–0.45 mm long, surface flattish, marked in rows and sometimes bearing low tubercles; occasional larger seeds more fully formed, 0.65–0.95 mm, cylindrical with tubercular surface.



FIGURE 2. *Epilobium × obscurescens*. The stem on the right hand side is 23 cm long.

HOLOTYPE: East Cornwall, v.c. 2, Clicker quarry, near Liskeard, grid reference SX/288.614, on rubble and imported granite gravel, alt. 100 m, 27 July 1995, coll. M. Atkinson (E).

***Epilobium × obscurescens* Kitchener & McKean, hybr. nov.**

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. obscurum* Schreber) (Fig. 2)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. obscurum* Schreber, characteribus inter parentes variantibus; planta semi-prostrata, stigmatibus clavatis, et seminibus praecipue sterilibus, eorum pagina laevi et reticulatovenosa, et in ovario pilis nonnullis glandulosis praedito, eis ad pedicellos haud extensis.

Herb, conspicuously reddish, with stems well branched mainly at ground level, creeping at first and then curving up to erect position, 8–23 cm high, sharply quadrangular and with raised lines running from one node to the next, with fairly sparse short crisped hairs, more numerous in upper parts. Leaves mainly opposite, but largely alternate on upper part of stems, ovate-lanceolate to elliptic with a few, 2–3(–5) obscure teeth, glabrous except for short marginal pubescence, sessile or with petioles not exceeding 1(–2) mm; cauline leaves 0·6–1·5 × 0·3–0·65 cm, average ratio of length to width 1·0·42–0·44. Sepals 3–3·5 × 1 mm, bearing crisped hairs. Flowers very pale pink, petals 5–6

mm. Ovary 1·3–2·2 cm, with frequent crisped hairs and occasional patent glandular hairs, the latter not extending down to pedicel. Stigma entire, clavate. Capsules 1·5–3·1 cm, densely curly hairy; seeds mostly sterile, 0·6–0·8 mm long when fully formed but the sterile ones only averaging 0·32 mm, surface smooth but with reticulate veining.

HOLOTYPUS: Co. Antrim, v.c. H39, Magheramorne, grid reference J/43.98–44.98, on spoil tips of quarry, 1 July 1980, *D. Ledsham*, s.n., bar-code no. 33089 (**E**); isotypus (**BEL**).

The specific name is spelt *obscurescens* rather than *obscurascens* because it is an epithet derived from part of each of the parental epithets.

***Epilobium × chateri* Kitchener & McKean, hybr. nov.**

(*Epilobium brunnescens* (Cockayne) Raven & Engelhorn × *E. palustre* L.) (Fig. 3)

Hybrida inter *Epilobium brunnescens* (Cockayne) Raven & Engelhorn et *E. palustre* L., characteribus inter parentes variantibus; planta semi-prostrata stigmatibus clavatis, et seminibus praecipue sterilibus sed interdum fertilibus tum plus quam 1 mm longis.

Herb with prostrate leafy runners, from which arise erect stems, 20–25 cm high and scarcely branched above, with 2 broad lines of short crisped hairs, descending from each node; the density of the hairs increasing in the upper parts of the stem. Leaves opposite, largely alternate on the flowering part of the stem, reddish, sessile or with petioles to 1 mm; caudine leaves 0·6–1·2 × 0·2–0·4 cm, average ratio of length to breadth 1·0·29; narrow, lanceolate with a few obscure teeth, glabrous except sometimes pubescent on margins or upper midrib. Leaves on runners similar, but smaller, up to 0·6 cm long, 0·2 cm wide and with more distinct petioles. Sepals c. 2·2 mm long, lanceolate and strigillose. Flowers very pale pink. Four long stamens projecting to lower part of stigma, their anthers being 0·43–0·50 mm long; four short stamens extending to style below. Ovary c. 1·3 cm, covered with short crisped and patent hairs, some glandular. Stigma entire, clavate, 0·95–1·76 mm long; style longer, erect, 1·42–2·37 mm. Capsules 1·5–3·3 cm long, with numerous crisped hairs and some patent glandular hairs; mostly sterile, containing shrivelled, abortive seeds 0·4 mm long; also contained are a few larger seeds 1·0–1·3 mm long with tubercled surface, generally part collapsed longitudinally, but occasionally fully formed and fertile. The larger seeds bear a neck or appendage at the point of attachment of the coma.

HOLOTYPUS: Cardiganshire, v.c. 46, south of Hadre, Llyn Brianne, grid reference SN/804.512, on damp, acidic shaly soil by Forestry Commission road, alt. 370 m, 7 August 1995, *A. O. Chater*, s.n. (**E**); isotypus (**NMW**).

COMPARISON OF TAXA

Virtually all wild specimens were noticeable in the field as having red stems and leaves. Growth began as prostrate, often spreading radially, with flowering stems curving up to an erect or semi-erect position. That growth habit is less conspicuous in cultivation. A specimen of *E. × brunnatum* was grown on by A. O. Chater and assumed a sprawling, multi-branched erect habit. This was replicated by one of us (G.D.K.) in growing on both *E. × brunnatum* and *E. × obscurescens*. A similar result arose from cultivation of experimental hybrids made by Brockie between *E. brunnescens* and *E. ciliatum*, it being reported by Raven & Raven (1976) that plants grew into large mounds about 1 m across, with very little about them to remind one of *E. brunnescens*. The cultivation by one of us (G.D.K.) of F₂ specimens of *E. × brunnatum* and *E. × chateri* also gave analogous results, with plants demonstrating extensive scrambling growth. Reddening generally only occurred at a late stage, when plants were transferred outdoors: it may derive from stress or exposure.

There have been a few instances where plants have been found in the wild with a more vigorous and nearly erect growth habit. One such was the 1981 Irish specimen mentioned above, to which the name of *E. brunnescens* × *montanum* was initially applied, but which appears to be *E. × brunnatum*. This is a well-branched green specimen rising to 20 cm. Others are the two 1996 West Cornish *E. × brunnatum* plants discovered by D. T. Holyoak. These rise to 24 and 28 cm, bear leaves over twice as large as are normally seen in such hybrids, and in general seem much closer to the erect parent. More favourable growth conditions may be suspected, although these latter plants were apparently growing in stony mine waste.

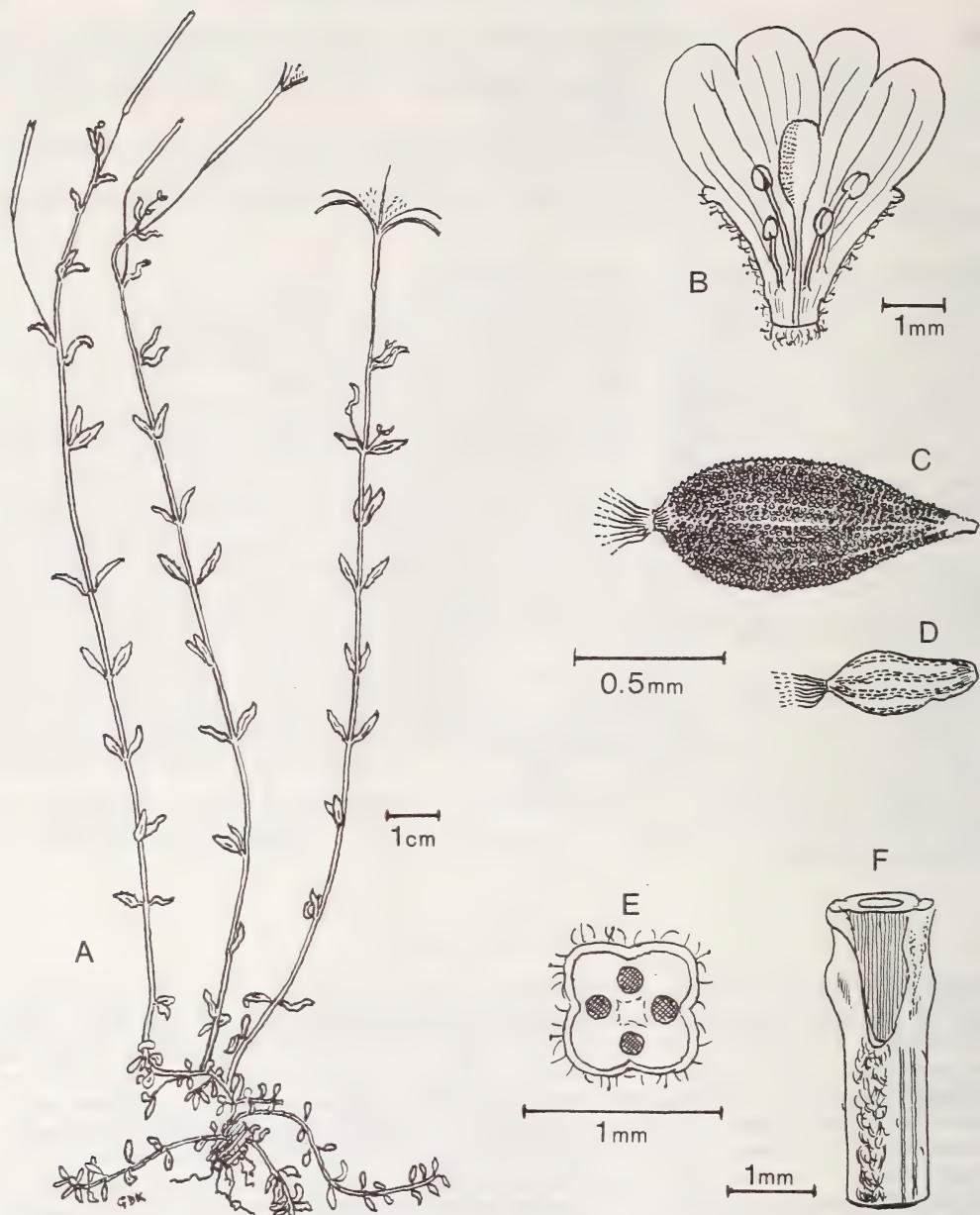


FIGURE 3. *Epilobium × chateri*. A. plant; B. flower; C. fertile seed; D. sterile seed; E. transverse section of ovary; F. mid-stem just below node.

The hybrids follow the erect species in bearing alternate leaves in the upper parts, instead of continuously opposite leaves with flowers borne individually in their axils, which is a characteristic peculiar to certain Australasian species of *Epilobium*, including *E. brunnescens* (Raven 1972). The wild specimens also show variable capsule length with very limited seed set, as is consistent with hybrid status. Their red colouring generally extends also to the sepals, which often bear an apical purple knob, as with *E. brunnescens*. The red sepals contrast with the greenish collar below. These sepal characteristics have not been repeated in each of the descriptions given above.

The morphological distinctness of prostrate *E. brunnescens* is so much greater than the differences between the various erect British species, however, that *E. brunnescens* is more readily identified as a parent than the other contributing species. In identifying the other parent, an analysis based on the species groupings put forward by Stace (1975) is of assistance. The initial grouping separates species with clavate stigmas and those with the stigmas four-lobed. As *E. brunnescens* has clavate stigmas, its hybrids with the former will carry similar stigmas, and its hybrids with the latter may be expected to bear variously intermediate stigmas (whose shapes are sometimes called "melted lobes" or "clenched fist").

The holotype specimens of *E. × cornubiense* and *E. × confusilobum* mentioned above indeed bear such intermediate stigmas. They are also distinct in carrying a fairly even spread of stem hairs which are short and crisped, representing the contribution of *E. montanum* or *E. lanceolatum*, as the case may be, and which are not conspicuously restricted to stem lines or bands. Some comment is perhaps due as regards the presence of glandular hairs on the upper parts of the specimens. Stace (1975) identifies *E. montanum* and *E. lanceolatum* as species which are not expected to contribute glandular hairs to a hybrid, and clearly they cannot be expected to do so to the same degree as, say, *E. ciliatum*. Many published descriptions do not mention glandular hairs in relation to these former species, although they do, nevertheless, occur. Exceptions are Stace (1991) and Haussknecht (1884): "Capsulis . . . junioribus tenuiter patentim glanduloso-pilosis" (*E. montanum*); and "Capsulis . . . pilis glandulosis brevissimis intermixtis obsitis; pedicellis glanduloso-puberulis" (*E. lanceolatum*).

The most apparent distinction between *E. × cornubiense* and *E. × confusilobum*, where (as with the Cornish mining or quarry sites) one hybrid combination cannot be ruled out by the absence of one of the potential parents, lies in the flower colour. The corollas of *E. lanceolatum* vary in the course of growth from white through to light and deep shell pink, each flower on a particular plant being a uniform colour, but perhaps differing from others on the same plant at that time. It appears that these colour characteristics can be inherited by *E. × cornubiense*. The 1995 specimen carries two flowers which were noted in the field as being white, as distinct from the very pale pink that characterizes most *E. brunnescens* hybrids so far found; and also as distinct from *E. × confusilobum*, whose corollas, on the material so far seen, are purplish pink. The 1996 specimens of *E. × cornubiense* carried several flowers which were noted in the field as ranging from pale pink to very pale pink, and that record of variability on one plant (while each flower was of uniform colour) is a valuable observation.

Hybrids with *E. palustre*, *E. ciliatum* and *E. obscurum* all involve parents with clavate stigmas. Distinguishing features are as follows:

E. × chateri is best recognised from leaf shape and (fertile) seed characteristics. *E. palustre* leaves are the narrowest of those of British species of *Epilobium*, and this character is not completely obscured by the broadly ovate to sub-orbicular leaf shape of *E. brunnescens*. The holotype hybrid specimen had a leaf length/breadth ratio of 1:0.29, significantly narrower than average measurements for material of *E. × brunnatum* (1:0.4–0.5), *E. × cornubiense* (1:0.57), *E. × confusilobum* (1:0.45) or *E. × obscurescens* (1:0.42–0.44). At the other end of the spectrum, the ratio for *E. brunnescens* is 1:0.7–0.85. *E. palustre* also has the largest seeds of British *Epilobium* species (1.6–1.8 mm), while *E. brunnescens* seeds, at 0.7 mm, are smaller than those of any of the native British species. The size of *E. palustre* seeds is reflected in the hybrid, whose fertile seeds (at 1.0–1.3 mm long) are longer than the fertile seeds of the other *E. brunnescens* crosses: *E. × brunnatum* (0.8–0.9 mm), *E. × cornubiense* (0.7–0.8 mm), *E. × confusilobum* (0.65–0.8 mm) and *E. × obscurescens* (0.6–0.8 mm). The fertile *E. × chateri* seeds also inherit beak characteristics from *E. palustre*, and bear a neck or appendage at the comal end.

E. × brunnatum and *E. × obscurescens* are very similar, but the former may be distinguished by the abundance of glandular hairs on the ovary deriving from *E. ciliatum* and descending at least down to the pedicels, such hairs being quite infrequent in the case of *E. × obscurescens*, and not present on the pedicels. The surface texture of the seeds also differs, with the sterile seeds of *E. × obscurescens* showing a pattern more reticulate than tuberculate (Fig. 4). It should be noted that the surface texture of fertile seeds is not necessarily the same as that of the sterile ones. That difference may perhaps be interpreted as a failure of the sterile seeds to develop fully their surface features, so presenting a somewhat desiccated effect. So the low ridging of sterile *E. × brunnatum* seeds (reflecting the ridged patterning of *E. ciliatum*) may become more prominent and tubercled in the fertile seeds. The reticulation of sterile *E. × obscurescens* seeds does not represent a reticulate

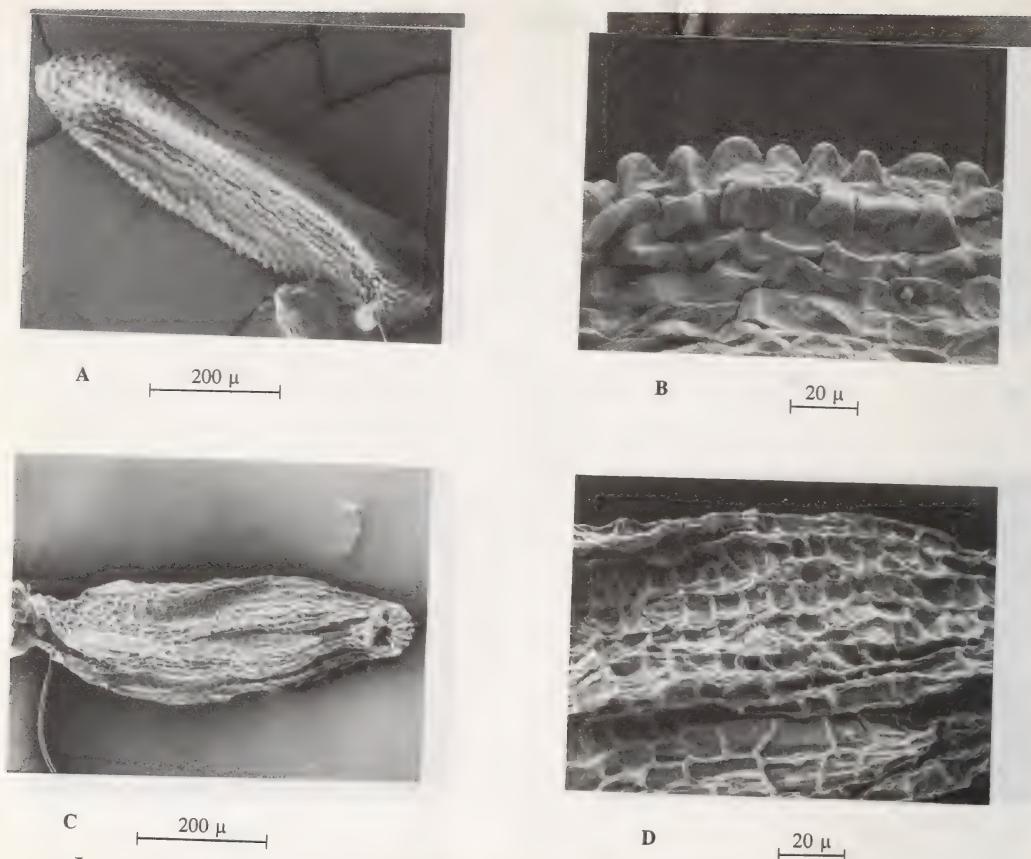


FIGURE 4. Scanning electron micrographs showing surface texture of sterile seeds of *E. × brunnatum* (A,B) and *E. × obscurescens* (C,D).

seeded parent. The surface of *E. obscurum* seeds is covered by narrow, wavy tubercles, and fertile *E. × obscurescens* seeds can repeat that appearance; so it seems likely that the reticulation of the sterile seeds also represents an undeveloped state of a tubercular surface. While it is often not easily observed, the presence of a short neck or appendage to the larger seeds, at the point of attachment of the coma, is an inheritance from *E. ciliatum*, and will clearly distinguish *E. × brunnatum* from *E. × obscurescens*.

STERILITY

Numerous hybrids were present at the recorded locations in v.cc. 1, 44 and H39. This opens the possibility of second or subsequent generations of hybrids, whether through back-crossing or self fertilisation. The presence of occasional seeds, either fully formed or only in part malformed (generally through longitudinal collapse of one side) has been noted in the specimens examined. A sample capsule from the v.c. 1 material of *E. × brunnatum* yielded 85 small abortive seeds and six larger ones. If fertile, the latter such seeds might account for at least some plants where hybrid populations exist.

Experimental sowing was undertaken in September 1995 using larger seeds taken from two of the v.c. 1 specimens of *E. × brunnatum*. Seeds were sown from each plant indoors, in small pots

containing a mixture of John Innes No. 3 and ballast sand; moisture was conserved by enclosing each in transparent plastic bags. Seeds were not covered, since Brockie (1966), working with New Zealand *Epilobium* hybrids, considered that light appears necessary to ensure good germination. From 18 seeds taken from one plant, nine seedlings germinated after 8 to 14 days. From 14 seeds taken from the other, five seedlings germinated over 14 to 39 days. The F_2 seedlings were transplanted into individual pots and, with some losses in cultivation, six plants survived successfully into the next year.

Germination of four F_2 seedlings was also achieved from material of *E. × chateri*.

The F_2 plants themselves set occasional apparently fertile seeds, as with the F_1 generation; one plant of *E. × brunnatum* was, however, apparently totally sterile, with collapsed, malformed stigmas. Apart from the general differences in cultivated material mentioned above, the F_2 plants showed a degree of variation which, if replicated in the wild, would render it even more difficult in some cases to identify what taxa were involved. The progeny of *E. × chateri*, for example, did not exhibit leaves quite as narrow as those from the original find (these wider leaved forms have been discounted in calculating the leaf length/breadth ratio given in the description of that hybrid).

DISTRIBUTION AND HABITAT

The occurrence of *E. brunnescens* hybrids in eleven localities in the British Isles up to 1996 (v.cc. 1, 2, 44, 46, H36, H39) provides limited scope for generalization. But data sufficient for mapping purposes have seldom been gathered in respect of any *Epilobium* hybrids – see Kitchener (1990), where it is concluded that “the real barrier to a fair assessment of the occurrence of willowherb hybrids has been lack of recognition, rather than scarcity”. Common to most of these localities, however, is an acid substrate, generally damp, open and of artificial origin; mining spoil appears particularly suitable.

The importance of open, disturbed habitats (e.g. quarries and wasteland) has been emphasised by Stace (1975) as affording a range of suitable opportunities for the establishment of *Epilobium* hybrids. But, in order for these opportunities to be taken up, there are at least two other relevant factors: the relative genetic compatibility of potential parents, and the availability of those parents themselves.

As regards the availability of the other parents, each of the species examined in this paper is readily to be found within the distributional range of *E. brunnescens*. As a limited measure of this – and taking into account the warning given that the data are not to be interpreted as showing comprehensive distribution – one may take the results of the B.S.B.I. sample survey under its Monitoring Scheme of 1987–8 (Palmer & Bratton 1995). *E. brunnescens* is recorded as present in 1987–8 in 125 of the sample squares, primarily in the damper western and northern parts and uplands of the British Isles. A high degree of coincidence is shown by the ubiquitous *E. montanum* (present in 90% of the same squares), by *E. palustre* (95%) and *E. obscurum* (82%).

The coincidence level of *E. ciliatum* is less (46%), as this species began its spread from the south-east, and has consolidated in the drier parts of the British Isles, from which *E. brunnescens* is largely absent. It has, however, been appearing increasingly within the range of *E. brunnescens*, as demonstrated by Preston (1989), with substantial spread in Wales and Cornwall occurring in the period 1959–69, and in Scotland and Ireland through to 1986. There is no reason to suppose that the spread of *E. ciliatum* has yet ceased; it has since appeared in vice-counties additional to those stated by Preston for the period up to 1986 (personal observation, and Palmer & Bratton 1995).

The increase of *E. ciliatum* may be relevant to the future occurrence of *E. brunnescens* hybrids if, as is possible, it is more ready to hybridize than other species, or such hybrids establish themselves with greater success. This is a matter for speculation, but some hybrid combinations of *Epilobium* are encountered more frequently in the field, and some species encountered more frequently as parents. Stace (1975) comments on this, and *E. ciliatum*, *E. montanum* and *E. obscurum* figure most prominently in the crosses which he regards as most frequently encountered. In our experience, within the range of *E. ciliatum*, it is the most frequently encountered parent in *Epilobium* hybrids. Further data are required before any assertion can be made about the relative frequency with which that species, in comparison with others, may hybridize with *E. brunnescens*.

CONCLUSION

It is perhaps surprising that these taxa have not been recognized until relatively recently in the British Isles, despite their potential occurrence having been publicised by Stace (1976). The confused history of the Irish records and the temporary loss of several specimens has not assisted that situation. It seems at least possible that, with further fieldwork, *E. brunnescens* hybrids may be found not to be so rare as the hitherto limited number of records suggests.

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A reassessment of the hybrid *Potamogeton × gessnacensis* G. Fisch. (*P. natans* × *P. polygonifolius*, Potamogetonaceae) in Britain

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ABSTRACT

Potamogeton × gessnacensis G. Fisch. (*P. natans* L. × *P. polygonifolius* Pourr.), hitherto known in Britain from Caernarvonshire (v.c. 49) and East Ross (v.c. 106), was discovered in 1996 in Shetland (v.c. 112). Cytological examination of plants from Caernarvonshire and Shetland shows that they are similar, with a chromosome number of $2n = c. 39$. This is intermediate between *P. natans* ($2n = 52$) and *P. polygonifolius* ($2n = 28$), both counts previously reported from British material. Populations of *P. × gessnacensis* are variously intermediate in morphology between the putative parents, the Caernarvonshire plants being closer to *P. natans* than the others; they are highly sterile. The habitat of *P. × gessnacensis* at its British sites is described. *P. natans* has not been recorded from any of the sites, which suggests that it may have been eliminated by competition with the hybrid.

KEYWORDS: *Potamogeton coloratus*, *P. epihydrus*, cytology.

INTRODUCTION

Potamogeton natans L. (Broad-leaved Pondweed) and *P. polygonifolius* Pourr. (Bog Pondweed) are the most frequent broad-leaved species of *Potamogeton* in the British Isles (Preston & Croft 1997). However, the hybrid between them appears to be very rare. Dandy (1975) reported "British plants which appear to be this hybrid" from two localities, Llyn Anafon, Caernarvonshire (v.c. 49) and Hill of Nigg, E. Ross (v.c. 106). Dandy's cautious wording contrasts with his normally confident phraseology (other hybrids in the same account are described as "clearly intermediate", "obviously intermediate", "manifestly intermediate" and "strikingly intermediate" between the parental species) and suggests that he regarded the identification as in need of confirmation. Preston (1995a) also described *P. × gessnacensis* as a hybrid requiring further research, pointing out that plants in the two British populations differed in morphology, with those at Llyn Anafon approaching *P. natans* very closely.

In August 1996 P.M.H. and C.D.P. discovered a further population of plants (at Loch of Gards, Shetland v.c. 112) which were morphologically intermediate between *P. natans* and *P. polygonifolius* and appeared to be highly sterile. As *P. natans* and *P. polygonifolius* differ in chromosome number, fresh material was sent to J.P.B. for cytological study. His results supported the provisional identification of the Shetland plant as the hybrid *P. × gessnacensis*. The plant from Llyn Anafon was also examined cytologically and proved to be similar. The results of these cytological studies are presented in this paper, and discussed in relation to the morphology of the plants.

CYTOLOGICAL STUDIES

Fresh material of putative *Potamogeton* × *gessnacensis* collected at Loch of Gards, Shetland (v.c. 112) on 1 August 1996 and Llyn Anafon, Caernarvonshire (v.c. 49) on 2 September 1996 was cultivated at the University of Leicester. Roots were pretreated in 8 hydroxyquinoline at 4°C for 8 hours, then fixed in fresh 3:1 ethyl alcohol:glacial acetic acid. The roots were then hydrolysed for 10 minutes at room temperature in 5N hydrochloric acid. The meristem was then dissected out in a drop of aceto-orcein using fine tungsten needles and tapped, flamed and squashed. Voucher specimens from both populations have been deposited in CGE.

Chromosome counts of $2n = c. 39$ were obtained from plants from Llyn Anafon (Fig. 1) and Loch of Gards (Fig. 2). The material is rather difficult cytologically. The chromosomes are rather numerous, very small (most are less than 1 μm long) and there is considerable variation in size between chromosomes within the complement. Another difficulty is that the chromosomes seem to be of two types (possibly the complements of the two parental taxa). One complement has a quadripartite appearance and resembles the textbook chromosome; it is clearly comprised of two chromatids, a centromere and four ends. The other sort of chromosome appears diffuse, without an obvious centromeric constriction and with only two ends apparent. The quadripartite chromosomes are easy to interpret even when adjacent, but this is not the case with the diffuse ones. In Fig. 1b (hollow arrow), the torpedo-shaped "body" has been interpreted as two adjacent chromosomes, though a case could be made for interpreting it as a single chromosome. However, other preparations from the same plant do not have a similarly shaped large chromosome. In Fig. 2b the V-shaped chromosome has been interpreted as a single chromosome with the chromatids splitting apart, rather than two small abutting chromosomes. The presence of a homologous chromosome is often useful in interpreting cases like this, but homologues need not be present in a hybrid (see the single strongly satellite chromosome arrowed in Figs 1a and 2a). A more certain count might be obtained by looking at the size and range of morphology of the chromosomes of the two parental taxa and checking the interpretation of the metaphase squashes in the light of this information. These interpretative difficulties are reflected in the fact that only approximate counts are presented here.

Interpretative difficulties apart, the Llyn Anafon and Shetland karyotypes of *P. × gessnacensis* have a number of features in common. Both have a single very distinctive satellite chromosome (arrowed in Figs 1a and 2a), and the same mixture of "quadruplicate" and "diffuse" chromosomes.

Potamogeton natans has a chromosome number of $2n = 52$. This statement is based on eight

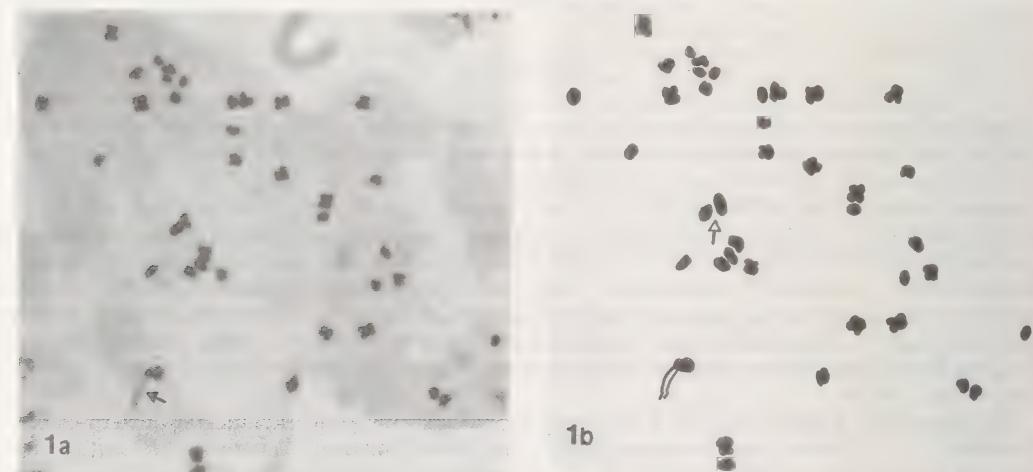


FIGURE 1. Cytological preparation of *Potamogeton* × *gessnacensis* from Llyn Anafon, Caernarvonshire (Fig. 1a) and the interpretation of this preparation as $2n = c. 39$ (Fig. 1b). The solid arrow in Fig. 1a indicates a conspicuous satellited chromosome. The hollow arrow in Fig. 1b indicates an area which is difficult to interpret (see text). Scale: as Fig. 2.

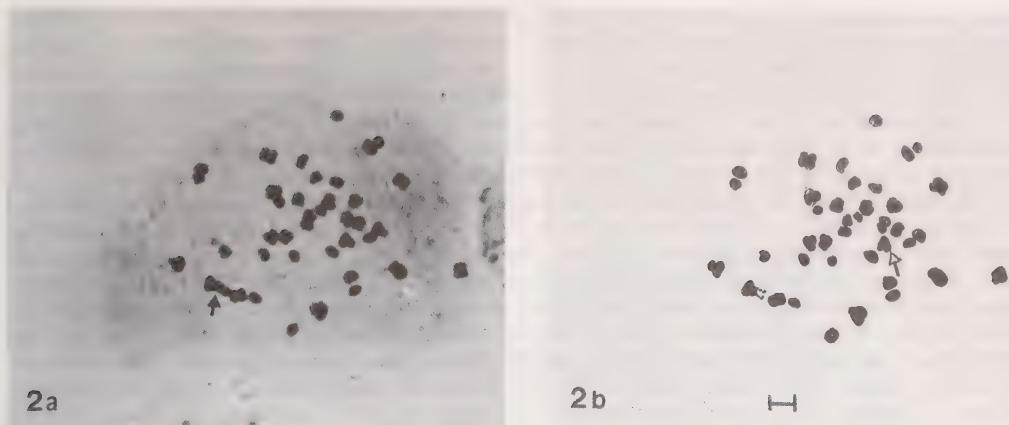


FIGURE 2. Cytological preparation of *Potamogeton* \times *gessnacensis* from Loch of Gards, Shetland (Fig. 2a) and the interpretation of this preparation as $2n = c. 39$ (Fig. 2b). The solid arrow in Fig. 2a indicates a conspicuous satellited chromosome. The hollow arrow in Fig. 2b indicates an area which is difficult to interpret (see text). Scale bar = 2 μm .

separate counts, one (as $2n = c. 52$) from English material (Hollingsworth *et al.* 1995; Hollingsworth *et al.* submitted). In this paper we have adopted, for convenience, the usual assumption that this represents the tetraploid level in *Potamogeton*. A count of $2n = 42$ has also been reported for *P. natans* from two localities, in N. America (Stern 1961, as $n = 21$) and eastern Asia (Probatova & Sokolovskaya 1984, as $2n = c. 42$). *P. polygonifolius* is a diploid species: $2n = 26$ is reported for this species by Palmgren (1939, as $n = 13$), Fernandes (1950) and Ficini *et al.* (1980). However, the three English counts of this species all unambiguously gave a count of $2n = 28$ (Hollingsworth 1995; Hollingsworth *et al.* submitted). In his summary of the chromosome numbers of *Potamogeton*, Les (1983) attributed the chromosome number $2n = 52$ to *P. polygonifolius* on the basis of two (uncited) counts. We have only been able to trace a single apparent count of $2n = 52$ for this species, by Takusagawa (1961). Although this count has been cited by abstracters (e.g. Moore 1973), a close reading of the text reveals that this count was never made, but was merely the chromosome number which Takusagawa would expect this species to have on the basis of the chromosome number of similar species.

Judging by the chromosome counts cited above, one would expect the hybrid *P. × gessnacensis* to be a triploid with $2n = 39$ or $2n = 40$. The cytological results show that the plants from Llyn Anafon and Shetland are indeed triploid, with a number which is certainly close to the expected number. They are therefore almost certainly a hybrid between a diploid and a tetraploid species. The tetraploid species is clearly *P. natans*, on morphological grounds. Although the morphological evidence for the involvement of *P. polygonifolius* is less strong, this is almost certainly the diploid parent. The only other broad-leaved pondweeds in the British flora which are diploids are *P. coloratus* and *P. epihydrus*, neither of which are likely parents of a hybrid which grows in upland N. Wales and Shetland.

RECOGNITION OF *P. × gessnacensis*

One of the features which distinguishes the hybrids of *P. natans* with the broad-leaved species *P. gramineus* (*P. × sparganiifolius*), *P. lucens* (*P. × fuitans*) and *P. nodosus* (*P. × schreberi*) is the presence of narrow, laminar submerged leaves intermediate between the phyllodes of *P. natans* and the laminar leaves of the other parent (Preston 1995a, b). Similar leaves might be expected to occur in the hybrid between *P. natans* and *P. polygonifolius*. However, the submerged leaves of the

British populations of *P. × gessnacensis* are much closer to the phyllodes of *P. natans* than they are to the laminar submerged leaves of *P. polygonifolius*. Plants of *P. × gessnacensis* from Llyn Anafon collected in May have phyllode-like submerged leaves which are sometimes expanded above the petiole into a very narrow lamina, and can occasionally resemble the narrowest submerged leaves of *P. × sparganifolius*. These leaves have usually decayed by August or September, although they can sometimes be found on axillary shoots. The plants from Scotland have either phyllodes or phyllodes which are expanded at the tip into a lamina which resembles a rudimentary floating leaf.

In the absence of leaves which are clearly intermediate between phyllodes and submerged leaves, the identification of *P. × gessnacensis* has to be based on features of the stipules and the floating leaves, which combine the characters of both parents (Table 1). Plants from Shetland are more easily recognised as intermediate than those from elsewhere, as they have short stipules which, when dry, are more or less translucent, lacking the very opaque, buff-coloured appearance of the *P. natans* stipule. When considered in conjunction with the phyllode-like submerged leaves and the presence on some leaves of at least a trace of the flexible junction between the petiole and lamina of the floating leaves, they clearly indicate that the plants are intermediate between the putative parents. The stipules of the other populations are closer to those of *P. natans*, but the floating leaves have longitudinal veins which are less markedly translucent than in that species. The flexible junction between the petiole and the lamina is also absent or poorly developed in these populations, but this character has to be used with caution as it is not always present in *P. natans*.

The inflorescences of *P. × gessnacensis* are usually shorter than those of *P. natans* and even in the field it is possible to obtain some indication that it is a sterile hybrid. The perianth segments of plants at Llyn Anafon and Loch of Gards remain closed and the stigmas protrude through them. This behaviour is typical of sterile hybrids (Preston 1995a, p. 46) and contrasts with that of fertile species where the perianth segments open to expose anthers which shed copious amounts of pollen. At Llyn Anafon on 2 September 1996 the old inflorescences of the hybrid were rotting, and being replaced by newly developed inflorescences. Examination of the pollen of plants from Llyn Anafon has shown that it is sterile (G. C. S. Clarke, in litt. to J. E. Dandy, 10 July 1973, BM). Plants from Llyn Anafon sometimes produce easily detached fascicles of short phyllodes or phyllode-like leaves in the leaf axils; these were first noted by A. Fryer on a specimen collected by C. Bailey on 29 September 1884 (BM). Similar structures are occasionally produced by *P. natans* and may act as vegetative propagules.

Material from Llyn Anafon is illustrated by Preston (1995a) and plants from Shetland are drawn as Fig. 3.

BRITISH POPULATIONS OF *P. × GESSNACENSIS*

Potamogeton × gessnacensis is now known from three sites in Britain. It has been collected at Llyn Anafon, Caernarvonshire, since 1884, the early specimens being originally named *P. natans*, *P. polygonifolius* or (in the case of plants collected by E. F. Cooper in 1890) *P. natans × polygonifolius*. At Llyn Anafon *P. × gessnacensis* grows in water from 0.3 to at least 0.8 m deep around the edge of the lake. The stands of the hybrid are extensive, especially in relatively sheltered bays, typically occupying several square metres in area. They flower freely, but the inflorescences rot rather than set fruit. Llyn Anafon is a base-poor upland lake (altitude 500 m), although there may be slight base-enrichment from a small outcrop of dolerite and a larger outcrop of less basic andesite south of the lake. Its flora includes *Callitricha hamulata*, *Isoetes lacustris*, the aquatic variant of *Juncus bulbosus*, *Littorella uniflora*, *Lobelia dortmanna*, *Menyanthes trifoliata*, *Myriophyllum alterniflorum*, *Potamogeton berchtoldii*, *Ranunculus omiophyllum*, *Sparganium angustifolium*, *Subularia aquatica*, *Utricularia vulgaris* sensu lato and *Chara globularis* var. *virgata*. *Potamogeton polygonifolius* occurs in runnels leading into the lake and in water up to 0.5 m deep near the edge, but *P. natans* is apparently absent. A second rare *Potamogeton* hybrid, *P. × griffithii*, also occurs at Llyn Anafon with one parent (*P. alpinus*) but not the other (*P. praelongus*).

The record of *P. × gessnacensis* from a small stream on the Hill of Nigg, East Ross, is based on a single collection made by U. K. Duncan on 10 August 1970. In a letter to J. E. Dandy dated 5 November 1970 and now kept with the specimen in BM, she commented "I noted at the time that there was no typical *natans* to be seen in the vicinity on the Hill of Nigg. In fact I thought this must be

TABLE 1. A COMPARISON OF SOME CHARACTERS OF *POTAMOGETON NATANS*, *P. POLYGONIFOLIUS* AND THE THREE BRITISH POPULATIONS OF THEIR HYBRID *P. \times GESSNACENSIS*

	<i>P. natans</i>	<i>P. \times gessnacensis</i>	<i>P. polygonifolius</i>
Stipules			
Length (mm)	40–170	30–85	20–42
Colour (when dry)	Green or buff, opaque	Brown or buff, \pm opaque	Brown, \pm translucent
Floating leaves			
Longitudinal veins of fresh leaves (when held up to light)	Translucent	Opaque or translucent (if translucent usually very narrow)	Opaque (sometimes paler than lamina but not translucent)
Discoloured junction between petiole and lamina	Usually present, rarely absent	Absent or trace visible	Absent or trace visible
Inflorescences			
Length (mm)	20–60	11–28	8–20
Capacity to produce well-formed fruits	Present	Absent	Absent
			Present

* Observations based on a single dried specimen consisting of two vegetative plants (BM).



FIGURE 3. *Potamogeton × gessnacensis*, drawn by L. T. Ellis from herbarium specimens collected at Loch of Gards, Shetland, by C.D.P. & P.M.H. on 1 August 1996 (Preston 96/145, 146, CGE). Scale bars = 3 cm.

a form of that species . . . there were only four plants, all nearly the same, growing in a colony in the small streamlet at GR 28/828708. I had followed up the stream from the coast expecting to find the loch at approximately that locality, but to my disappointment it had completely disappeared, having become a "bog" full of moss, rushes etc., without even a pool of water left . . ."

The third site, Loch of Gards, Shetland, is a shallow coastal lake. *P. × gessnacensis* grows in water 0·2–0·3 m deep, forming small patches over a sandy substrate around the edge of the lake, and larger stands by a wall which crosses the lake at the south end. The plants were flowering when first discovered on 1 August 1996 and still flowering when W. Scott revisited the site on 4 September 1996. There was no sign of fruit developing on either date. Loch of Gards is a relatively eutrophic lake which (judging by its situation) must receive some input of salt-spray. Few aquatic plants grow with the *P. × gessnacensis*, but the deeper water in the centre of the lake is dominated by *Potamogeton pusillus* and *Ranunculus baudotii*. Other species present include *Littorella uniflora*,

Myriophyllum alterniflorum, *Persicaria amphibia*, *Potamogeton filiformis* and *P. perfoliatus*. Neither *P. natans* nor *P. polygonifolius* was recorded at Loch of Gards in 1996.

It is remarkable that *P. natans* has not been recorded from any of the British *P. \times gessnacensis* sites. At Llyn Anafon and Loch of Gards the habitat which appears to be suitable for this species is occupied by the hybrid, suggesting that if *P. natans* was formerly present it may have been out-competed by the hybrid. *P. polygonifolius* is present at Llyn Anafon in a different habitat.

DISCUSSION

The results of the cytological studies outlined above support the conclusion that the plants from Llyn Anafon and Loch of Gards are *P. \times gessnacensis*. However, the evidence is not yet absolutely conclusive, and more detailed cytological study, or isozyme or other molecular studies, would be worthwhile.

P. \times gessnacensis is a difficult hybrid to detect in the field. In order to identify it one needs to recognise that it is intermediate between the parents, and resist the temptation to ascribe it to one parent or the other. It is unlikely that a population such as that at Llyn Anafon, which has a close resemblance to *P. natans*, could be identified on a single visit to a site, as the characteristic features of the submerged leaves are apparent only in the early season whereas the sterility of the plants can be established only later in the summer. The hybrid is more difficult to detect as a herbarium specimen, and the fact that J. E. Dandy was able to identify the plant from Llyn Anafon as *P. \times gessnacensis* provides remarkable testimony to his knowledge of the genus. In view of these difficulties of identification, it seems likely that there are further populations of the hybrid in Britain that have hitherto escaped detection; the hybrid is also likely to occur in Ireland.

The variation between the British populations of *Potamogeton \times gessnacensis* is apparently paralleled by variation in the type locality, the Gessnach stream in Germany. In his initial description of the hybrid as *P. \times gessnacensis*, Fischer (1907) recognised three varieties, one variety closer to *P. natans*, one closer to *P. polygonifolius* and one intermediate between the other two.

SPECIMENS EXAMINED

The above account is based on the following specimens of *P. \times gessnacensis*. Determinations attributed to J. E. Dandy (J.E.D.) were made in 1973 unless otherwise stated.

BRITISH ISLES

WALES: Caernarvonshire, v.c. 49: Llyn Anafon, SH/69.69., 29 September 1884, C. Bailey, BM, det. J.E.D.; August 1890, E. F. Cooper, BM, det. J.E.D.; 5 July 1905, H. W. Pugsley, BM, det. J.E.D.; 1 October 1906, J. F. Dutton, BM, det. J.E.D.; 30 July 1910, G. Goode, LTR, det. J.E.D., 1975; 4 August 1928, A. Wilson, YRK, det. C.D.P., 1997; 4 July 1946, R. Ross, BM, det. J.E.D.; 4 July 1984, M. Wade, UTLH; 28 May 1988, C. D. Preston & N. F. Stewart, Preston 88/35, 37, 38, BM, CGE, NMW; 27 August 1989, C.D.P. & N. F. Stewart, Preston 89/462, 464, 465, CGE, NMW; 2 September 1996, T. D. Dines & C.D.P., Preston 86/231, 232, 233, BM, CGE, NMW.

SCOTLAND: East Ross, v.c. 106: N. side of Hill of Nigg, NH/828.708, 10 August 1970, U. K. Duncan, BM, det. J. E. D. Shetland, v.c. 112: Loch of Gards, Scat Ness, HU/38.09., 1 August 1996, P.M.H. & C.D.P., Preston 96/145, 146, 147, BM, CGE, E; 4 September 1996, W. Scott, Scott 3527, CGE, E, det. C.D.P., 1996.

GERMANY

In der Gessnach zwischen Ödhof und Schaufling b. Deggendorf (Bayer. Wald), 17 August 1921, L. Oberneder, BM.

ACKNOWLEDGMENTS

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Potamogeton pectinatus L. × *P. vaginatus* Turcz. (*P. × bottnicus* Hagstr.), a newly identified hybrid in the British Isles

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ABSTRACT

A hybrid *Potamogeton* (Potamogetonaceae) which grows in shallow, rapidly flowing water in the River Till (Cheviot) and River Tweed (Berwickshire (v.c. 81) and Cheviot (v.c. 68)) is apparently referable to *P. × bottnicus* Hagstr. (*P. pectinatus* L. × *P. vaginatus* Turcz.). Both morphological and isozyme characters are consistent with this hybrid combination rather than with the previous identification of these plants as *P. × suecicus* K. Richt. (*P. pectinatus* × *P. filiformis* Pers.). British plants of *P. × bottnicus* and European plants of *P. vaginatus* are described and the differences between them, *P. pectinatus* and *P. × suecicus* outlined. Possible explanations for the presence of *P. × bottnicus* in Britain in the absence of *P. vaginatus* are discussed. The name *P. × bottnicus* is lectotypified by a syntype referable to *P. pectinatus* × *P. vaginatus*. Examination of type material of *P. × meinshausenii* Juz., described from the vicinity of St Petersburg, indicates that it is not a hybrid between *P. pectinatus* and *P. vaginatus* as hitherto supposed.

KEYWORDS: Potamogetonaceae, *Potamogeton filiformis*, *P. × suecicus*, *P. × meinshausenii*.

INTRODUCTION

Two species in *Potamogeton* subgenus *Coleogeton* Rchb. are found in the British Isles, *P. filiformis* Pers. (Slender-leaved Pondweed) and *P. pectinatus* L. (Fennel Pondweed). The hybrid between them, *P. × suecicus* K. Richt., is one of the more difficult *Potamogeton* hybrids to identify, partly because of the extreme variability of the commoner parent, *P. pectinatus*, and partly because the crucial character which separates this parent from the hybrid, the structure of the leaf sheaths, can only be ascertained by dissection under the microscope. The first correct records of *P. × suecicus* in the British Isles were published by Dandy & Taylor (1940). The hybrid has subsequently been discovered in scattered localities in Scotland and Ireland, where both the widespread *P. pectinatus* and the more northerly *P. filiformis* occur (Preston & Croft 1997). More significantly, *P. × suecicus* was reported by Dandy & Taylor (1946) from the River Tweed in Berwickshire (v.c. 81) and Cheviot (v.c. 68), and the River Wharfe and River Ure in Yorkshire (v.c. 64 and v.c. 65); a similar plant has subsequently been found in a tributary of the Tweed, the River Till (Dandy 1975; Holmes & Whitton 1975a, b; Swan 1993). At the time of Dandy & Taylor's paper these localities all lay south of the extant sites for *P. filiformis* in Britain. *P. filiformis* has since been found in Rayburn Lake, S. Northumberland (v.c. 67), south of the Tweed and the Till, but the Yorkshire sites are still some 150 km south of the nearest known *P. filiformis* population.

We have recently re-investigated *P. × suecicus* in Britain, examining the morphology of populations and using isozyme electrophoresis to investigate the variation in both the hybrid and its putative parents (Hollingsworth *et al.* 1996a, b). Most populations hitherto identified as *P. ×*

suecicus, and a number of new populations discovered during the course of this study, have proved to be intermediate morphologically between *P. filiformis* and *P. pectinatus*, and the results of the isozyme analysis offered strong support to the hypothesis that they represent the hybrid between these two species. This applies both to plants in sites in Scotland, where the hybrid often grows in proximity to both parents, and to the outlying populations in the River Wharfe and River Ure. Hollingsworth *et al.* (1996a) concluded that the evidence that the populations studied are the hybrid between *P. filiformis* and *P. pectinatus* is "virtually conclusive". An updated account of the distribution of *P. × suecicus* in the British Isles is in preparation.

Although the identity of most populations of *P. × suecicus* was confirmed by our recent study, the plants in the River Till and River Tweed were a conspicuous exception. We were unable to identify them as *P. × suecicus* either on morphological grounds or from the isozyme evidence. Both morphology and isozyme evidence is, however, consistent with the hypothesis that these plants are *P. × bottnicus* Hagstr., the hybrid between *P. pectinatus* and the third European member of subgenus *Coleogeton*, *P. vaginatus* Turcz. This is a surprising conclusion, as in Europe *P. vaginatus* is confined to Norway, Sweden and Finland (Elven & Johansen 1984); the nearest population lies some 1500 km from the sites in the River Tweed and River Till. The species is also found in central Asia and is widespread in North America (Hultén & Fries 1986). The hybrid is described below, and the evidence for its identity outlined.

POTAMOGETON × BOTTNICUS IN BRITAIN

DESCRIPTION

The following description of *P. × bottnicus* is based on fresh material and herbarium specimens collected from the British sites.

Plants forming large and vigorous clumps. Rhizomes to at least 0·45 m long, 1·5–6·5 mm in diameter. Stems up to 1·5 m long, 1·7–4·3 mm in diameter, terete, with frequent branches lying more or less parallel to the main stem; nodal glands absent. Scales 10–64 mm long, present on lowest (0–)1–3 nodes of the stem, clasping the stem throughout their length or with the distal part free, incurved and leaf-like, or bearing rudimentary leaves. Submerged leaves linear, mid to dark green, sometimes tinged with brown when growing near the surface of the water, leaves at the first 4 nodes above the basal scales 25–206 × (1·2–)2·0–3·5 mm, 11–90 times as long as wide, 0·8–3·7 times as long as the sheath, stiff, markedly canaliculate, acute; leaves towards the apex of mature stems (72–)110–200(–250) × 0·8–3·1 mm, (45–)60–110(–140) times as long as wide, (2·6–)3·0–5·7 times as long as the sheath, canaliculate, more or less truncate, rounded or obtuse at the apex, sometimes slightly mucronate and often slightly asymmetrical, sometimes more or less acute on flowering stems, entire and plane at the margin, the midrib bordered on each side by 1–2 inconspicuous lateral veins and several air channels. Floating leaves absent. Leaf sheaths green with hyaline margins, the margins sometimes with a brownish tinge, open and usually convolute unless forced apart by branches arising at the node, 25–78 × 2·1–5·5 mm at the first 4 nodes above the basal scales, 23–70 mm long towards the apex of mature vegetative stems, only 17–28 mm long towards the apex of flowering stems; ligules 6–17 mm, hyaline, rounded or truncate at the apex. Turions absent. Inflorescences 10–26 × 4–5·5 mm; peduncles 36–90 × 0·6–0·7 mm, pale pink, terete, flexuous. Flowers 5–10, in 3–5 groups of 1–2; anthers small, hidden by the tepals, not filled and not dehiscing readily, the pollen misshapen; carpels 4, the stigmas sessile. Fruits not seen, and almost certainly do not develop. Vegetative reproduction by small plantlets which develop on short axillary stolons; perhaps also by tubers which are formed on the rhizomes of both parents but these not yet seen on the hybrid.

COMPARISON OF *P. × BOTTNICUS* WITH *P. PECTINATUS* AND *P. × SUECICUS*

The salient characters distinguishing the three European species in subgenus *Coleogeton* and the hybrids *P. × bottnicus* and *P. × suecicus* are set out in Table 1. British and Irish botanists are most likely to overlook *P. × bottnicus* as a form of the variable *P. pectinatus*. Fortunately, both *P. pectinatus* and *P. × bottnicus* grow together in the River Tweed on the S. side of St Thomas's Island, Norham Mains, and in July 1995 the differences between the taxa were clearly apparent in this mixed stand. The clumps of *P. × bottnicus* reached the surface, where the leaves were brownish green, and scarcely moved in the current. The leaves had blunt apices and long, broad sheaths. The

clumps were flowering rather sparingly, with approximately 160 inflorescences per square metre, and the anthers were hidden by the tepals and did not appear to be releasing pollen on to the water surface. *P. pectinatus* formed bright green clumps which at that time did not reach the surface of the water but were waving in the current. The plants were richly branched, and it was difficult to distinguish a single main stem. The leaves were narrower and more finely tapered towards the apex than those of *P. × bottnicus*, and their sheaths were shorter and more slender. Flowers were more frequent than on the clumps of *P. × bottnicus*, with approximately 600 inflorescences per square metre of water surface; the anthers exceeded the tepals, were clearly full, and dehisced on the surface of the water to release pollen which drifted downstream. Pollen from both taxa in this stand was subsequently examined microscopically, and the well-formed pollen of *P. pectinatus* contrasted with the misshapen pollen of *P. × bottnicus* (Table 2).

Measurements based on stems of *P. × bottnicus* and *P. pectinatus* collected at random from the mixed stand in the R. Tweed and the population of *P. × bottnicus* in the River Till are presented in Table 3 and Fig. 1. These clearly illustrate the vegetative differences between the two taxa at these sites. One complicating factor in comparing the two taxa is the ontogenetic variation which is shown by most members of subgenus *Coleogeton*: lower leaves (especially on short pioneer shoots) tend to be broader and more obtuse than upper leaves, and leaves on vegetative stems tend to be broader than those on flowering stems. The leaves at the apex of long flowering shoots of *P. × bottnicus* are, therefore, more like those of *P. pectinatus* than other leaves. *P. pectinatus* is a very variable species and some populations, such as those which were formerly segregated as *P. flabellatus* Bab., may be indistinguishable vegetatively from *P. × bottnicus*. However, the sessile stigmas of the hybrid are crucial in distinguishing it from all forms of *P. pectinatus* which may resemble it vegetatively.

In vegetative characters *P. × bottnicus* is usually closer to *P. × suecicus* than *P. pectinatus*, and in particular it resembles the robust forms of that hybrid in the R. Wharfe and R. Ure. Characteristic specimens of *P. × suecicus* from these rivers are illustrated by Dandy & Taylor (1946) and Preston (1995). *P. × bottnicus* and *P. × suecicus* are both sterile hybrids with obtuse leaves and sessile stigmas. The large lower leaf sheaths of *P. × bottnicus* might be thought to be derived from the similar sheaths of *P. vaginalis* (which they closely resemble) and thus provide a character to distinguish it from *P. × suecicus*, but some pioneer shoots of the latter have surprisingly large sheaths, as do some plants of *P. pectinatus*. The crucial distinction between *P. × bottnicus* and *P. × suecicus* lies in the fact that the leaf sheaths of the former are open whereas at least some of the sheaths of *P. × suecicus* are closed and tubular at the base. Data for selected populations are provided in Table 4. In interpreting this table it should be remembered that a closed sheath is an unambiguous character, whereas a sheath may be recorded as open because it actually is open, or because it is closed for an indetectably short distance above the base, or because it is a closed sheath which has split. Nevertheless, the data in Table 4 (which are based on the dissection of young and apparently intact sheaths) demonstrate that in some *P. × suecicus* populations all the sheaths are tubular, whereas others consist of plants with a mixture of open and tubular sheaths.

The following key to the British and Irish taxa in subgenus *Coleogeton* can be used in place of that presented by Preston (1995, p. 133).

- 1a. All sheaths open to the base 2
- 1b. Some or all sheaths tubular at the base 3
- 2a. Mature leaves on the vegetative stems usually acute to finely acuminate at the apex; stigmas borne on a distinct style c. 0.2 mm long; pollen well-formed; fruits 3.3–4.7 mm *P. pectinatus*
- 2b. Mature leaves on the vegetative stems more or less truncate, rounded or obtuse at the apex; stigmas sessile; pollen misshapen; fruits not developing *P. × bottnicus*
- 3a. Stems branched at base, otherwise unbranched or very sparingly branched; all sheaths tubular at the base; stigmas sessile; pollen well-formed; fruits 2.2–2.8(–3.2) mm *P. filiformis*
- 3b. Stems usually sparingly or richly branched above the base; all sheaths tubular at the base or some tubular and others open and convolute; stigmas sessile or borne on a distinct style; pollen misshapen; fruits not developing *P. × suecicus*

TABLE 1. COMPARISON OF SOME CHARACTERS OF *POTAMOGETON FILIFORMIS*, *P. PECTINATUS*, *P. × SUECICUS* (*P. FILIFORMIS × PECTINATUS*) AND *P. × BOTTNICUS* (*P. PECTINATUS × VAGINATUS*) FROM THE BRITISH ISLES, AND *P. VAGINATUS* FROM SCANDINAVIA

	<i>P. filiformis</i>	<i>P. × suecicus</i>	<i>P. pectinatus</i>	<i>P. × bottanicus</i>	<i>P. vaginalis</i>
Leaf sheaths	Tubular	Tubular or some tubular, some open	Open	Open	Open
Short, broad stem leaves differing from branch leaves	Absent	Sometimes present	Sometimes present	Present	Present
Apex of branch leaves	Obtuse to acute	Subacute to acuminate	Acute to acuminate	Truncate to acute	Obtuse to acute
Ligules (mm)	5-15	7-24	5-15	6-17	0.5-4
Stigmas	Sessile	Sessile or stalked	Stalked	Sessile	Sessile
Pollen	Fertile	Sterile	Fertile	Sterile	Fertile
Fruit (mm)	2.2-2.8(-3.2)	-	3.3-4.7	-	2.6-3.8

TABLE 2. POLLEN STAINABILITY OF *POTAMOGETON PECTINATUS* AND *P. \times BOTTNICUS* FROM A MIXED STAND IN THE RIVER TWEED, AND *P. VAGINATUS* FROM FINLAND

Taxon	Locality	Date	Pollen stainability (%)
<i>P. pectinatus</i>	St Thomas's Island, Norham Mains	1995	86.6
<i>P. \times bottnicus</i>	St Thomas's Island, Norham Mains	1995	0.8
<i>P. vaginatus</i>	Kuljunnieniemi, Saloainen, Raahe	1987	93.9
<i>P. vaginatus</i>	Martinlahti, Piehinki, Raahe	1992	95.9

Stainability based on at least 300 grains from at least three anthers stained with safranin in glycerol. Based on material of *P. pectinatus* and *P. \times bottnicus* collected by the authors and herbarium specimens of *P. vaginatus* collected by J. Särkkä (OULU and herb. J.Särkkä).

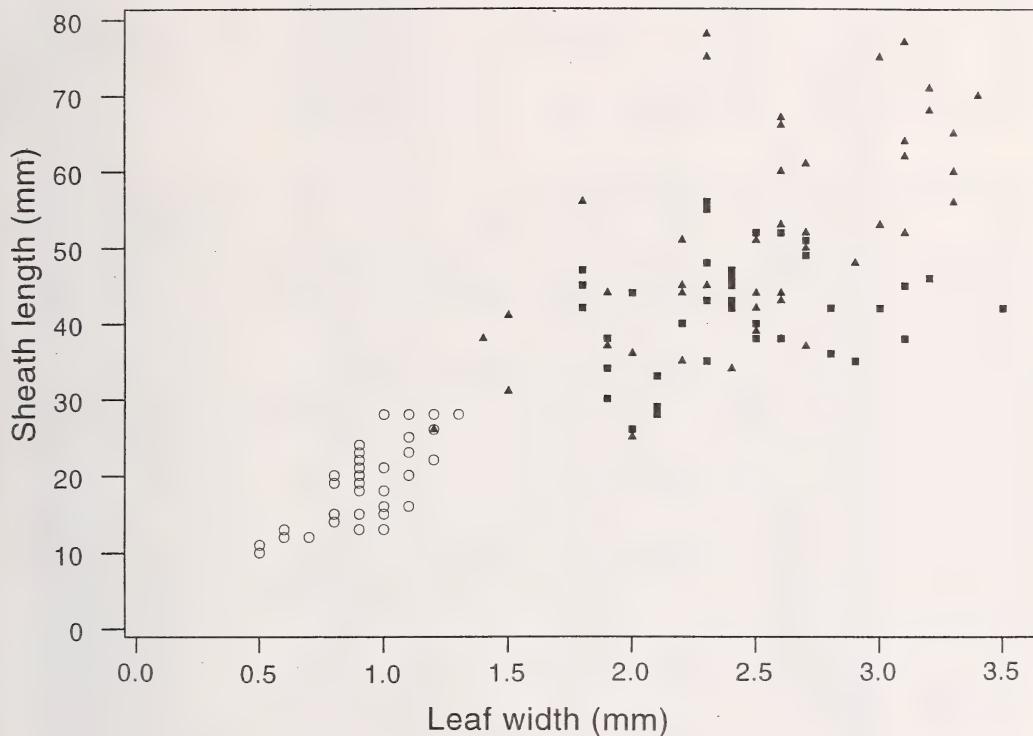


FIGURE 1. Sheath length (mm) plotted against leaf width (mm) for *Potamogeton \times bottnicus* and *P. pectinatus*, based on measurements at the lowest four leaf-bearing nodes of randomly sampled fresh vegetative stems collected on 18–19 July 1995. Samples of *P. \times bottnicus* collected from the River Tweed at Norham Mains (solid squares; n = 40) and the River Till below Twizel Bridge, NT/883.433 (solid triangles; n = 46). Samples of *P. pectinatus* (open circles; n = 43) collected from the same site as the River Tweed *P. \times bottnicus*.

COMPARISON OF *P. \times BOTTNICUS* WITH *P. VAGINATUS*

In Europe *Potamogeton vaginatus* is restricted to Norway, Sweden and Finland. We are not aware of a detailed description of the European plant in English, and therefore include one here. The following description has been drawn up primarily from Finnish material in OULU and in the private herbarium of J. Särkkä, supplemented by specimens from Finland and Sweden in BM, CGE and LTR. As it is based entirely on dried specimens, it is likely to under-estimate the range of variation of the species, especially in features such as stem length, and it lacks characters which cannot be deduced from pressed plants. The illustration of *P. vaginatus* in Fryer & Bennett (1915) is based on

TABLE 3. SHEATH AND LEAF DIMENSIONS OF *P. × BOTTNICUS* AND *P. PECTINATUS* SAMPLES FROM A MIXED STAND IN THE RIVER TWEED, AND *P. × BOTTNICUS* SAMPLES FROM THE RIVER TILL

	Sheath length (mm)						Leaf length (mm)						Leaf width (mm)					
	1	2	3	4	V	F	1	2	3	4	V	F	1	2	3	4	V	F
<i>P. × bottnicus</i> (R. Till)																		
Minimum	25	31	36	37	30	—	25	66	98	107	112	—	1.2	1.5	1.4	1.5	1.1	—
Mean	44	49	56	56	46	—	46	95	139	163	173	—	2.5	2.6	2.5	2.5	2.2	—
Maximum	65	75	77	78	70	—	81	137	170	206	252	—	3.3	3.3	3.4	3.2	3.1	—
<i>P. × bottnicus</i> (R. Tweed)																		
Minimum	26	28	30	29	23	17	33	57	87	79	87	72	2.0	1.8	1.8	1.8	0.8	0.8
Mean	38	41	44	44	39	23	47	88	117	119	151	108	2.5	2.5	2.4	2.4	1.8	1.1
Maximum	46	51	56	55	55	28	65	106	154	173	215	155	3.2	3.5	3.0	2.8	2.5	1.3
<i>P. pectinatus</i> (R. Tweed)																		
Minimum	10	11	11	12	—	—	11	17	20	23	—	—	0.5	0.5	0.5	0.6	—	—
Mean	17	18	20	20	—	—	36	37	53	53	—	—	0.9	0.9	0.9	0.9	—	—
Maximum	26	25	28	28	—	—	74	51	92	91	—	—	1.2	1.2	1.2	1.3	—	—

Measurements based on randomly sampled stems collected on 18–19 July 1995 from the River Tweed at Norham Mains, NT923.493, and River Till below Twizel Bridge, NT883.433. Values are provided for the lowest four leaf-bearing nodes, numbered from the base (1) upwards, and the upper nodes of vegetative (V) and flowering (F) stems. The differences between *P. pectinatus* and the *P. × bottnicus* populations are statistically significant except those for leaf length at node 1 (Mann-Whitney U test, $p < 0.001$). There are also statistically significant differences between the *P. × bottnicus* populations themselves for leaf length at node 4 ($p < 0.05$), and for sheath length ($p < 0.05$), leaf length ($p < 0.01$) and leaf width ($p < 0.01$) on the upper vegetative stems. Sample size: 7–12 (nodes 1–4), 20–33 (V) and 12 (F). A dash indicates measurements which were not made.

TABLE 4. SHEATH MORPHOLOGY OF POPULATIONS OF *POTAMOGETON* × *BOTTNICUS* AND *P. × SUECICUS* FROM THE BRITISH ISLES

Taxon	Locality	Grid ref.	No. of sheaths examined		
			Open	Tubular	Total
<i>Potamogeton</i> × <i>bottnicus</i>	R. Till, Twizel Bridge, v.c. 68	NT/88.43	60	0	60
	R. Tweed, Norham Mains, v.c. 68	NT/92.49	68	0	68
<i>Potamogeton</i> × <i>suecicus</i>	R. Wharfe, Harewood Bridge, v.c. 64	SE/26.78	37	21	58
	Loch Fitty, v.c. 85	NT/12.91	0	21	21
	R. Lossie, v.c. 95	NT/2.6	0	20	20
	Loch of Strathbeg, v.c. 95	NK/08.58	17	25	42
	Little Loch Borve, v.c. 110	NF/91.81	2	13	15
	Loch a'Chalaig, v.c. 110	NF/89.78	22	14	36
	Loch an Duin Bhig, v.c. 110	NF/75.46	1	21	22
	Loch Bhrui, v.c. 110	NF/91.82	5	34	39
	Loch of Langamay, v.c. 111	HY/74.44	4	12	16
	Loch of Clickimin, v.c. 112	HU/46.41	15	15	30
	Lough Gill, v.c. H1	Q/61.13	5	58	63
	Rosapenna, v.c. H35	C/11.38	17	23	40

correctly identified Swedish material, although the British records of this species cited in the same work are erroneous.

Rhizomes to at least 0·45 m long, 1·0–6·0 mm in diameter. Stems up to at least 1·6 m long, 1·2–5·5 mm in diameter near the base, with 1–5 branches emerging from most of the leaf sheaths on the main stem, some or all of these branches long and richly branched; nodal glands absent. Scales 18–70 mm long present on the lowest 0–3 nodes of the stem, clasping the stem throughout their length or with the distal part free, incurved and leaf-like or with rudimentary leaves at the apex. Submerged leaves linear; leaves on the main stem 17–82 × 0·7–2·5(–3·3) mm, 13–67 times as long as wide, 0·5–2·2 times as long as the sheath, more or less canaliculate, truncate, rounded or obtuse at the apex, the midrib bordered on each side by 2–4 inconspicuous lateral veins; mature leaves on the branches 39–125 × 0·3–0·8(–1·25) mm, (30)–100–420 times as long as wide, (1·4)–2·0–6·2 times as long as the sheath, obtuse or more or less acute at the apex, the midrib bordered on each side by an inconspicuous lateral vein. Floating leaves absent. Leaf sheaths green with hyaline margins and ligules, open, sometimes convolute, the sheaths on the main stem 16–80 × (1·5)–2·0–7·0 mm, more or less inflated, with ligules 0·5–3·0 mm, the sheaths on the branches 15–30 mm, slightly inflated at the base of the larger branches, otherwise tightly enclosing the stem, with ligules 2·5–4·0 mm. Turions absent. Inflorescences (25)–35–55(–80) × 3–5 mm; peduncles (33)–45–140(–165) mm, very slender, flexuous. Flowers 9–20, in 5–9(–11) groups of (1)–2, the group more or less evenly spaced approximately 5–10 mm apart at maturity; carpels 4, the stigmas sessile. Fruits 2·6–3·8 × 1·8–3·0 mm, olive green or brown; beak 0·1–0·3 mm, ventral, subventral or subapical, verruciform. Vegetative reproduction by tubers 40–50 mm long formed on the rhizome is described and illustrated by Hagström (1916) and Elven & Johansen (1984).

P. vaginatus is more likely to be mistaken for *P. pectinatus* than for *P. filiformis*, as it is a robust, richly branched plant with open leaf sheaths. It differs from *P. pectinatus* in its distinctive habit, with short, broad, blunt leaves borne on large inflated sheaths on the main stem. The branches emerge from these sheaths, and are often leafless close to the sheaths but richly branched above, giving rise to a mass of leafy shoots. The branch leaves are much more like those of *P. pectinatus* than those on the main stems, with narrower sheaths and longer, narrower leaves but with apices which are more obtuse than those of that species. A further difference lies in the short ligules, which are often less than 1·5 mm long on the stem leaves and together with the more or less hyaline upper edge of the sheath form a "dog collar" at the top of the sheath. The mature inflorescences of *P. vaginatus* have a distinctive appearance, as the pairs of flowers on the axis of the inflorescence are more or less evenly spaced, although the proximal two pairs tend to be further apart and the distal two pairs nearer together than the others. A more critical difference from *P. pectinatus* lies in the sessile rather than stalked stigmas. The fruits of *P. vaginatus* are intermediate in size between those of *P. filiformis* and *P. pectinatus*, and the stigmas persist as a very small boss at the distal end.

TABLE 5. SPECIES ASSOCIATED WITH *POTAMOGETON* × *BOTTNICUS* IN TEN QUADRATS RECORDED IN THE RIVER TWEED AND RIVER TILL

	16	26	23	22	20	21	25	19	17	18	Quadrat no.
<i>Potamogeton</i> × <i>bottnicus</i>	10	10	10	10	6	6	5	9	7	8	
<i>Ranunculus</i> × <i>kelchoensis</i>			2	1	7	7	9		5		
<i>Potamogeton</i> <i>perfoliatus</i>				2	5						
<i>Ranunculus</i> <i>penicillatus</i> subsp. <i>pseudofluitans</i>						5				4	
<i>Potamogeton</i> <i>pectinatus</i>								5			
Bare substrate (%)	0	0	0	5	20	5	0	8	35	20	
Substrate	s	s	s	s	s	s	s	s	m	s	
Water depth (cm)	55	35	20	30	25	25	20	45	20	25	

Based on 1 × 1 m quadrats recorded on 18–19 July 1995 at R. Till below Twizel Bridge, NT/883.433 (quadrats 16–18) and R. Tweed S. of St Thomas's Island, Norham Mains, NT/923.493 (quadrats 19–23, 25–26). Cover-abundance of plants estimated on the Domin scale. Substrates recorded as s (stones) or m (mixture of fine sediment, stones and rocks). The identity of the *Ranunculus* taxa is discussed in the text.

As *P. pectinatus* and *P. vaginatus* are similar, the hybrid *P. × bottnicus* is not easy to identify on morphological grounds. However, the plants from the Rivers Tweed and Till differ from *P. vaginatus* in the absence of the characteristic habit of that species (although they grow in a very different habitat from that of *P. vaginatus* in the Gulf of Bothnia), in the longer ligules, especially on the lower stem leaves, the shorter inflorescences and the sterile pollen.

ISOZYME EVIDENCE

The isozyme evidence for the identity of *P. × bottnicus* is derived from work which we have reported in detail elsewhere (Hollingsworth *et al.* 1996a, b). In this study, 26 populations (447 plants) of *P. pectinatus*, 13 populations (270 plants) of *P. filiformis* and eleven populations (275 plants) of *P. × suecicus* were analysed. Although most of these samples were collected in Britain, material of *P. filiformis* from Sweden and *P. pectinatus* from Sweden and Crete was also included. In addition, we collected material from two populations (32 plants) of *P. × bottnicus* from the Rivers Till and Tweed and from a single population of *P. vaginatus* (24 plants) from Sweden.

Two of the nine enzyme systems which we studied (G6PDH, LDH) proved to be invariant across all the taxa and therefore offer no evidence about their inter-relationships. For the remaining seven systems, *P. × suecicus* showed additive banding patterns consistent with the hypothesis that it is a hybrid between *P. filiformis* and *P. pectinatus*. These systems included four which differed consistently between the putative parents in banding pattern (AAT, FBA and IDH) or in staining intensity (PGD).

The plants from the Till and Tweed differed in banding pattern from all the *P. × suecicus* populations studied in three enzyme systems (AAT, PGM and SKD). They also differed in staining intensity in a fourth system (PGD). The isozyme results are consistent with the hypothesis that these populations are of hybrid origin and that *P. pectinatus* is one of the parents, but do not support the suggestion that the other parent is *P. filiformis*. They are, however, explicable as the result of additive inheritance between *P. pectinatus* and *P. vaginatus*. The 32 plants sampled from the Till and Tweed showed no variation, suggesting that they may represent only a single clone (although the isozyme loci studied represent only a minute proportion of the total genome, and there may be variation which we have not detected).

DISTRIBUTION AND HABITAT

The plants referred here to *P. × bottnicus* are known from two rivers. Quadrats illustrating the vegetation in which they grow are presented in Table 5. In the River Till downstream of Twizel Bridge *P. × bottnicus* grows in rapidly flowing water 20–55 cm deep, where the plants are rooted in a stony substrate or in a mixture of fine sediment, stones and rocks. Beds of *P. perfoliatus* also grow in this stretch of river, and there are also stands of *Ranunculus* spp. A few fronds of *Lemna minor* are

found in places where rooted macrophytes reach the water surface and impede the flow of the river. *P. pectinatus* does not occur in this stretch of the river, but it does grow elsewhere in the River Till. At Ford Bridge, 13–14 km upstream of the *P. × bottnicus* colony, *P. pectinatus* is found with *Myriophyllum spicatum*, rooted in fine silt. *P. pectinatus* is also found in the River Tweed at its junction with the River Till, some 1·5 km downstream of Twizel Bridge, where it grows in a sandy substrate. *P. filiformis* is not recorded from the River Tweed or any of its tributaries.

The lower stretches of the River Tweed are difficult to survey, and we have not been able to examine the entire length of the river. We know of only one colony of *P. × bottnicus*, in a swiftly flowing stretch of river on the south side of St Thomas's Island. Here it grows in some quantity in water 15–45 cm deep, rooted in a substrate of stones. *P. pectinatus* is occasionally mixed with *P. × bottnicus* but usually grows nearby as separate clumps. *P. × bottnicus* also grows with clumps of *Ranunculus* spp. and is occasionally associated with small quantities of *P. crispus* and *P. × salicifolius*. *P. × bottnicus* is absent from deeper stretches of the river immediately upstream and downstream of this colony; these areas are characterised by large beds of the broad-leaved species *P. lucens* and *P. perfoliatus* and their hybrid *P. × salicifolius*. There are earlier records of "*P. × suecicus*" from stretches of the Tweed between the River Till and St Thomas's Island (including some herbarium specimens now re-identified as *P. × bottnicus* and cited below). The hybrid is often washed up by the edge of the river downstream of St Thomas's Island, and we have regularly found it in flotsam at Union Bridge. Existing records and our own fieldwork suggest that *P. × bottnicus* has a restricted distribution in the lower stretches of the river.

The *Ranunculus* plants in the River Tweed and its tributaries are difficult to identify as they include at least three sterile hybrids of uncertain parentage (Holmes & Whitton 1975b). The most frequent associate of *P. × bottnicus* at St Thomas's Island is a very robust sterile *Ranunculus* hybrid with capillary leaves which have rather few segments, and intermediate and laminar leaves on some (but not all) stems. This is the plant which Holmes & Whitton (1975a, b) refer to as "*R. fluitans* × ?" and which appears to us to be the hybrid subsequently described by Webster (1990) as *R. × kelchoensis* (*R. fluitans* × *R. peltatus*). Robust *Ranunculus* plants which grow with *P. × bottnicus* in the R. Till resemble this hybrid in most characters, but we have not seen any intermediate or laminar leaves on this population. Nevertheless, we have also (albeit rather tentatively) referred these to *R. × kelchoensis*. At both sites there is also a less robust *Ranunculus* with bushier capillary leaves and no laminar leaves. This closely resembles *R. penicillatus* subsp. *pseudofluitans* and is named as such in Table 5. However, it is less vigorous than typical material of that taxon and we did not collect any fruiting plants, so we cannot rule out the possibility that it is a sterile hybrid which has *R. penicillatus* subsp. *pseudofluitans* as one parent.

The herbarium specimens of *Potamogeton* × *bottnicus* from Britain that we have seen, or collected, are listed below:

ENGLAND: Cheviot, v.c. 68: River Tweed, Bankhead, Loanend, 30 August 1942, G. Taylor (BM, E). Right bank of River Tweed, Norham, NT/901.477, 3 August 1972, N. T. H. Holmes (BM). South bank of River Tweed, Norham Mains, NT/920.496, 20 September 1971, N. T. H. Holmes (BM). River Tweed near Tweed Villa, Norham, NT/893.467, 25 May 1974, G. A. Swan (BM). River Tweed opposite St Thomas's Island, Norham Mains, NT/919.494, 25 May 1974, G. A. Swan (BM). River Tweed S. of St Thomas's Island, Norham Mains, NT/923.493, 19 July 1995, R. J. Gornall, P. M. Hollingsworth & C. D. Preston (Preston 95/43) (BM, CGE, E, LD, LTR). River Till below Twizel Bridge, Tillmouth Park, Twizel, NT/885.434, 15 May 1972, N. T. H. Holmes (BM). River Till below Twizel Bridge, NT/883.433, 25 June 1992, P. M. Hollingsworth & C. D. Preston (Preston 92/88, 92/89) (BM, CGE, LTR); —, 26 August 1994, P. M. Hollingsworth & C. D. Preston (Preston 94/210, 94/217) (CGE, E, LTR); —, 18 July 1995, R. J. Gornall, P. M. Hollingsworth & C. D. Preston (Preston 95/45) (BM, CGE, LTR).

SCOTLAND: Berwicks., v.c. 81: River Tweed above Union Bridge, Hutton, 30 August 1942, G. Taylor (BM).

P. × BOTTNICUS IN EUROPE

The centre of diversity of *Potamogeton* subgenus *Coleogeton* in Europe is the Gulf of Bothnia, where all three European species occur, and where the three possible hybrids have all been

reported, *P. filiformis* × *P. pectinatus* (*P. × suecicus*), *P. filiformis* × *P. vaginatus* (*P. × fennicus* Hagstr.) and *P. pectinatus* × *P. vaginatus* (*P. × botnicus*). A thorough understanding of *P. × botnicus* in Europe would require a detailed study of the subgenus in this area. We have not had the opportunity to make such a study, so we have restricted our remarks to two topics. These are the lectotypification of *P. × botnicus*, which is necessary in order to justify the use of this binomial, and the identity of *P. × meinshausenii*, a robust plant described as the hybrid between *P. pectinatus* and *P. vaginatus* from rivers in Europe south of the range of *P. vaginatus*, and therefore a potential parallel to the British *P. × botnicus*.

LECTOTYPIFICATION OF *P. × BOTNICUS* HAGSTR.

In his description of *P. × botnicus*, Hagström (1916) mentioned material from three localities. C. W. Fontell first discovered the plant near Jakobstad, Finland, but although he published a description of the plant (Fontell 1902, 1903, 1909) he did not give it a binomial. In addition to this locality, Hagström reported the hybrid from two Swedish localities, Tynderö near Sundsvall in Medelpad and Hernösand to Angermania. Hagström also mentioned a specimen from a Russian site, but as he only identified this as either *P. × botnicus* or *P. × fennicus*, this plant need not be considered further.

We requested type material of *P. × botnicus* from a number of herbaria (**BM**, **C**, **H**, **LD**, **OLU**, **RIG**, **S**, **TURA**) and located possible syntypes from all the localities cited by Hagström. These collections are listed below, preceded by the name given originally to the material by the collector if this is apparent from the label.

A. *P. pectinatus* × *vaginatus*. Östrobotnia media. Pedersöre. Sandön prope Jacobstad in mare, 15 July 1898, C. W. Fontell (C). Apparent duplicates with less detailed labels at **LD** (ex herb. J. O. Hagström), **S**.

B. *P. pectinatus* × *vaginatus*. Ostrobotnia media: på sandbotten invid Sandön i Bottniska viken, 18 July 1899, C. W. Fontell (TURA).

C. *P. pectinatus* × *vaginatus*. Ostrobotnia media. Pedersöre. På sandbotten invid Sandön, 19 September 1900, C. W. Fontell (TURA).

D. Medelpad. Tynderö, undated, K. A. Holm (LD). Determined as *P. pectinatus* L. × *vaginatus* Turcz. (*P. botnicus* m. in mscr.) by J. O. Hagström, 1 May 1909.

E. *P. vaginatus*. Suecia: in prov. Ångermanland, in mari ad oppidum Hernösand, freto australi, 62°, 37' lat. bor, 29 July 1899, G. Tiselius, Pot. scand. no. 207 (S). Determined as *P. pectinatus* L. × *vaginatus* Turcz. (*P. botnicus* Hagstr.) by J. O. Hagström, 1910.

Two other collections may be mentioned. A specimen at **LD** collected as *P. pectinatus* by J. A. Sandman on 20 July 1884 at Karlö, Ostrobotnia borealis, was determined as *P. pectinatus* L. × *vaginatus* Turcz. (*P. botnicus* m.) by Hagström on 8 October 1906 but is not cited in the protologue. Secondly, specimens collected by E. af Hällström from Kuolajärvi, Finland, on 29 August 1910 and distributed from **H** were initially determined as *P. filiformis* × *vaginatus* by Hagström but redetermined by him as *P. pectinatus* × *vaginatus* in 1920, after the publication of the binomial *P. × botnicus*. Some of these specimens bear modern labels on which the date of the redetermination is not apparent.

The lectotype of *P. × botnicus* should be selected from collections A-E above. We have chosen collection D. Although this is undated and has a modern label, it also bears a note signed by Hagström and dated 1 May 1909. P. Lassen has kindly provided an approximate translation:

This plant ought to be among the most fine and precious in your herbarium. Because it is the hybrid *P. pectinatus* L. × *vaginatus* Turcz. (*P. botnicus* m. in mscr.). It is not known before from Sweden, but from the Finnish coast of the Gulf of Bothnia. I have eagerly looked for it in herbaria and am happy to have found it now from the Swedish side. Please make a trip to Tynderö this summer and try to find its growing-place. There is a locality for *P. vaginatus* there and there it should be sought. I believe the Reverend Holm would like to accompany you, because he is evidently a keen botanist. Possibly you could also find there the hybrid *P. filiformis* × *vaginatus* as well as *P. filiformis* × *pectinatus*!

The lectotype conforms to Hagström's description of the hybrid, and the citation "m. in mscr." clearly links it to the protologue. Curiously, Hagström did not describe the morphology of the

sheaths despite the fact that he usually stressed the taxonomic importance of closed as opposed to open stipules and sheaths. However, we dissected twelve young sheaths of specimen D, all of which were open, and the carpels have sessile stigmas. We therefore conclude that it is indeed *P. pectinatus* × *P. vaginatus*.

Of the other collections, A also has open sheaths (26 dissected, 23 open, three inconclusive) and is also referable to *P. pectinatus* × *P. vaginatus*, although all the specimens lack flowers. There is no direct evidence that Hagström saw collections B and C. Specimen B is probably erroneously identified as *P. pectinatus* × *P. vaginatus*. We dissected 31 sheaths of which 27 were open but two appeared to be distinctly tubular (two were inconclusive), but it must be admitted that the interpretation of the sheath morphology of old herbarium specimens is not easy, even after the material has been rehydrated. We found no evidence to doubt the identity of C. Collection E bears Hagström's determinavit slip as *P. × botnicus*, but of the 15 sheaths we dissected six were tubular and five open (with four inconclusive), and this plant is therefore a hybrid of *P. filiformis* (possibly *P. filiformis* × *P. vaginatus*).

The nomenclature and typification of *P. × botnicus* can be summarised as follows:

Potamogeton × botnicus Hagstr., *Kungl. Svenska Vet.-Akad. Handl.* 55(5): 52 (1916). Lectotype: Medelpad. Tynderö, undated, K. A. Holm (LD), designated here. Hybrid formula: *P. pectinatus* L. × *P. vaginatus* Turcz.

THE IDENTITY OF *P. × meinshausenii* JUZ.

Juzepczuk (1955) reported *P. pectinatus* × *P. vaginatus* from the River Pudostj near Gatchina, S.W. of St Petersburg, Russia. This grew "in aqua frigida e pura fluminis (celeriter fluentis)". It was originally discovered by K. F. Meinshausen, who had collected it on several occasions between 1887 and 1896, but named it *P. pectinatus* var., *P. flabellatus* and, subsequently, *P. vaginatus*. Juzepczuk gave his plant the binomial *P. × meinshausenii*, distinguishing it from *P. × botnicus* by a number of characters including its much more robust habit, wider sheaths, longer leaves and longer inflorescences. Although he accepted that both *P. × botnicus* and *P. × meinshausenii* were hybrids between *P. pectinatus* and *P. vaginatus*, he had a number of reasons for giving the Russian plant a new binomial including the fact that *P. × botnicus* is a product of recent hybridisation and grows with its parents, whereas the Russian plant is probably a very ancient and relict clone growing in the absence of closely related species. *P. × meinshausenii* has subsequently been reported by Galinis (1977) from lakes and a number of strongly flowing rivers near Trakai and Vilnius in Lithuania. Both the Russian and the Lithuanian sites for the hybrid are well south of the current distribution of *P. vaginatus*.

Isotypes of *P. meinshausenii* were widely distributed, and we have seen them in BM, E and H. The appearance of this hybrid is extremely similar to that of the British *P. × botnicus*. At first we thought that these populations represented a parallel situation to the one we have described in the Rivers Tweed and Till, citing them as such in Hollingsworth *et al.* (1996a). However, we have subsequently examined the material more closely and find that the sheaths of *P. × meinshausenii* are consistently and manifestly tubular (17 examined). The stigmas are sessile and the pollen appears to be sterile. These characters suggest that *P. × meinshausenii* is referable to *P. × suecicus*, but the very robust sheaths which are clearly tubular differ from those of the British populations of *P. × suecicus*, which have sheaths with a very thin, hyaline adaxial side which has to be dissected very carefully in order to establish its tubular nature. An isozyme study of *P. × meinshausenii* would be rewarding. Whatever its identity, the morphology of the sheaths rules out *P. × botnicus*, unless the type population is displaying a character found in neither of the parental species.

DISCUSSION

Dandy & Taylor (1946) first identified plants from the Rivers Ure, Wharfe and Tweed as *P. × suecicus*. Their paper was based on a very detailed study of material from the Wharfe and Ure in Yorkshire, which Taylor collected repeatedly from different sites along these rivers over a period of

six years. By contrast, they only knew the plant from the Tweed from Taylor's collections made at two sites on a single day (the population in the Till was not discovered until later). Bance's (1946) detailed anatomical studies of *P. × suecicus*, which provided powerful support for Dandy & Taylor's hypothesis, was based exclusively on material from the Wharfe and the Ure.

The identification of *P. × suecicus* from the Yorkshire rivers has been supported by recent studies (Hollingsworth *et al.* 1996a). However, the morphological and isozyme evidence reviewed in this paper have thrown great doubt on the previous identification of *P. × suecicus* in the Till and Tweed. Plants of *P. × suecicus* either have all the leaf sheaths tubular or a mixture of tubular and open sheaths, whereas the sheaths of the plants in the Till and Tweed are consistently open. If only morphological evidence were available, one might argue that this merely represents one extreme in the range of variation of *P. × suecicus*. However, the isozyme evidence has virtually ruled out this possibility. We must admit, however, that one cannot use isozyme evidence to categorically disprove a suggested parentage of a hybrid growing in the absence of one or both parents, as it is impossible to rule out the possibility that the hybrid may have been the product of parental genotypes which have not been detected. Despite these caveats, the suggestion that the Till and Tweed plants are *P. × suecicus* is scarcely tenable in the light of recent evidence.

We have published the identification of the Till and Tweed plants as *P. × botnicus* as all the evidence we have is consistent with this hypothesis, and we cannot come up with any other explanation of the data. However, we regard the identification as a hypothesis to be tested by future work rather than an established fact. Further isozyme studies involving *P. vaginatus* and *P. × botnicus* from the Gulf of Bothnia, and other molecular studies, would be likely to provide valuable additional evidence.

If we assume that our identification of the Till and Tweed plants as *P. × botnicus* is correct, how can we account for its presence in these rivers? The Quaternary history of many *Potamogeton* species is relatively well known, as their fruits are often preserved in lake sediments (Godwin 1975). The same evidence is not available for sterile hybrids, and we can only speculate about their history. One possible explanation for the presence of *P. × botnicus* in the Rivers Tweed and Till is that it is a relict hybrid. Although *P. vaginatus* is now restricted in Europe to Scandinavia, there is fossil evidence that it formerly grew as far south as Britain and the Netherlands. Fruits of *P. cf. vaginatus* have been found in deposits near Mundesley, Norfolk, which date from the first British glacial period, the early Anglian (West 1980). *P. vaginatus* fruits have been found in deposits from the last (Weichselian) glacial period at Sourlie, S.W. of Glasgow, dating from 30,000 BP (H. Bos & J. H. Dickson, pers. comm.), and from the Netherlands where they have been dated at 45,000 BP (Cappers 1993; Cappers *et al.* 1993). It seems unlikely that a sterile hybrid could have persisted in our area for 30,000 years, and the hypothesis that *P. × botnicus* is a relict hybrid would be more plausible if there were evidence that *P. vaginatus* had survived in Britain after the last glacial period. An alternative explanation for the presence of *P. × botnicus* in the Rivers Tweed and Till is long-distance dispersal of vegetative fragments, or seed resulting from a cross between *P. pectinatus* and *P. vaginatus*, from northern Europe.

It is not unusual for *Potamogeton* hybrids to occur in lakes or rivers from which one or both parents are absent, although these sites usually lie within the total range of both parents. There are, however, some *Potamogeton* and other hybrids in Britain which occur naturally outside the current distributional limit of the rarer parent. A striking parallel to *P. × botnicus* is provided by *Carex recta*. This is usually treated as a species, but it is derived from hybridisation between *C. aquatilis*, which is widespread in northern Britain, and *C. paleacea*, which is confined in Europe to the coasts of Scandinavia and N.W. Russia (Faulkner 1972, 1973). Other hybrids which extend outside the limit of the rarer parent include *Circaeaa × intermedia* (Raven 1963), *Nuphar × spenneriana* (Heslop-Harrison 1953), *Potamogeton × suecicus* (Dandy & Taylor 1946) and *Ranunculus × levenensis* (Padmore 1957; Gibbs & Gornall 1976; Gornall 1987), although both parents of these hybrids are found in Britain. It has been suggested that all these hybrids may be relicts persisting by vegetative reproduction in an area where the rarer parent formerly grew or, in the case of *R. × levenensis*, in areas to which the seeds of *R. reptans* are thought to be repeatedly introduced by waterfowl. *Circaeaa × intermedia* is also capable of vegetative spread from these relict populations into disturbed habitats. In Ireland the fertile hybrid *Saxifraga × polita* is present north of the current range of *S. hirsuta*, and its presence is thought to indicate that *S. hirsuta* was once more widespread (Webb 1948, 1975). All these hybrids were known for many years before their origin was

appreciated, and their hybrid nature was often revealed by detailed morphological or genetical studies. This suggests that there may be further rather cryptic hybrids awaiting discovery in the British Isles.

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Five new species of *Rubus* L. (Rosaceae) with transmarine ranges

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ABSTRACT

Five new species of *Rubus* L. (Rosaceae) are described, all with ranges extending to more than one country and across a wide expanse of sea. *R. waddellii* D. E. Allen, sp. nov. (ser. *Sylvatici* (P. J. Mueller) Focke) occurs in quantity in one part of the Isle of Man and is known also from two counties in the far north of Ireland, where it may well prove to be widespread. *R. anglobelgicus* D. E. Allen & H. Vannerom, sp. nov. (ser. *Anisacanthi* H. E. Weber), is widespread in the west half of Belgium and locally common in one district of Hampshire by the south-east shore of Southampton Water. *R. davisi* D. E. Allen, sp. nov. (ser. *Rhamnifolii* (Bab.) Focke), confined to heaths and locally abundant in south-east Dorset, is known elsewhere in Wessex as well as in Pembroke and Jersey. *R. sempernitens* D. E. Allen & L. J. Margetts, sp. nov. (ser. *Radula* (Focke) Focke), is widely distributed in Devon and known from one wood in the Cotentin Peninsula, dép. Manche, France. *R. venetorum* D. E. Allen, sp. nov. (ser. *Hystrix* Focke), is locally abundant in Brittany and neighbouring parts of north-west France and in the largest of the Isles of Scilly; isolated patches have also been found in four counties in the far south of the English mainland.

KEYWORDS: apomictic species, Brambles, distribution.

INTRODUCTION

It is now the convention among *Rubus* specialists to privilege with published descriptions only morphotypes with at least a “regional” (as opposed to no more than a “local”) distribution, in order to keep within manageable limits the very great number of potential taxa in this mainly apomictic genus. The five new species here described would not all have been considered to have ranges sufficiently wide to merit having a name conferred on them had not those ranges been found in each case to extend across a wide expanse of sea to a second country. Such a distribution in itself would seem to be of sufficient interest phytogeographically to warrant any morphotypes displaying it being accorded taxonomic recognition.

DESCRIPTIONS OF NEW SPECIES

1. *Rubus waddellii* D. E. Allen, sp. nov.

Turio altissime arcuatus, obtusangulus faciebus parum vel profunde excavatis, purpureo-rufescens, glaber vel glabrescens, aculeolis paucis minimis interdum praeditus, aculeis crebris 8–12 per 5 cm subaequalibus ad angulos dispositis mediis (3–7 mm) tenuibus e basi lata compressa rectis vel curvatis declinatis vel subpatulis interdum confluentibus munitus. Folia 3–5-nata, pedata, saepissime imbricata, crassiuscula et duriuscula, superne nitentia strigosa, inferne sparsim pubescentia vel glabra, quorum petioli aculeis (1–4 mm) numerosis curvatis muniti. Foliolum terminale rotundum vel ovatum, apice acuminatum, basi emarginatum vel cordatum, inaequaliter dentato-serratum dentibus primis nonnullis saepe patulis, ad marginem undulatum, eiusdem petiolulo quadruplo vel triplo longius; foliola infima brevissime (1–2 mm) petiolulata. Inflorescentia usque ad apicem non vel vix foliata, foliis ternatis inferne et saepe usque ad decem simplicibus et trilobatis bracteisque foliosis saepissime nonnullis magnis superne instructa, late vel anguste pyramidalis ad apicem truncata vel rotundata congesta, ramulis axillaribus omnibus erectis vel adscendentibus multifloris aucta. Rachis flexuosa, pilos numerosis vestita, aculeis crebris saepe basi latis purpureis plerumque

declinatis vel curvatis munita. Pedicelli sicut rachis vestiti aculeis nonnullis tenuibus (1–5 mm) muniti. Flores c. 2 cm diametro, cupulati. Sepala viridia vel grisea, albo-marginata, pilis densis aciculisque brevibus sparsim vel nullis praedita, non attenuata, patentia vel reflexa. Petala alba subrotunda vel late obovata, ad marginem pilis longis sparsim praedita, non contigua. Stamina alba stylos virideos-flavescentes parum vel multo superantia. Antherae glabrae. Carpella glabrescentia vel pilis interdum longis ornata. Receptaculum pilosum. Fructus rotundus.

Stem high-arching, bluntly angled with shallowly to deeply furrowed sides, dull reddish-purple, pruinose, glabrous or glabrescent, with many sessile glands and sometimes a few very small pricklets; prickles 8–12 per 5 cm, confined to the angles, tending to cluster, subequal, 3–7 mm, the longer ones equalling the stem diameter, slender from a broad compressed base, straight or curved, slanting or subpatent, sometimes confluent, crimson with a yellow point. Leaves pedate; leaflets 3–5, usually partly imbricate, thick and hard to the touch, shining dark green and strigose above, green and thinly pubescent or glabrous beneath; terminal leaflet 5–7(–9) × 4–6(–7) cm, rotund or ovate, with an acuminate (1–1.5 cm) apex and emarginate or cordate base, irregularly dentate and slightly compound serrate with often several principal teeth patent, undulate on the margin, the petiolule $\frac{1}{2}$ as long as the lamina; petiolules of basal leaflets 1–2 mm; petiole longer than the basal leaflets, yellowish becoming dark purple, with many short and medium simple and tufted hairs, many sessile and subsessile glands and 6–10(–13) curved prickles 1–4 mm. Flowering branch with 3-foliate leaves below and up to 10 simple and trifid leaves above together with usually several conspicuous leaf-like simple and trifid axillary bracts, not or not quite leafy to the apex; inflorescence a broad or narrow pyramid with a truncate or rounded congested top and erect or ascending axillary peduncles, the upper and middle ones many-flowered and divided above the middle and usually shorter than but sometimes as long as their leaves; rachis flexuous, with numerous patent short to medium simple and tufted hairs, numerous sessile and subsessile glands and frequent often broad-based purple prickles 2–7 mm varying much in length and direction but mostly declining or curved; pedicels clothed like the rachis, with several slender prickles 1–5 mm. Flowers c. 2 cm in diameter, cupped; sepals green or greyish, white-bordered, with dense short simple and stellate hairs, numerous sessile and subsessile glands and rare or no short acicles, with a short but distinct point, patent or reflexed; petals 6–9 × 5 mm, pure white, roundish or broadly obovate, irregularly ciliate with occasional long simple and stellate hairs on the sinuate margin, not contiguous; stamens slightly to far exceeding styles, filaments white, anthers glabrous; styles yellowish-green; young carpels hairy or glabrescent, the hairs sometimes long; receptacle hairy; fruit globose. Flowering in July and August.

HOLOTYPE: bank of ditch of hill lane below Bulbin, near Glenmullan, N.N.W. of Drumfree, East Donegal, v.c. H34, C/38.41, 9 August 1992, D. E. Allen s.n. (**BM**).

Exsiccatae (all BM):

- v.c. 71, Man: hedge-top, Glenmaye village, SC/23.79, 4 July 1960 and 4 August 1963; hedge of lane N. of Fairy Dam, SC/296.782, 20 July 1960; old lane between Ballanank and Orrisdale farms, 2 km N.N.E. of Ballasalla, SC/290.717, 20 July 1960; bank of Cronk Road, Union Mills, SC/350.775, 10 August 1975; side of track just N. of Lonan church, SC/430.833, 11 August 1975, D.E.A. s.n.
 v.c. H38, Down: N. of Banbridge, side of a lane branching off road to Belfast, c. J/15.47, 13 July 1901, W. M. Rogers s.n. as *R. hesperius* (herb. Barton & Riddellsell, no. 8529).

This member of ser. *Sylvatici* can be identified at once by its cupped flowers of broad white petals, its dark, thick, shining stem leaves with roundish or ovate leaflets at most thinly hairy beneath, its more or less glabrous stem and a flowering branch, when well-developed, with conspicuously numerous leaves as well as leaf-like bracts. It is one of several *Rubus* species widespread in the Isle of Man for which a serial number ("M39") has for many years now stood in for a scientific name. There it is "thinly scattered over the mid-eastern section of the central and south-central lowlands . . . especially up to 700 ft [213 m] on the slopes overlooking the central valley, with a main concentration between the headwaters of the River Dhoo and the Santon Burn" (Allen 1986). Isolated bushes also occur far to the north and west of this core range. In all it has been noted in seven 10-km grid squares: SC/2.7, 2.8, 3.7, 3.8, 4.7, 4.8, 4.9, all on the Manx Slates, which constitute the near-universal formation of the island's southern three quarters. Tolerant of a considerable degree of exposure, it is

the ecological counterpart of *R. silurum* (Ley) Ley of the upland areas of Wales, a species which it also superficially resembles. Initially, B. A. Miles and E. S. Edees, to whom material was submitted in the 1960s, respectively suggested *R. sciocharis* (Sudre) W. C. R. Watson and "*R. carpinifolius*" (i.e. *R. platyacanthus* P. J. Mueller & Lef.) as the bramble's identity, determinations which they both, however, subsequently withdrew, concluding that it matched no British *Rubus* species so far described, a verdict with which A. Newton was to concur some years later.

As the Manx *Rubus* flora contains, at least at the present day, no two species, either described or undescribed, from which this very distinct bramble could have arisen by hybridization within the island, it has always seemed likely that it might also occur in one or more of the neighbouring regions bordering the Irish Sea. Its reported presence in Scotland in Kirkcudbright, v.c. 73 (Allen 1986), was based on a specimen collected c. 1975 which is unfortunately no longer extant (O. M. Stewart, in litt. 1993); the necessary verification of that record accordingly remains outstanding. In 1993, however, two bushes were recognised as being this same bramble in a hill lane in East Donegal (Allen 1994). A further Ulster specimen, collected in Down at the turn of the century, has since come to light in BM. The species may well prove to be widespread in the far north of Ireland, where the *Rubus* flora has been investigated so far at best only patchily. One other species, *R. lettti* Rogers, is similarly known as yet only in the Isle of Man and the north half of Ireland. In recognition of this dual range, it seems appropriate that the name should commemorate the Rev. Cosslett Herbert Waddell (1858–1919), who, uniquely, was a pioneer in the study of the group in both the Isle of Man and his native Ulster.

The distribution of the species is shown in Fig. 1.

2. *Rubus anglobelgicus* D. E. Allen & H. Vannerom, sp. nov.

Planta robusta. Turio altissime arcuatus, obtusangulus faciebus concavis, purpureus, glabrescens, glandulis stipitatis longis et aciculis longis et aculeolis sparsim praeditus, aculeis crebris 5–20 per 5 cm subaequalibus plerumque ad angulos dispositis tenuibus e basi lata compressa plerumque declinatis munitus. Folia 5-nata, digitata, plana vel concava, non vel vix imbricata, superne glabrescentia, inferne subcinerea tomentosa et sparsim breviter pilosa (praesertim ad venos), quorum petioli petiolulique glandulis stipitatis et aciculis et aculeolis saepe glanduliferis paucis, petioli aculeis (3–4 mm) numerosis curvatis vel declinatis muniti. Folium terminale ovatum vel anguste obovatum vel ellipticum, apice acuminatum, basi integrum vel emarginatum, inaequaliter serratum dentibus primis nonnullis patulis, ad marginem undulatum, eiusdem petiolulo triplo vel quadruplo longius; foliola infirma breviter (3–6 mm) petiolulata. Inflorescentia usque ad apicem non foliata, foliis ternatis inferne et uno vel duo simplicibus et trilobatis superne instructa, longa, subpyramidalis ad apicem rotundata congesta, ramulis axillaribus infimis saepe longissimis distantibus adscendentibus vel mediis erectis vel patulis aucta. Rachis flexuosa, acute angulata sulcata, pilis numerosis vestita, aculeolis paucis et aculeis (4–7 mm) numerosis declinatis curvatisque, ad apicem saepe glandulis stipitatis crebris munita. Flores c. 3 cm diametro. Sepala griseo-viridia tomentosa et sparsim pilosa, glandulis stipitatis aciculisque numerosis munita, anguste albo-marginata, omnia attenuata, reflexa vel tandem erecta. Petala roseola vel alba, ovata vel obovato-cuneata vel elliptica, ad apicem sparsim pilosa, vix emarginata, remota. Stamina alba, stylos flavescentes vel virides, basi rufescentes, multo superantia. Antherae glabrae vel pilis rarissimis praeditae. Carpella dense pilosa. Receptaculum glabrum vel pilis rarissimis praeditum. Fructus parum oblongus. Facies Rubum geniculatum Kalt. revocat.

Robust. Stem tall (up to c. 2 m) and high-arching, stout (6–10 mm in diameter), bluntly angled with furrowed sides, dull purple, glabrescent, with rare long stalked glands, long acicles and prickles; prickles c. 7–9 per 5 cm, mostly confined to the angles, subequal, 5–10 mm, slender from a broad compressed base, mostly slanting or a few subpatent, crimson. Leaves digitate; leaflets 5, flat or concave, not contiguous or slightly imbricate, yellowish-green and glabrescent above, pale or greyish green and felted and with sparse short mostly simple hairs chiefly on the veins beneath; terminal leaflet c. 9–13 × 5–8 cm, ovate or narrowly obovate or elliptical, with an acuminate apex c. 2 cm and entire or emarginate base, unequally and slightly compound-serrate with several of the principal teeth patent (rarely, one or two retrorse), with undulate margins, the petiolule $\frac{1}{4}$ – $\frac{1}{3}$ as long as the lamina; petiolules of basal leaflets 3–6 mm; petiole about as long as the basal leaflets, dark purple, with occasional to numerous short or medium simple and tufted hairs and 15–20 curved



FIGURE 1. The distribution of *Rubus waddellii* in the British Isles.

or declining prickles 3–4 mm, both petiole and especially the petiolules with occasional and varying numbers of short and medium and long stalked glands, medium and long acicles and pricklets (often gland-tipped). Flowering branch with 3-foliate leaves below and 1–2 simple and trifid leaves above, not leafy to the apex; inflorescence long, subpyramidal with a congested rounded top, the many-flowered peduncles all ascending or the middle and upper ones erect or patent, the axillary ones 3–10 cm, the lowest one 6–11 cm distant from the next, often very long and subequalalling the main axis, all shorter than their leaves and divided well above the middle; rachis somewhat flexuous, sharply angled and furrowed, with numerous patent and adpressed simple and tufted hairs, numerous sessile glands, occasional pricklets and numerous subequal broad-based slender-pointed mixed declining and curved prickles 4–7 mm with a tendency to cluster, the uppermost rachis and pedicels often with rather numerous stalked glands of varying lengths. Flowers (2–)3(–4) cm in diameter; sepals greyish-green, white-bordered, felted, with sparse short and medium simple and tufted hairs, numerous sessile glands and usually many very short and medium stalked glands and few to many medium acicles, long-pointed, reflexed in flower, reflexed or erect in fruit; petals 12–13 × 5–7 mm, pale pink to white, ovate or obovate-cuneate or elliptical, with sparse short hairs on the margin at the apex, erose, distant; stamens much exceeding styles, filaments white, anthers glabrous or with

rare long hairs; styles yellowish or green, sometimes reddish-based; young carpels densely hairy; receptacle glabrous or with a few hairs; fruit large, longer than broad. Flowering in July and August. Facies recalling that of *Rubus geniculatus* Kalt.

HOLOTYPUS: hedgebank, Zichem, near Diest, Belgium, 8 July 1994, H. Vannerom no. 940708.5 as *R. spinuliferus* [sic] (**BM**).

This very distinct, strikingly tall and robust bramble, with long elliptical leaflets with conspicuously "jagged" dentation and long, narrow, usually pale pink petals, is widely distributed in the west half of Belgium, where it is known from 28 4 × 4 km grid-squares (H. Vannerom, in litt.). It has passed there till now as *R. spinulifer* P. J. Mueller & Lef., but that determination cannot be sustained, for excellent photographs taken by W. C. Barton of the holotype of that species in Lausanne (**LAU**) show that it possesses, inter alia, prickles of a different shape. Sudre (1912), who saw at least one specimen of Lefèvre's from the type locality (Waligny, Forêt de Retz, dép. Aisne, France), pronounced *R. spinulifer* intermediate between *R. fuscus* Weihe and *R. koehleri* Weihe, a verdict which implies a heavily glandular plant. This is borne out by the two numbers, 554 and 555, he distributed of *R. spinulifer* in his *Batotheca*, which are both patently different from the Belgian plant here described. This latter, by contrast, has only a very thin scatter of glands, acicles and prickles, to the extent that it seems to belong best in series *Anisacanthi*.

In 1993 a specimen of the Belgian "*R. spinulifer*" sent to me by Vannerom in a miscellaneous exchange parcel struck me as suspiciously similar to an unnamed bramble ("H494") locally common in one district on the Tertiary gravels of the far south of Hampshire, v.c. 11, between Gosport and the River Hamble (to the north bank of which it extends in just the one place), by the south-east shore of Southampton Water. Apparently confined to the two 10-km squares SU/5.0 and SU/5.1, it occurs in shady places in general but more especially on wood margins. A series collected from one of these localities the following summer was sent to Vannerom, who confirmed it as indeed the plant well-known to him in Belgium. Other British *Rubus* specialists who subsequently saw specimens from both countries side-by-side at the 1994 B.S.B.I. Exhibition Meeting concurred with that opinion.

R. anglobelgicus is close in many respects to another British bramble, *R. celticus* Newton, a species apparently endemic to north-west Wales. *R. celticus*, however, is normally much more glandular (and accordingly regarded as best placed in series *Radula*) and typically has an inflorescence with a long, narrow, subracemosous top and much more numerous, often subpatent prickles on the rachis. Its petals are also much broader and its pedate leaves hairier beneath, their terminal leaflets much more often having straight sides converging to a narrow base.

Representative exsiccatae from six localities in v.c. 11 have been deposited in **BM**. Specimens from various Belgian localities collected by J. van Winkel and labelled "*R. diestemius* Vannerom ined." are in Brussels (**BR**). In Vienna (**W**) and Hamburg (**HBG**), in the herbaria of A. Neumann and A. Schumacher respectively, there are also examples labelled "*R. lejeunei* var. *bracteatus* Sudre" collected by Vannerom (no. 66/59) from Assent, Belgium, on 16 July 1966.

The distribution of the species in the British Isles is shown in Fig. 2.

3. *Rubus davisii* D. E. Allen, sp. nov.

Turio arcuato-decumbens, obtusangulus faciebus concavis, purpureus vel atrorufescens, glabrescens, aculeis 8–12 per 5 cm subaequalibus patulis longis (6–10 mm) tenuibus e basi lata compressa plerumque ad angulos dispositis interdum confluentibus ± rectis munitus. Folia 4–5-nata, digitata vel subpedata, imbricata vel non contigua, superne glabra, inferne subcinerea tomentosa et praesertim ad venos numerosis satis longis pilis vestita, quorum petioli aculeis (3–4 mm) numerosis curvatis muniti. Foliolum terminale subrotundum vel ovatum, apice acutum vel acuminatum, basi integrum vel emarginatum, dentato-serratum, planum, eiusdem petiolulo duplo vel triplo longius; foliola infima brevissime (1–3 mm) petiolulata. Inflorescentia saepe fere usque ad apicem foliata, foliis ternatis inferne et 1–8 simplicibus et trilobatis superne instructa, late pyramidalis, truncata, ad apicem congesta, ramulis axillaribus omnibus adscendentibus infimis longis distantibus paniculatis aucta. Rachis flexuosa, pilis numerosis vestita, aculeis (5–9 mm) numerosis inaequalibus patulis et declinatis et curvatis munita. Flores c. 2–3 cm diametro. Sepala grisea, albo-marginata, pilis numerosis et aciculis saepe conspicue numerosis praedita, nonnulla attenuata, reflexa. Petala roseola vel rosea vel purpureo-rosea, obovata interdum attenuata, ad marginem sparsim pilosa, denticulata, non contigua. Stamina alba vel rosea, stylos flavescentes vel virides, basi erubescentes



FIGURE 2. The distribution of *Rubus anglohericus* in the British Isles.

vel rufescentes vel purpureos, aequantia vel vix superantia. Antherae glabrae. Carpella barbata. Receptaculum hirsutum. Fructus rotundus.

Stem low-arching, bluntly angled with furrowed sides, purple or dark red, glabrescent with a few long simple and tufted hairs and many sessile glands; prickles 8–12 per 5 cm, mostly confined to the angles, subequal, (4)–6–10 mm, exceeding the stem diameter, slender from a broad compressed base, often somewhat curved above, patent, sometimes confluent, purple or red with a yellow point. Leaves digitate or subpedate; leaflets 4–5, imbricate or not, dark or yellowish green and glabrous above, greyish and felted with also numerous spreading medium and long simple and tufted hairs along the main veins beneath; terminal leaflet 5.5–8 × 4–7 cm, subrotund or ovate, with an acute or acuminate (1 cm) apex and entire or emarginate base, dentate and slightly compound serrate with sometimes one principal tooth patent, flat, the petiolule $\frac{1}{2}$ – $\frac{3}{4}$ as long as the lamina; petiolules of basal leaflets 1–3 mm; petiole much longer than the basal leaflets, dark purple, with few to many long simple and tufted hairs and 14–17 curved prickles 3–4 mm. Flowering branch with 3-foliate leaves below and 1–8 simple and trifid leaves above, often leafy almost to the apex; inflorescence a broad pyramid with a congested flat top, the peduncles all ascending, the lower ones long (c. 20–25 cm) and paniced, the lowest one 5–10 cm distant from the next, divided above the middle; rachis

flexuous, with numerous medium and long simple and tufted hairs and numerous unequal mixed patent, declining and curved prickles 5–9 mm in shape and colour like those on the stem. Flowers c. 2–3 cm in diameter, cupped; sepals greyish, white-bordered, shaggy with medium and long simple and tufted hairs and often conspicuously numerous short and medium acicles, short- or long-pointed, reflexed; petals c. 8 × 5 mm, pale to bright pink or puce, obovate, sometimes attenuate below, with sparse short simple and tufted hairs on the margin, denticulate, well spaced; stamens equalling or slightly exceeding styles, filaments white or pink, anthers glabrous, sutures sometimes purple; styles yellowish or green, pink- or reddish- or purple-based; young carpels bearded; receptacle hairy; fruit globose. Flowering in July and August.

HOLOTYPE: 1·6 km N. from Corfe, Dorset, v.c. 9, c. SY/96.83, 3 August 1892, E. F. Linton s.n. as *R. incurvatus* ("the usual S. England form of *Handbk. Br. Rubi* p. 27" – W. M. Rogers) (BM).

This member of ser. *Rhamnifolii* has been known since the 1890s on the heaths of south-east Dorset, v.c. 9, where it is widespread and locally abundant. Though rendered distinctive by its dark glabrescent stem with long patent prickles, roundish terminal leaflets of the stem leaves and strongly aciculate sepals, it has, even so, perplexed successive generations of *Rubus* specialists and been referred over the years to as many as eight different species. Its closest affinity among British species seems to be with *R. rhombifolius* Weihe ex Boenn. Friderichsen considered specimens sent to him by Rogers to be identical with the Scandinavian plant he understood as *R. insularis* F. Aresch. Rogers began by calling it "*R. villicaulis* strong luxuriant form" and then settled on the manuscript name of *R. incurvatus* var. *rotundifolius* (meaning by *R. incurvatus* the species now known to British batologists as *R. rhombifolius*), but it was not among his several manuscript names published after his death (Rogers & Riddelsdell 1925) because Riddelsdell acknowledged himself insufficiently conversant with the plant. That name is not, however, available for reviving, for the epithet *rotundifolius* is preoccupied at the specific level. The species is therefore named instead in honour of the late T. A. Warren Davis (1899–1980), whose intensive study of the Rubi of Pembrokeshire in the 1960s led him to distinguish it independently and to circulate material from there to the leading specialists of the period.

As demonstrated by the list of representative exsiccatae cited below, *R. davisii* appears to have a mid-western distribution in England and Wales, extending diagonally from Pembroke to Dorset and the west margin of the New Forest, while its presence on a heath in the Channel Islands suggests that it may prove to occur on the European mainland as well:

v.c. S, Channel Is: occasional in maritime heathy scrub E. and S. of Gros Nez, Jersey, WV/55.56, 18 July 1994, D.E.A. s.n. (BM).

v.c. 6, N. Somerset: near Shapwick, c. ST/42.40, 6 August 1891, D. Fry s.n. (BM). Peat moor N. of Shapwick, c. ST/41.39, 9 September 1891, J. W. White s.n. as *R. cariensis* (BM). Shapwick moor to Ashcott, ST/4.3, 10 August 1892, E. F. Linton & R. P. Murray s.n. as *R. nemoralis* (BM: herb. Barton & Riddelsdell no. 9839). Ashcott Heath, near Shapwick, ST/44.39, 21 July 1856, E. S. Edees nos 12132, 12147 (NMW).

v.c. 9, Dorset: Corfe Castle, c. SY/95.82, 24 July 1891, R. P. Murray s.n. as *R. villicaulis* var. *insularis* (BM, CGE, LIV). Norden Heath, SY/94.83, 24 July 1891, W. M. Rogers s. n. as *R. villicaulis* (BM: herb. Barton & Riddelsdell no. 9848). Half-way between Swanage and Corfe, SY/99.80, 12 July 1894, F. A. Rogers s.n. as *R. incurvatus* (BM). Furzebrook, between Wareham and Corfe, SY/93.83, 2 August 1955; Bere Wood, c. SY/87.94, 4 August 1955, E. S. Edees nos 11153, 11155 respectively (NMW). Corfe Common, SY/95.80, 31 July 1991, D.E.A. s.n. (BM).

v.c. 11, S. Hants.: plentiful among gorse, hillside behind Blissford, near Fordingbridge, SU/176.139, 18 July 1984; gorse scrub, Godshill Ridge, SU/182.150, 14 July 1987, D.E.A. nos H827A, H827B respectively (BM).

v.c. 45, Pembroke: open scrub on side of a cwm, Ramsey Island, SM/70.24, 23 July 1965; raised area in river-side marsh, Letterston, SM/92.29, 16 July 1966, T. A. W. Davis nos 65/956, 66/1059 respectively (CGE, NMW: herb. Edees nos. 23350, 23372 respectively).

The distribution of the species in the British Isles is shown in Fig. 3.

4. *Rubus sempernitens* D. E. Allen & L. J. Margetts, sp. nov.

Turio alte arcuatus, acutangulus faciebus planis vel parum excavatis, brunneus vel purpureus, striatus, glaber vel interdum leviter pilosus, glandulis stipitatis paucis plerumque

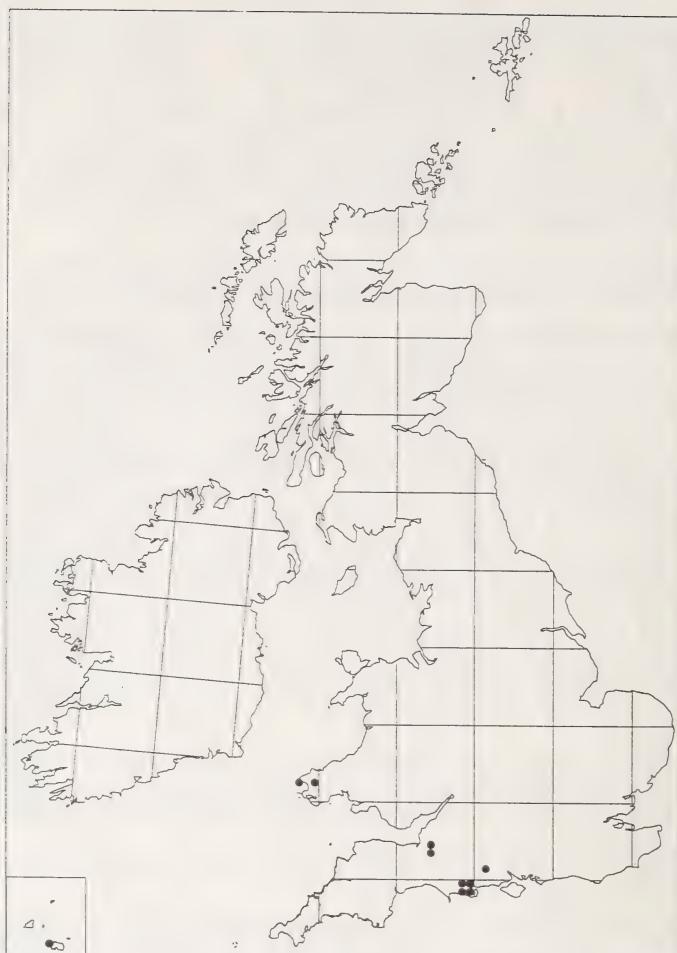


FIGURE 3. The distribution of *Rubus davisii* in the British Isles.

brevibus et aciculis crebris brevibus mediisque cum paucis longis nonnullis glanduliferis et aculeolis paucis vel numerosis patulis et aculeis crebris c. 15 per 5 cm inaequalibus ad angulos dispositis mediis (2–6 mm) tenuibus e basi lata compressa plerumque curvatis munitus. Folia 3–5-nata, pedata, interdum imbricata, crassiuscula, superne nitentia atrovirideo-flavescentia, inferne pallido-vel griseo-viridia sparsim pubescentia (praesertim ad venos), quorum petioli aculeis (1.5–2.5 mm) numerosis curvatis et superne (cum petiolulis) glandulis stipitatis crebris longis et aciculis longis nonnullis glanduliferis muniti. Foliolum terminale ovatum vel obovatum, apice longe acuminatum, basi emarginatum vel subcordatum, inaequaliter subdentato-serratum dentibus fere tenuibus primis nonnullis interdum patulis, planum, eiusdem petiolulo quadruplo vel triplo longius; foliola infima brevissime (2–3 mm) petiolulata. Inflorescentia usque ad apicem interdum foliata, foliis ternatis inferne et simplicibus et trilobatis saepissime duo usque quinque superne instructa, longa, pyramidalis ad apicem truncata vel acuta saepe congesta, ramulis axillaribus omnibus adscendentibus (vel superioribus patulis) infimis paniculatis aucta. Rachis flexuosa, pilis numerosis densius superne vestita, glandulis stipitatis numerosis et aciculis numerosis (longis nonnullis glanduliferis) et aculeolis paucis vel crebris et aculeis (1–6 mm) crebris declinatis curvatisque munita. Pedicelli sicut rachis superior aculeis nonnullis tenuibus 2–3 mm muniti. Flores c. 2 cm diametro, plani. Sepala

grisea, anguste albo-marginata, tomentosa glandulis stipitatis aciculisque numerosis munita, attenuata, apice saepe foliata, reflexa. Petala rosea, anguste obovata vel subrotunda, denticulata, sparsim pubescentia, ad marginem pilis numerosis praedita, ad apicem saepe emarginata, non contigua. Stamina alba stylos pallidos superantia. Antherae saepissime pilis raris ornata. Carpella pilis numerosis nonnullis longis (1 mm) praedita. Receptaculum dense pilosum. Fructus oblongus.

Stem high-arching, sharply angled with flat or shallowly furrowed sides, brown or purple, striate, with sparse to frequent simple and tufted hairs or (more usually) none, scattered mostly short stalked glands, more numerous short and medium and a few long (sometimes gland-tipped) acicles and few to many patent pricklets; prickles c. 15 per 5 cm, confined to the angles, unequal, 2–6 mm, slender from a broad compressed base, typically curved, tawny or purple with a yellowish point. Leaves pedate; leaflets 3–5, sometimes imbricate, relatively thick, conspicuously shining and dark yellowish-green and thinly hairy above, pale to greyish-green and with a thin clothing of mostly simple adpressed hairs mostly along the veins beneath; terminal leaflet c. 7–9 × 5–6 cm, ovate or obovate, with a long acuminate apex c. 1·5–2·0 cm and an emarginate or subcordate base, unequally rather finely subdente-serrate with a principal tooth sometimes subpatent, flat, the petiolule $\frac{1}{4}$ – $\frac{1}{3}$ as long as the lamina; petiolules of basal leaflets 2–3 mm; petiole as long as or shorter than the basal leaflets, coloured and armed like the stem but with frequent long stalked glands and long sometimes gland-tipped acicles at the apex of the petiole and on the lower parts of the petiolules, with c. 10–17 curved prickles 1·5–2·5 mm. Flowering branch with 3-foliate leaves below and (1–)2–5(–7) simple and trifid leaves above, sometimes leafy to the apex; inflorescence long, pyramidal with a flat or acute and often congested top, the peduncles all ascending or one or more mid or upper ones patent, the lowest ones c. 15 cm long, panicled, divided around the middle; rachis flexuous, with numerous white medium mostly tufted hairs increasing in denseness upwards, numerous short and medium stalked glands, numerous short and medium and long acicles (some of the long ones gland-tipped) occasional to frequent pricklets of various lengths and frequent declining and curved prickles 1–6 mm long in shape and colour like those on the stem; pedicels clothed like the upper part of the rachis, with several slender prickles 2–3 mm long. Flowers c. 2 cm in diameter, flat; sepals greyish, narrowly white-bordered, woolly with dense short or medium simple and tufted hairs, with many sessile glands and usually many short and medium stalked glands and acicles, long-pointed from bud and often leafy-tipped, reflexed; petals 7–10 × 4–7 mm, pink, narrowly obovate to subrotund, denticulate, with sparse adpressed hairs above and many tufted and a few simple short and medium hairs on the margin, often notched, well separated; stamens exceeding styles, filaments white, anthers usually with one or two hairs; styles pale; young carpels densely hairy and with some hairs 1 mm long; receptacle densely hairy; fruit oblong. Flowering in June and July.

HOLOTYPUS: Core Copse, near Ottery St Mary, SY/132.945, S. Devon, v.c. 3, 30 June 1992, L. J. Margetts s.n. (BM).

This member of ser. *Radula* is readily told by its long leafy pyramid of relatively small pink flowers, long-pointed sepals, shining ("sempernitens") dark yellowish-green leaflets with a long acuminate tip, densely hairy young carpels with a few much longer hairs and – in most cases – the contrasting glabrous stem and very hairy rachis. The presence of long, gland-tipped acicles on the petiolules and at the apex of the petiole is also a distinctive character.

R. sempernitens has escaped notice till only the last few years because its chief area of occurrence, south-east Devon, was previously neglected by batologists. Since 1987, on taking up residence there, L. J. Margetts has found what has become familiar to him as "the shiny-leaved Radulan" to be frequent to common in the east of the county, v.cc. 3 and 4, in hedgerows and light woodland and especially on commons, both on the Triassic pebble beds and on a combination of Greensand and Clay-with-Flints. Scattered colonies extend its distribution into the more central parts of Devon, but none have been observed as yet further west. A single bush has also been detected just inside Dorset, v.c. 9. The 10-km grid-squares in which the species has been noted now total 15: SS/4.1, 8.2, 9.0, 9.1; ST/0.0, 0.2, 2.0; SX/8.8, 9.8, 9.9; SY/0.8, 0.9, 1.9, 2.9, 3.9.

So wide a range would in itself justify privileging this bramble with a published name, but in addition it has emerged that the species is to be found on the other side of the English Channel as well, in the Cotentin Peninsula of Normandy. A specimen, now in BM, collected by D.E.A. in 1993 in local abundance in open oak-chestnut woodland (les Maresquiers) near le Vréton, 4·5 km west of



FIGURE 4. The distribution of *Rubus sempernitens* in the British Isles.

Bricquebec, dép. Manche, is, in the opinion of both myself and L. J. Margetts, *R. sempernitens* too, displaying the same unusual pattern of carpel hairiness and differing only from the general run of English plants in having quite glabrous anthers and a rather hairy stem. It may well turn out to occur more widely in that part of France.

This French specimen and the holotype are currently the only exsiccatae in public herbaria as far as we have been able to establish. **Herb.** L.J.M., however, contains a range of further material, on which the description above has been partly based.

The distribution of the species in the British Isles is shown in Fig. 4.

5. *Rubus venetorum* D. E. Allen, sp. nov.

Turio arcuato-decumbens, obtusangulus faciebus planis vel parum excavatis, atropurpureus, copioso pilosus, glandulis stipitatis numerosis plerumque brevibus et aciculis paucioribus et aculeolis numerosis nonnullis glanduliferis et aculeis c. 20–30 per 5 cm inaequalibus patulis vel curvatis mediis (3–6 mm) tenuibus e basi lata compressa plerumque ad angulos dispositis munitus. Folia 3–5-nata, digitata vel pedata, utrinque viridia, imbricata, superne sparsim pilosa, inferne sparsim pubescentia, quorum petioli aculeis (2–3.5 mm) numerosis curvatis muniti. Foliolum terminale subrotundum vel obovatum, apice cuspidatum vel acuminatum, basi emarginatum vel

subintegrum, inaequaliter saepe tenuissime serrato-dentatum dentibus primis interdum patulis, planum vel ad marginem undulatum, eiusdem petiolulo quadruplo vel triplo longius; foliola infima brevissime (2 mm) petiolulata. Inflorescentia usque ad apicem non foliata, foliis ternatis inferne et saepissime uno solo integro superne instructa, longa, pyramidalis ad apicem rotunda vel truncata, ramulis axillaribus omnibus adscendentibus vel mediis patulis infimis distantibus aucta. Rachis flexuosa, copiose pilosa, glandulis stipitatis numerosis brevibus et mediis et longis, aciculis mediis paucioribus, aculeolis numerosis interdum glanduliferis, aculeis numerosis inaequalibus tenuibus declinatis vel parum curvatis purpureis munita. Flores c. 2–3 cm diametro. Sepala griseo-viridia, dense pilosa, glandulis stipitatis aciculisque brevibus et mediis munita, albomarginata, attenuata, in flore laxe reflexa, tandem fructum amplexantia. Petala rosea vel roseola, obovata vel ovata vel elliptica, ad marginem pilis numerosis vestita, saepe emarginata, non contigua. Stamina rosea stylos virides vel flavos vel erubescentes, basi roseos vel rufescentes, aequantia vel parum superantia. Antherae glabrae. Carpella dense pilosa. Receptaculum glabrum. Fructus rotundus.

Stem low-arching, bluntly angled with flat or shallowly furrowed sides, blackish purple, with many simple and tufted hairs, numerous short and a few long stalked glands, fewer acicles and numerous pricklets (some gland-tipped); prickles c. 20–30 per 5 cm, mostly confined to the angles, unequal, 3–6 mm, slender from a typically broad compressed base, patent to (mainly) curved, purple or red with a sometimes yellowish point. Leaves digitate or pedate; leaflets 3–5, tending to be imbricate, medium to dark green and thinly hairy above, pale green and with a usually thin clothing of simple adpressed hairs beneath; terminal leaflet c. 6–7 × 4·5–6 cm, subrotund or obovate, with a cuspidate or acuminate apex c. 0·5 mm and an emarginate or subentire base, unequally and often finely serrate-dentate with the principal teeth sometimes patent, flat or with the margins undulate, the petiolule $\frac{1}{4}$ – $\frac{1}{2}$ as long as the lamina; petiolules of basal leaflets 2 mm; petiole as long as or shorter than the basal leaflets, coloured and clothed like the stem, with 15–25 curved prickles 2–3·5 mm. Flowering branch with 3-foliate leaves below and 1(–3) simple entire leaves above, not leafy to the apex; inflorescence long, typically pyramidal with a rounded or sometimes flat top, all the peduncles ascending or the middle ones patent, the axillary peduncles 4–10 cm, the lowest one 5–7 cm distant from the rest, all shorter than their leaves and divided about halfway or well above the middle; rachis flexuous, dark purple, with numerous to dense patent and adpressed medium simple and tufted hairs, numerous (but varying proportions of) short and medium and long stalked glands, fewer short and medium acicles, numerous sometimes gland-tipped pricklets and rather numerous, unequal, triangular-based, slender-pointed, declining or slightly curved, purple prickles 2–5 mm. Flowers c. 2–3 cm in diameter; sepals greyish-green, shaggy with numerous white or yellowish short and medium simple and tufted hairs, usually many subsessile and short and medium stalked glands and short and medium acicles, white-bordered, long-pointed, loosely reflexed in flower patent then erect in fruit; petals 8–13 × 4–4·5 mm, pale or deep pink (to whitish in shade), obovate or ovate or elliptical, with numerous short to long simple and tufted hairs on the margin, often notched, distant; stamens equalling or slightly (rarely, much) exceeding the neat head of styles, filaments pink (or green in shade), anthers glabrous, sutures pink; styles pale green or yellow or pink, and pink- or reddish-based; young carpels densely hairy; receptacle glabrous; fruit globose. Flowering in June and July.

HOLOTYPUS: locally abundant in open areas, Bois du Rabey, Quettehou, dép. Manche, France, 3 July 1991, D. E. Allen no. C87, specimen "A" (**BM**).

Exsiccatae:

ENGLAND

v.c. 1a, Scilly: Low Pool, Rose Hill, St Mary's, SV/912.108; Carn Morval Down, St Mary's, SV/90.12, both 3 July 1954, J. E. Lousley nos 660 and 672 respectively, both det. B. A. Miles 1967 as *R. hastiformis* (**BM**). Abundant in hedges and among bracken on slopes to the sea, Halangy Down, St Mary's, SV/90.12, 26 June 1995; wall-top, Back Lane, Tresco, SV/890.156, 7 July 1995, D.E.A. s.n. (**BM**).

v.c. 2, E. Cornwall: wood near Polbathic, SX/35.56, 25 July 1980, E. S. Edees no. 22641 (**NMW**) – shade form.

v.c. 4, N. Devon: "North Devon", 1880, H. A. Evans s.n. as *R. pallidus*, comm. Botanical Record Club 1883 (**BM**). Great Odam Moor Plantation, SS/74.18, 10 July 1990, L. J. Margetts & W. H. Tucker no. 444 (**herb. L.J.M.**).

v.c. 9, Dorset: hedgebank, Redbridge Road, near Moreton station, SY/776.885, 29 June 1996, D.E.A. s.n. (**BM: herb. H. Vannerom**).

v.c. 10, Wight: Combley Great Wood, one patch only among tall bracken, SZ/547.888, 19 July 1995, D.E.A. no. H337 (**BM**).

FRANCE

Representative specimens collected by me in 1994 and 1996 have been deposited in **BM** from: dép. Ille-et-Vilaine: hedgebank outside Tremblay.

dép. Côtes-du-Nord: Lande de Fréhel; clay copse, La Poterie, near Lamballe.

dép. Loire-Inférieure: near Pénestin, under pines; wood W. of Herbignac, in open heathy ground; Forêt de Princé, S.W. of Nantes, in abundance.

This member of ser. *Hystrix* is named after the Veneti, the powerful Celtic tribe defeated in a naval battle by the Romans under Julius Caesar in 56 B.C. Their territory supposedly extended over much of the present-day département of Morbihan, on the west coast of Brittany, where this bramble occurs in local abundance (in the pinewoods bordering the prehistoric alignments at Carnac, for example). It seems to be predominantly a Breton species, populating broad-leaved and coniferous woodland alike, often in great quantity, and spilling over into hedges and heath scrub. I have seen it in every département of that region except Finistère and south of the Loire in the Forêt de Princé, near Nantes. It may well extend further south still, into dép. Vendée, though it is not represented in the extensive *Rubus* collection from the east of that département made by J. Charrier and now in **BM**. The holotype locality in dép. Manche, in the north-east corner of the Cotentin Peninsula of Normandy, is so far the only one known in France outside Brittany and the region of the Western Loire.

A bramble with showy pink flowers and occurring so widely in such profusion would surely have been described long since had the north-west corner of France received more attention from batologists. In the principal account to have been published of the Rubi of any part of Brittany, by Arrondeau (1863), a resident of Vannes in dép. Morbihan, there is indeed a mention of a plant which from its description might be a shade form of this species; wrongly identified by Arrondeau with *R. scabripes* Genev., it was later described by Sudre (1905) as *R. strictispinus* and later still reduced by him (Sudre 1910) to a variety of *R. muelleri* Lef., a member of ser. *Vestiti* (Focke) Focke. Unfortunately, I have been unable to trace any specimen of this. Sudre himself made only one fleeting visit to Brittany, to the neighbourhood of Quimper in dép. Finistère (Sudre 1904), on which occasion he recorded what might also have been *R. venetorum* under the aggregate and widely-misapplied name of "*R. fuscoater* Weihe".

Essentially a French bramble, *R. venetorum* is as yet known in Britain in quantity only in the sheltered north-east coastal district of the main island of the Scilly archipelago, St Mary's, v.c. 1a. The species evidently requires a milder climate than most parts of the English mainland can produce. Its absence from the extensive collections of Cornwall and Devon Rubi made by B. A. Miles (CGE), F. Rilstone (**BM**) and H. J. Riddelsdell (**BM**) and single representation only in those made by L. J. Margetts (**herb. L.J.M.**) and E. S. Edees (NMW) suggest that elsewhere in the far south-west of England it is distinctly rare. That must be even more the case further east, in the region centred on the Solent, for the *Rubus* flora of Hampshire and the Isle of Wight has been investigated by now with considerable thoroughness. Several of these English mainland occurrences have the appearance of being the product of separate recent introductions by migrant birds, possibly direct from France.

R. venetorum exhibits considerable variation but, when typical, is rendered distinctive by the round terminal leaflets of the stem leaves only thinly hairy beneath, dark stem, Hystrican armature and narrow, bright pink petals, pink filaments, usually red-based styles and ultimately erect sepals.

Putative hybrids of *R. venetorum* with *R. prolongatus* Boulay & Letendre and *R. iricus* Rogers have been observed on St Mary's, Scilly. One of those with *R. prolongatus* extends for some distance along hedgebanks on both sides of a metalled road (SV/916.118) and also occurs in a nearby green lane, so is evidently fertile. Examples of these have been deposited in **BM** as well.

The distribution of the species in the British Isles is shown in Fig. 5.



FIGURE 5. The distribution of *Rubus venetorum* in the British Isles.

ACKNOWLEDGMENTS

I am particularly indebted to H. Vannerom and L. J. Margetts for their assistance with the respective accounts of *R. anglobelgicus* and *R. sempervirens*, including commenting on the draft descriptions, and for providing the excellent specimens here designated as their holotypes; records of the latter's English distribution were also kindly provided by L. J. Margetts. I am also grateful to A. Newton for helpful comments, on different occasions, on material of most of the species described, and to Miss P. Hodson and Miss R. Fitzgerald for introducing me to the flora of East Donegal and leading my footsteps to an extra-Manx station at last for *R. waddellii*. Fuller study of *R. davisii* in its Jersey locality was made possible by a grant from the B.S.B.I. Welch Bequest Fund, which I also acknowledge with gratitude.

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Four new species of *Rubus* L. (Rosaceae) from eastern England

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ABSTRACT

The history of the study of Brambles in East Anglia is summarised and four new species are described: *Rubus gariannensis* A. L. Bull, sp. nov.; *Rubus villosior* A. L. Bull, sp. nov.; *Rubus cromerensis* A. L. Bull, sp. nov.; and *Rubus hindii* A. L. Bull, sp. nov.

KEYWORDS: Norfolk, W. M. Hind, E. F. Linton, cv ‘Bedford Giant’.

INTRODUCTION

The earliest student of the East Anglian *Rubus* flora was probably Charles Cardale Babington (1808–95), Professor of Botany at Cambridge University and author of *British Rubi* (1869). His record of *Rubus althaeifolius* Babington (Babington 1860) from Cambridgeshire and West Suffolk was later renamed *Rubus babingtonianus* by Watson (1946) as the name had been applied to another species by Trattinnick in 1823.

The Rev. W. M. Hind, an Irishman who was rector of Honington with Sapiston in West Suffolk for nearly twenty years, made a collection of Rubi which are with his herbarium in IPS. He published a *Flora of Suffolk* in 1889, much of the work for which had been done by the Rev. Dr Churchill Babington (1821–89), cousin of Charles and Professor of Archaeology at Cambridge until 1866, when he took the living of Cockfield in Suffolk. A distinguished lichenologist, in addition to his work towards the *Flora*, published after his death by Hind, he also published a volume on the *Birds of Suffolk* (Britten & Boulger 1931).

Hind’s *Flora* reveals that a good number of students of the genus *Rubus* visited Suffolk in the latter half of the 19th century, drawn particularly to the area round Nayland and Polstead which was particularly rich at that time. The Rev. J. D. Gray features prominently, as does the Rev. E. F. Linton, rector of Sprowston in Norfolk from 1878 to c. 1888. So far as one can judge from Petch & Swann’s *Flora of Norfolk* (1968), it would appear that Linton was almost alone in his studies of Norfolk brambles, and apart from a few additions made by H. J. Riddelsdell in 1925, these authors accepted Linton’s records as the basis for *Rubus* in their *Flora* nearly 80 years later.

The early part of the present century appears to have been the botanical dark ages in eastern England, though Linnaeus Cumming visited Polstead in 1915, and a specimen from there bearing his name is in NWH and is undoubtedly *Rubus hindii*. Specimens collected from Suffolk by W. H. Mills in 1947 are to be found in CGE and the late B. A. Miles also visited that county (Simpson 1982). During the 1950s, the late E. S. Edees paid regular visits to the Swaffham district of Norfolk, Mrs Edees being from a local family. From 1968, he helped the present author become established as a botanist, and also had a week-long stay in Suffolk which resulted in a paper in the county *Transactions* (Edees 1974).

The present author’s paper (Bull 1985) on the *Rubus* flora of Norfolk and Suffolk made mention of a “Corton *Rubus*” and a “Thursford *Rubus*”. These are published here as *Rubus gariannensis* and *R. villosior* respectively, whilst *R. hindii* was mentioned under *R. ferox* agg. as being “near *R. tuberculatus* (Babington 1860) but not identical with it.”

Rubus gariannensis A. L. Bull, sp. nov. (Series *Sylvatici*)

Turio arcuatus, angulatus, sulcatus, roseo-griseus subrubescens, sparsis pilis simplicibus fasciculatisque et nonnullis (pilis) longioribus vestitus et glandulis nonnullis brevissime stipitatis instructus. Aculei 8–15 per 5 cm in angulis dispositi non numquam geminati, subaequales, robusti, longi et

abrupte e basi dilatati acutati, declinati vel decurvati, 7–10 mm, rubiginosi vel rubri et in apricis ad apicem flavescentes.

Folia subpedata, non contigua, fuscoviridia pilosaque supra praesertim in venis, subter quoque pilis brevibus, simplicibus fasciculatisque obtecta. Foliolum terminale 5·5–7·5 × 8–10 cm (cum cuspide e basi angusta orta, 1·5 ad 2 cm) obovatum, e basi integra vel emarginata et margine subaequaliter serrato, interdum nihilominus dentibus principalibus retroflexis. Foliolorum basium petioluli 3–5 mm longi. Petiolus foliolis basalibus usque duplo longior, brunneus vel rubiginosus, multis pilis brevibus simplicibus fasciculatisque vestitus, glandulis sessilibus et brevissime stipitatis instructus, aculeis subflavis c. 12 acute deflexis vel paulum decurvatis armatus.

Rami floriferi foliis subter 3-natis et saepe uno duobusve supra simplicibus praeditus, non ad apicem foliosus. Inflorescentia laxa. Pedunculi pauci vel sat multi, rigiduli divaricate ascendentes, supra medium divisi, ramulis 3–7 floris ad angulum 60–90° a pedunculis, 1–3 cm, divergentibus. Rachis flexuosior, brunneopurpurea, multis vel etiam densis pilis brevibus simplicibus fasciculatisque vestita, paucis vel interdum multis glandulis subsessilibus instructa, sat multis aculeis tenuibus, subflavis, acute declinatis, 3–6 mm longis, armata. Pedicelli tenues, rigiduli, pilis densis brevibusque, interdum simplicibus numerosioribus longioribusque vestiti multis aculeis tenuibus, subflavis declinatis, 3–5 mm longi, armati. Flores 2·5 cm diametro. Sepala griseo-viridia, albomarginata, pilis densis appressis et simplicibus longis sparsis vestita, reflexa. Petala lactea, leviter obovata, 8–9 × 4 mm, in marginibus pilosa, vix contigua. Stamina stylis superantia. Filamenta alba. Antherae glabrae. Styli virides. Carpella et receptaculum glabra.

Stem arching, angled, furrowed, pinkish grey becoming light red with mainly sparse, simple and tufted hairs and scattered longer hairs, and with few to rather many sessile, subsessile and very short stalked glands. Prickles 8–18 per 5 cm on the angles, sometimes in pairs, strong, long and abruptly needle like from a broad base, sharply declining or curved, 7–10 mm, reddish brown, or red with a yellow tip in exposure. Leaves subpedate, not contiguous, dark green and pilose above, especially along the veins, shortly pilose below, with a covering of short, simple and tufted hairs. Terminal leaflet 5·5–8 × 7·5–10 cm, including the narrow based terminal cusp, 1·5–2 cm, obovate, the base entire or emarginate, the margin more or less evenly serrate, though the principal teeth are sometimes retrorse, the petiolule 2/5 as long as the lamina. Petiolules of basal leaflets 3–5 mm. Petiole to twice as long as the basal leaflets, brown, or reddish brown, pilose, with numerous short, simple and tufted hairs, sessile glands, very short stalked glands, and about 12 sharply deflexed or somewhat curved yellowish prickles.

Flowering branch with 3-foliate leaves below and often 1–2 simple leaves above, not leafy to the apex. Inflorescence lax, with few or rather many, wiry, ascending, divaricate peduncles divided above the middle, the branches 3–7 flowered, set at 60–90° to the peduncles, 1–3 cm. Rachis slightly flexuose, brownish purple with numerous to dense, short to medium simple and tufted hairs, few to occasionally many subsessile glands, and fairly many sharply declining yellowish prickles 3–6 mm. Pedicels slender, wiry, with dense short hair and fairly numerous simple longer hairs, and numerous slender, slanting yellowish prickles 3–5 mm. Flowers 2·5 cm diameter. Sepals greyish green with a white border, with dense appressed hairs and scattered, long simple hairs, reflexed. Petals milk white, slightly obovate, 8–9 × 4 mm, pilose on the margin, scarcely contiguous. Stamens exceeding the styles, filaments white, anthers glabrous, styles green, carpels and receptacle glabrous. Unripe fruit brownish red. Flowering from late June to early August.

Diagnostic features: the long, hard, slender and needle like declining prickles which are frequently in pairs; the neat, obovate terminal leaflet with a long, narrow based cusp, and the ample panicle with long, wiry, divaricate branches, or occasionally with a broad-truncate terminal panicle, the branches interwoven. Flowers milk white.

HOLOTYPUS: Howard's Common, Belton near Great Yarmouth, GR TM/475.025, v.c. 25, 23 July 1993, A. L. Bull (BM). Isotype in **herb. A. Newton**.

The name *gariannensis* is derived from Gariannonum, the well preserved Roman fort at Burgh Castle, 2 km north of the type locality.

Specimens have been circulated to Mr H. Vannerom in Belgium and to Prof. H. E. Weber in Germany. It was suggested to the latter that the present plant might be close to *R. schlechtendalii*

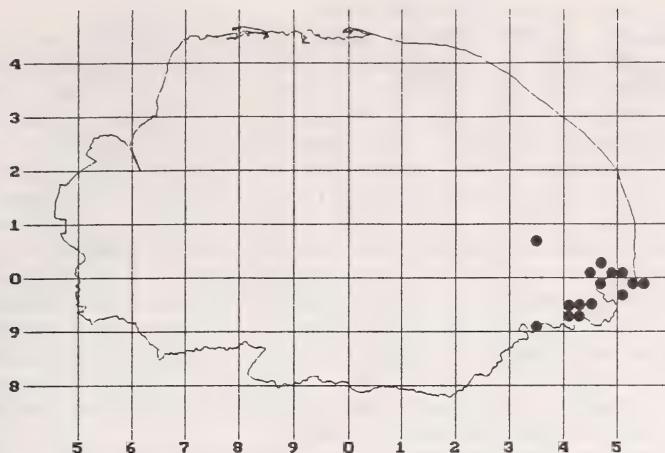


FIGURE 1. Distribution of *Rubus gariannensis* A. L. Bull in Norfolk. • all records.

Weihe. In reply, Prof. Weber stated that it appeared to be closer to *R. maassii* Focke ex Bertram, but differing in a number of key points. In his account of Suffolk brambles, Hind claims to have collected *R. maassii* from Henstead, near Beccles in 1886, though his specimen cannot now be traced as it is not in his herbarium at IPS. It was collected from the general area where the present plant occurs, and may well have been this plant.

Rubus gariannensis grows in a wide range of habitats on relatively poor, sandy soils. It grows throughout the afforested area of v.c. 25 in the arc formed by the River Waveney and Breydon Water, and occurs on the other side of this peninsula on the cliff edge at Corton, just north of Lowestoft. In east Norfolk, v.c. 27, it occurs on the sea bank of the River Waveney at Aldeby near Beccles; on the marsh wall on the Haddiscoe levels, the only *Rubus* other than *R. ulmifolius* Schott to be found there; throughout several woods on the higher ground between the Waveney and the Yare, and on the north side of the latter river on heathy ground at Strumpshaw, only a few km from Norwich. Local endemic. The distribution of this species is shown in Fig. 1.

Representative exsiccatae (all herb. A. L. Bull): v.c. 25: TM/4.9, Herringfleet and Blundeston; TM/5.9, Corton; TG/4.0, Belton and TG/5.0, Lound; v.c. 27: TM/4.9, Aldeby and TG/4.0, Haddiscoe.

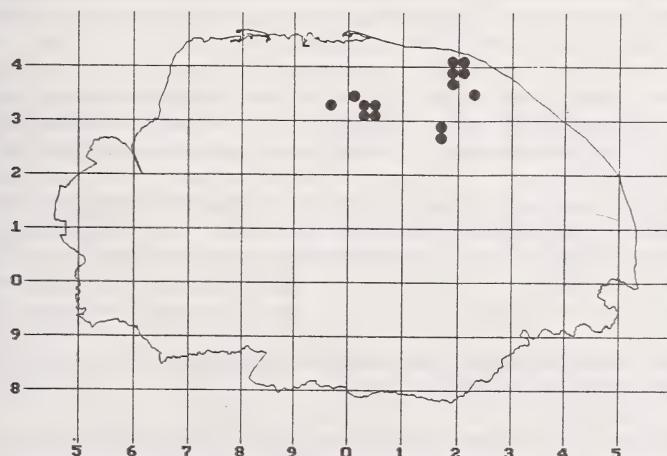


FIGURE 2. Distribution of *Rubus villosior* A. L. Bull in Norfolk. • all records.

Rubus villosior A. L. Bull, sp. nov. (Series *Micantes*)

Turio arcuato-decumbens, angulatus, sulcatus, griseo-purpureus, sat multis longis pilis simplicibus fasciculatisque vestitus sparsis vel crebris longis glandulis pallido-stipitatis nigro-capitatisque intractus. Aculei tenues, e basi longa declinati, 8–12 per 5 cm, 3–5 mm longi, rubri ad apicem flavescentes. Folia 5-nata fuscoviridia, digitata vel subpedata, subimbricata, pilis supra praesertim in venis, longis simplicibus lucidis vestita, subter quoque pilis longis simplicibus lucidis (in venis pectinatim dispositis) tomento que obiecta nec sine pilis brevioribus densioribus appressis. Folium terminale 8.5–11 × 4.5–7 cm (ita ut cuspis terminalis 1.5–2 cm includatur), obovatum, e basi integra vel emarginata cuspidatum, Margines subaequaliter serrati. Petiolulum, longitudine quartae fere partis laminulae, pilis simplicibus lucidis c-lmm. vestitum, aculeis tenuibus 4–5 declinati vel decurvatis et aciculis longis, tenuissimis et ad apicem glanduliferis ad 1.25 armatum.

Rami floriferi ad apicem paene foliosi. Folia inferiora 3–5 nata, uno vel duobus foliolulis ad basim peduncularum superiorum dispositas. Inflorescentia pyramidalis dense supra conglomerate, longis subter ramis axillaribus ascendentibus. Pedunculi 3–7 flori, 1–3 cm longi. Rachis flexuosa, longis pilis sericeis obiecta. Pedunculi et pedicelli pilis confertissimis et subflavis, praesertim aestate proveta, obiecta ita ut multae glandulae pallidae nigrocapitate videri non possint et pauci vel numerosiores aculei tenues et declinati paene celentur.

Flores 2–2.5 cm. Sepala pallidoviridia, dense pubescentia et pilis longis sericeis vestita qui paucas vel multas breves glandulas pallidostipitatas nigrocapitatisque celant, brevi mucrone fuscoviridi praedita, laxe reflexa vel patentia. Petala non contigua, alba vel primo subrosea, late elliptica, marginibus pilosis. Filamenta alba. Antherae glabrae. Styli pallidovirides. Carpella et receptaculum glabra. Fructus immaturus pallidoviridis, maturus parvus et durus.

Stem low arching, angled, furrowed, greyish purple, with moderately numerous long simple and tufted hairs, and with occasional to numerous pale stalked, blackheaded long glands. Prickles slender, slanting, from a long base, 8–12 per 5 cm, 3–5 mm, red with a yellow tip. Leaves 5-nate, dark green, digitate to subpedate, subimbricate, pilose above with long, simple hairs that glisten in the sun, and especially along the veins, pilose and tomentose below, with long, shining simple hairs, pectinately pilose on the veins, and shorter, denser appressed hairs, terminal leaflet 8.5–11 × 4.5–7 cm, including the terminal cusp 1.5–2 cm. Obovate cuspidate, with entire or emarginate base and straight sides, the margins more or less evenly serrate, the petiole about as long as the lamina with shining simple hairs c. 1 mm, 4 or 5 slender, slanting or curved prickles and long, very slender gland tipped acicles to 1.25 mm.

Flowering branch leafy almost to the apex, with 3–5 foliate leaves below and one or two simple leaves at the base of the upper peduncles. Inflorescence pyramidal, the upper part dense, with long/ ascending axillary branches, the peduncles 3–7 flowered, 1–3 cm. Rachis flexuose, covered with long silky hairs which become very dense and somewhat yellowish on the peduncles and pedicels, especially later in the season, the hair obscuring many long stalked pale, black headed glands, and almost obscuring the few to rather many, slanting prickles.

Flowers 2–2.5 cm. Sepals pale green, densely pubescent, with long, silky hairs obscuring few to many short, pale stalked, black headed glands, and with a short, dark green mucro, loosely reflexed to patent. Petals not contiguous, white, or pale pink at first, broadly elliptic, pilose on the margins. Filaments white, anthers glabrous, styles pale green. Carpels and receptacle glabrous. Young fruit pale green. Ripe fruit small, hard.

Diagnostic features: *Rubus villosior* is characterised by its remarkably shaggy panicle, especially when in shade, a point remarked upon by Prof. H. E. Weber, who at first suggested that the specimen had felt disease. When told that the indumentum was typical of the species, he referred to it as the “mite imitating blackberry.” It is also noteworthy for the consistently long, buried glands under the hair on both stem and panicle, which always have transparent stalks and black heads.

HOLOTYPUS: Thursford Wood, Fakenham, West Norfolk, v.c. 28, GR TF/977.332, 29 July 1994, A. L. Bull (BM). Isotype in **herb.** A. Newton.

This species is a dominant feature of many woods across north central Norfolk on the south facing slopes of the high ground which culminates in the Cromer Ridge, the glacial moraine from the last Ice Age. Although this species and the next are dominant through the area in which they occur,

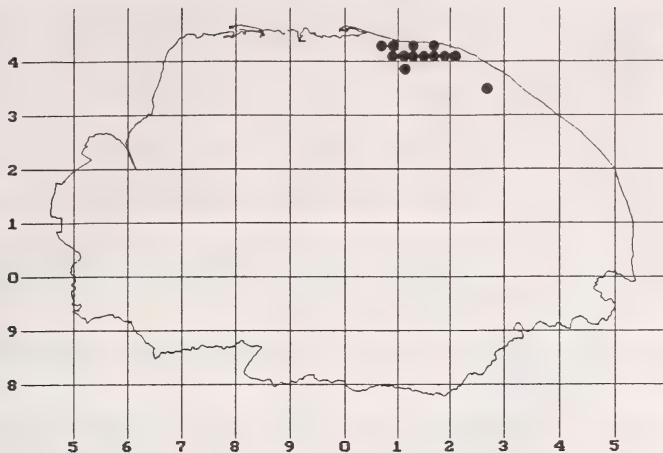


FIGURE 3. Distribution of *Rubus cromerensis* A. L. Bull in Norfolk. • all records.

neither seems to have appeared in any of the earlier herbaria. This may possibly be due to the fact that both are associated with the Cromer Ridge, erroneously described by W. C. R. Watson as "poor bramble country. Norfolk has no brambles due to the Ice Age!" (E. L. Swann, pers. comm.) Local endemic. The distribution of this species is shown in Fig. 2.

Representative exsiccatae (all **herb.** A. L. Bull): v.c. 27: TG/0.3, Swanton Novers Great Wood, 14 July 1993; TG/1.2, Blickling Great Wood, 11 August 1995; TG/1.3 and TG/1.4, Felbrigg Great Wood, 17 August 1995; TG/2.3, Old John's Wood, Gunton, 22 July 1973.

Rubus cromerensis A. L. Bull, sp. nov. (Series *Anisacanthi*)

Turio arcuatus, pruinosis, brunneo-nigrescens, angulatus vel sulcatus, multis plerumque pilis simplicibus stellatisque vestitus, paucis vel multis glandulis sessilibus brevissimeque stipitatis instructus. Aciculi pauci vel nulli. Aculei multi vel plurimi ad 20–25 per 5 cm, patentes plerumque et ad apicem flavi, ad 6–7 mm, saepe geminati et ad angulos plerumque sed non omnino dispositi nec sine minoribus aculeis numerosioribus interspersis.

Folia 3–5 nata pedata, viridia vel fuscoviridia, pilis supra sparsis simplicibus, multis subter simplicibus stellatisque vestita, mollia sed non dense obtecta. Foliolum terminale obovatum, longe e basi angusta, integra, saepe cuneata acuminatum, petiolulo terminale brevi, ad quintam partem laminae longitudine, multis aculeis leviter curvatis armato.

Inflorescentia anguste pyramidalis apice brevi subracemoso rotundato et ramis inferioribus ascendentibus, 5–7 floris, non ad apicem foliosis. Rami axillares nonnumquam longitudine crescentes ita ut in corymbum densum rotundatumque disponantur, uno vel duobus foliis plerumque supra comitantibus, multis tenuibus aculeis declinatis vel decurvatis armati, et paucis subnigris glandulis stipitatis brevibus vel paulo longioribus instructa. Rachis pilosa. Sepala pilis griseis dense obtecta apicibus plerumque brevibus, multis aculeis pallidis vel purpureus armata, reflexa.

Flores 2–2.5 cm. Petala alba nonnumquam emarginata. Filamenta alba. Styls albovirides. Carpella glabra. Fructus magnus elongatus.

Stems arching, pruinose, brownish black, angled or furrowed with usually many simple and stellate hairs and few to many sessile and short stalked glands. Acicles few or none. Prickles many to very many, up to 20–25 per 5 cm, mainly patent, coloured like the stem but yellow tipped, 6–7 mm, often in pairs, mainly on the angles though not confined to them, and with fairly numerous pricklets. Leaves 3–5-nate, pedate, dark to mid-green, with scattered simple hairs above and many simple and stellate hairs beneath, soft but not felted. Terminal leaflet obovate, long acuminate from a narrow, entire, often cuneate base. Terminal petiole short, about 1/5 the length of the lamina, armed with slightly curved prickles.

Flowering branch narrowly pyramidal, with a short, subracemose rounded top and ascending lower branches, 5–7 flowered, not leafy to the top, sometimes with axillary branches lengthening to give a dense, rounded corymb, usually with one or two simple leaves above, armed with many slender declining or decurved prickles, and not very many short to longish black-stalked glands, the rachis pilose. Flowers 2–2.5 cm. Sepals greyish felted, usually with short tips and armed with many pale to purple prickles, reflexed. Petals white, elliptic, notched, filaments white, styles whitish-green, carpels glabrous. Fruit large, round to long and thimble shaped, with a rather sharp flavour. In shade, where the rachis stays green instead of adopting the normal blackish colour, this may go bright red at the time the fruit is ripe.

Diagnostic features: the very blackish-brown stem, the prickles mainly equal and patent, allied with the short stalked, obovate long acuminate leaves with markedly narrow to cuneate bases, renders this bramble very noticeable wherever it occurs.

HOLOTYPUS: Salthouse Heath, East Norfolk, v.c. 27, GR TG/071.422, 25 July 1996, A. L. Bull (BM). Isotype in **herb.** A. Newton.

Rubus cromerensis is often dominant on the higher parts and north facing slopes of the Cromer ridge between that town and Salthouse, in hedgerows and on heaths, not being found very often in woodland, and rarely more than 3 km from the sea. Local endemic. The distribution of this species is shown in Fig. 3.

Representative exsiccatae (all **herb.** A. L. Bull): v.c. 27: TG/1.3, Kelling Heath, 10 July 1975; TG/1.4, Beeston Regis Common, 17 July 1975; TG/1.4, Pretty Corner, Sheringham, 3 August 1992; TG/2.4, roadside, East Runton, 3 July 1987; TG/1.4, Roman Camp, Aylmerton, TG/1.4, 3 August 1992, and Muckleburgh Hill, Weybourne, 4 July 1973.

Rubus hindii A. L. Bull, sp. nov. (Section *Corylifolii*)

Turio arcuatus, pruinosis, rubropurpureus, paucis vel nonnumquam pluribus pilis simplicibus stellatisque vestitus, glabrescens, aculeis 15–25 per 5 cm, longis gracilibusque e basi longa ortis, rubropurpureis, magnitudine ad 9 mm gradatim accendentibus nec solum ad angulos dispositis armatus, aculeis minoribus, aculeolis et nonnullis aciculis, glandulis tamen stipitatis paucioribus instructus.

Folia subpedata. Foliola 3–5, mollia, saepe pilis canis dense subter obtecta, supra brevibus pilis appressis simplicibus stellatisque parce praedita, viridia vel fusco-viridia, subpedata, foliolorum inferiorum. petiolulis 2–3 mm. Foliolum terminale suborbiculare vel obovatum, 7.5 × 6.5 cm, apice cuspidato ad 1 cm, basi cordata vel emarginata, primo saepe concava postea convexa facta, margine leviter multiserrato, dentibus quaternis apiculatis praetexto. Petioli saepe ad tertiam vel dimidiam parti laminae longi, paucis vel pluribus aculeis gracilibus, patentibus vel curvatoribus armati, perpaucis glandulis instructi.

Inflorescentia recta, apice densiore rotundato et nonnullis inferioribus ramis angulo 45° ascendentibus, foliis infra ternatis superne singulis binis ornata. Rami ad 10 cm et ad 7 flori, sicut caulis armati et brevibus pilis simplicibus stellatisque, multis aculeis ad 6 mm patentibus vel paulum decurvatis, multis aciculis glanduliferis et glandulis stipitatis instructi. Flores ad 3.25 cm. Sepala canoviridia, ovata, longe acuminata sed apice non foliato, albo margine praetexta, multis glandulis subsessilibus instructa, laxe reflexa vel patentia, mox ascendentia et fructum immaturum amplectantia. Petala rosea, orbicularia vel rhombi fere forma, saepe subemarginata et basi angusta, margine ciliato. Filamenta subrosea vel alba, stylis rubris vel basi roseis, rarius subflavis, longiora. Carpella glabra. Fructus nonnumquam imperfectus, saepe magnus et succosus.

Stem arching, pruinose, becoming reddish purple with few to rather many simple and stellate hairs, glabrescent, with many long, slender prickles from a moderately long base, reddish purple, graduating in size up to 9 mm long, not confined to the angles, the main prickles 15–25 per 5 cm. Smaller prickles, pricklets and some acicles present but not many stalked glands.

Leaves (3–)5 nate, soft and often greyish white felted beneath, with short, simple and stellate hairs, sub-pedate, the basal leaf stalks 2–3 mm. Terminal leaflet almost round to shortly obovate, 7.5 × 6.5 cm with abrupt acuminate cuspidate tip to 1 cm. Some leaves may be more gradually acuminate, the base cordate or emarginate, often somewhat concave at first, but becoming convex later, the margin

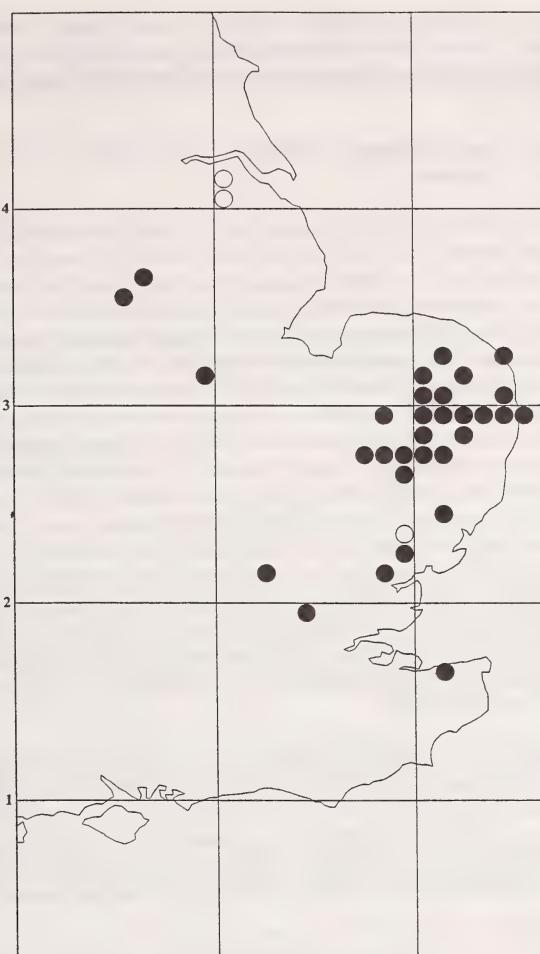


FIGURE 4. Distribution of *Rubus hindii* A. L. Bull in eastern England. ○ herbarium records; ● field records.

shallowly compound-serrate, the teeth in fours, each tooth apiculate. Petiole often long, 1/3 to 1/2 of the length of the lamina, armed with few to fairly many slender/patent to somewhat curved prickles and one or two stalked glands. Upper leaf surface thinly pilose, mid to dark green.

Flowering branch with 3-nate leaves and with one or two simple leaves above, straight, with a fairly dense rounded top and with several ascending lower branches at an angle of 45°, to 10 cm and up to 7-flowered, armed like the stem and clothed with short, simple and tufted hairs, and fairly many to many patent to somewhat decurved prickles to 6 mm, and fairly many gland tipped acicles and stalked glands.

Flowers to 3·25 cm. Sepals pale green with a white margin, ovate long acuminate but not leafy tipped, with many subsessile glands, loosely reflexed to patent but soon rising to clasp the unripe fruit. Petals pink to bright pink, round to roughly rhomboidal, often slightly notched and with a short claw, pilose on the margin. Filaments pale pink or white, longer than the pink based or red styles. These are rarely pale yellow or greenish. Carpels glabrous. Fruit sometimes partly defective, but often large and good.

Diagnostic features: *R. hindii* needs to be separated from *R. tuberculatus* Bab. It is less glandular than that species, especially on the stem. The terminal leaflet of the present plant is usually almost

round, and white felted beneath, and with a much longer petiole than is the case with *R. tuberculatus*. In addition *R. hindii* has the flowers pink or deep pink, with pink or white filaments, and usually pink or red based styles (sometimes pale yellow or greenish), whilst the flowers of *R. tuberculatus* are always white.

HOLOTYPUS: The King's Forest, Wordwell, Suffolk, v.c. 26, TL/835.735, 15 July 1995, A. L. Bull (BM). Isotype in **herb.** A. Newton.

A specimen of this bramble from Ixworth Thorpe, v.c. 26, was examined in the Hind collection in IPS in 1982. During the summer of 1983 a visit was made to Ixworth Thorpe Carr, the only remaining piece of woodland in the village, and the plant was found to be abundant. When it was later discovered to be of regional significance, a return visit was made in 1994 to collect holotype material, only to discover that, following "agricultural improvements" there was very little of the plant left. It is, however, one of the most frequent brambles in parts of north west Suffolk bordering Breckland, and across southeast and central Norfolk. It also occurs in east Suffolk, Herts., Essex as far south as Epping Forest; so far as is known, at a single station in east Kent; from the borders of south Lincs. and Rutland, and from Nottinghamshire. Whilst visiting MANCH during the autumn of 1995, A. Newton discovered a sheet of *R. hindii* collected by Augustin Ley under the name of *Rubus dumetorum* Weihe & Nees var. *raduliformis* Ley, from Elsham, North Lincs., v.c. 54, annotated "also at Barnetby and other stations" August 1907 (Alan Newton, pers. comm.). Thus, *R. hindii* occurs in much of eastern England south of the Humber, with a reasonable supposition that it may be found even further afield. It is not known to either Prof. Weber or Mr Vannerom on the continent. Regional endemic. The distribution of this species is shown in Fig. 4.

Whilst in Devon during 1995, A. Newton pointed out an "escaped" specimen of the cultivar 'Bedford Giant' at Shute, near Axminster. This was examined critically and compared with *R. hindii*. From the examination, it was deduced that cv. 'Bedford Giant' is probably a sport of the present plant with very weak armature.

Representative exsiccatae (all in **herb. A. L. Bull):** v.c. 15: TR/1.6, Clowes Wood, East Kent, 23 July 1996; v.c. 18: TQ/4.9, Strawberry Hill, Epping Forest, South Essex, 25 July 1995; v.c. 20: TL/2.1, Brockett Park, Welwyn, Herts., 14 July 1993; v.c. 26: TL/9.7 Thorpe Carr, Ixworth Thorpe, Suffolk, 19 July 1983; v.c. 27: TM/2.9, Green Lane, Hempnall, East Norfolk, 3 July 1992; v.cc. 53/55: TL/9.1, Pickworth Woods, on the county boundary between South Lincs. and Rutland, 25 September 1995; v.c. 56: SK/6.6, Robin's Dam picnic place, Nottinghamshire, 22 July 1994.

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The author would like to thank Mr W. H. Tucker for preparing the Latin descriptions and also Mr A. Newton for his help, encouragement and advice in the preparation of this paper. In addition, thanks go to Martin Sanford of IPS for help in tracing specimens, and for photocopying to me information on the Babingtons and W. M. Hind, also to Dr A. C. Irwin for allowing me to search through the Rubi at Norwich Castle Museum.

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A new variety of *Ophrys apifera* Hudson (Orchidaceae)

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ABSTRACT

Variation within *Ophrys apifera* Hudson (Bee Orchid) in Britain is briefly reviewed. A new variety, *O. apifera* var. **belgarum** D. M. T. Ettligner var. nov., is proposed for specimens with labella that lack side lobes and basal fields, and bear distinctive harness-shaped patterns of sharp-edged yellow bands.

KEYWORDS: Bee Orchid, variation, Britain.

INTRODUCTION

Ophrys apifera Hudson (Orchidaceae) is an almost, if not entirely, obligate autogam (occasional hybrids with other *Ophrys* species may be due to insect visitors removing excess pollen from already-fertilised flowers). Consequently, any variant tends to be perpetuated since there is no means apart from genetic drift by which mutated genes can be eliminated. The most frequent of these variants have been described and named, albeit at various ranks, over many years (e.g. the summary by Camus & Camus 1921).

In more recent times, Landwehr (1977) recognised and illustrated in great detail the following:

a. subsp. *jurana* Ruppert var. *friburgensis* (Freyhold) Ruppert: labellum normal; petals greatly enlarged into the shape of sepals, usually pink sometimes yellow-green or whitish speckled with pink spots;

b. subsp. *jurana* f. *botteronii* (Chodat) Ruppert: as for *friburgensis* but with the side-lobes, which are normally separated from the main labellum, reduced to unseparated pointed humps near its apex;

c. subsp. *jurana* f. *saraepontana* Ruppert: similar to *friburgensis* but with a marbled labellum pattern and side lobes either reduced or modified in the manner of f. *botteronii*;

d. var. *aurita* Moggridge: as normal *apifera* but with long, straight, yellow-green petals that appear very narrow because the edges are sharply reflexed;

e. var. *bicolor* (Naegeli) E. Nelson: labellum pattern replaced by a green or pale brownish area near the base, shading smoothly to a blackish-brown near the apex; basal field absent;

f. f. *chlorantha* (Hegetschweiler) K. Richter: lacking anthocyanin; the tepals are greenish white and the labellum greenish yellow with only the ghost of a pattern;

g. var. *flavescens* Rosbach: a less pronounced version of *chlorantha*, it has a pale brown labellum bearing a normal but faded pattern; and

h. var. *trollii* (Hegetschweiler) E. Nelson: labellum elongated, tapering to a pointed tip that is not or only slightly reflexed; side lobes prominent and often widely separated; labellum pattern asymmetric and diffusely marbled; basal field distorted or missing.

Sundermann (1980) limited his recognition to vars *flavescens* and *friburgensis* (in which latter he – reasonably – included all the variants with sepaloid petals, *friburgensis* having priority at varietal rank). It was also reasonable to discard *aurita*, which is poorly differentiated from the norm, but his reason for preferring *flavescens* to the more morphologically extreme *chlorantha* is unclear. His omission of the highly distinctive *trollii* and *bicolor* is also difficult to understand.

Buttler (1986) also preferred *flavescens*, which he included with *trollii*, *bicolor* and *botteronii* in his illustrations and descriptions but he refrained from quoting any formal ranks.

Baumann & Künkele (1988) mentioned *botteronii*, *trollii* and *bicolor* but only as synonyms of *apifera*.

Stace (1991) was sparing in his use of subspecies and variety, and admitted none to *apifera* in the British Isles.

Delforge (1994) mentioned and illustrated *jurana friburgensis*, *jurana botteronii*, *trollii* and *bicolor* but without assigning ranks to them; he also illustrated an unequivocal specimen of *chlorantha* but only as an unnamed example of "hypochromy" (abnormal absence of colour, in this case anthocyanins).

Devillers & Devillers-Terschuren (1994) did not formally recognise any taxon below the rank of species.

Sell & Murrell (1996) mentioned *bicolor*, *flavescens*, *trollii* and *botteronii*, and chose forma rank for all, with appropriate stat. nov. authorities. They also chose to equate *flavescens* with *chlorantha*, as apparently did Sundermann (1980) and Buttler (1986), though Landwehr (1977) clearly illustrates a distinction. Their preference for *botteronii* for the sepaloid-petal variant is logical at forma rank but their description is so unlike any published illustration (or specimen in the field) that one must suspect some accidental omission of text.

VARIATION IN BRITAIN

It is clear that, with time, infraspecific taxa have become progressively less often recognised among European orchids, Sell & Murrell (1996) being a welcome exception. This is not the place to discuss the reasons for this or to attempt a refutation; the problem seems to lie partly in the subjectivity surrounding the definitions of the terms species, subspecies, variety and forma. I believe that the infraspecific taxa as I would define them have evolutionary potential, even if it is sometimes slight, and suggest that the following taxa should be recognised within British *Ophrys apifera*. They invariably occur with normal *apifera* and varietal rank seems to me to be the most appropriate for all of them (the summarised descriptions are above; I am not in a position to comment on the validity of the authorities).

Var. *aurita*. Probably widely overlooked; distribution uncertain.

Var. *bicolor*. Recorded at one site in Anglesey (v.c. 52) in 1976 and one site in Dorset (v.c. 9) since 1993. A third British site was discovered in N. Essex (v.c. 19) in June 1997 by J. Tyler; c. 20 specimens (!) were growing with c. 35 var. *chlorantha* and 100+ var. *apifera*.

Var. *chlorantha*. Not uncommon in southern and eastern England, rare elsewhere but sometimes in large numbers (e.g. several hundred in a good year at one site in Yorkshire). Intermediates ("flavescens") seem to be very rare in the British Isles and should not be confused with normal flowers that have faded with age.

Var. *friburgensis*. Rare, mostly in south-western England. Intermediates, with pink petals larger than normal but not sepaloid in shape, occur more frequently.

Var. *trollii*. Uncommon in southern and south-western England, rare elsewhere. Intermediates occur occasionally but should not be confused with normal *apifera* with labellum apices that are for some reason not properly reflexed.

A NEW VARIETY

In July 1985, while examining a colony of *O. apifera* at a dune system near Rhosneigr, Anglesey (v.c. 52), I found a specimen whose flowers differed greatly from the norm and from any described variety; however, one plant at one locality does not justify taxonomic recognition. In June 1993 M. N. Jenkinson kindly drew my attention to the variants in a colony on a roadside verge near Winchester (v.c. 11). To my surprise, these were exactly the same as the Anglesey specimen and a rough count showed c. 200 flowering plants accompanied by c. 20 plants with normal flowers. Since the County Council was persuaded (at least temporarily) to change its mowing policy at the site, the numbers have remained satisfactory, though subject to the substantial fluctuations normal in the species. Identical flowers had been known in smaller numbers at Twyford Down, c. 4 km to the south west, since the 1960s (23 plants in 1964) by M. N. Jenkinson and R. J. Laurence (pers. comm., 1993, 1995). Personal enquiries, accompanied by colour transparencies at a reproduction ratio of 1:1, have shown that the new variety has also been found near Great Gaddesden (v.c. 20) by

R. M. Bateman in 1980 (though he recorded it at the time as non-standard var. *trollii* Bateman 1982), and at two sites near Bath (v.c. 6) by R. J. Laurence (pers. comm., 1995). Similar enquiries seem to show that it occurs only rarely on the Continent since it has only been seen at one site in France by P. Delforge and at "several" in Switzerland by H. R. Reinhard, whilst the equally experienced orchidologists P. Jacquet and D. Rückbrodt have never seen it (all replies in litt. 1996). If anyone has close-up photographs thought to be of this variety I should be very glad to see them, since I am confident that it occurs more widely in Britain and Ireland.

DESCRIPTION

Ophrys apifera Hudson var. *belgarum* D. M. T. Ettlinger var. nov.

HOLOTYPE: roadside verge on chalk near Winchester, Hampshire (v.c. 11), England, 18 June 1994, *D. M. Turner Ettlinger* now in the Orchid Herbarium at K.

Ab *apifera* typica non differt nisi labello. Labellum ± obovatum, apparerter globosum, hirsutum ad margines superiores. Lobi laterales absentes. Usualis parva area annularis basilis absens. Apex acutus plerumque sed non semper plene reflexus. Color atrocastaneus cum vitta aurea argutaque in medio et vittibus tenuibus unde versus humeros.

It differs from typical *apifera* only in its labellum which is more-or-less obovate, well rounded in appearance, the upper edges very hairy. Side lobes absent. Basal field absent. Apex sharply pointed, usually though not always well reflexed under the lip. Ground colour dark chestnut, with a clear-cut bright yellow band across the middle and smaller subsidiary bands extending from the sides of the middle band up to the shoulders.

Etymology: *belgarum* = "of the Belgae", the Celtic tribe who inhabited the type area in Roman times and whose chief town Venta Belgarum ("the market of the Belgae") evolved into the modern Winchester. Jenkinson (1995) has a good illustration of the variety in his book; he informally suggested the name *pseudotrollii* but I believe that that name would be more appropriate for normal *apifera* whose apices have failed to tuck themselves under the lip.

ACKNOWLEDGMENTS

I am grateful to all my correspondents in this matter, especially M. N. Jenkinson and R. J. Laurence the original discoverers of the variety. I also thank R. M. Bateman for his helpful comments on the manuscript.

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Notes

NORTHERN LIMITS ATTAINED BY NATIVE BRITISH PLANTS IN NORTH PEARY LAND, GREENLAND

In June 1995 I was able to visit North Peary Land, Greenland with an Arcturus Expedition led by Robert Burton. The botanists in the party were Dr Jean Balfour, Dr Hugh Lang, Dr Fritz and Mrs Elizabeth Schwarzenbach and myself. Our base camp was at the head of Frigg Fjord at 83° 11' N latitude some 50 km to the south of Kap Morris Jesup, the most northerly point of land in the world. Cape Columbia, the most northerly point of the Canadian arctic, on Ellesmere Island is at latitude 83° 08' N.

During our two week stay we recorded some 80 species of vascular plants. Twenty five of the species seen also occur in Britain and Ireland and of these, four were found at a new northern limit (Table 1). Apart from *Kobresia simpliciuscula* which also occurs in Upper Teesdale, these four species are confined to the Scottish Highlands. Christian Bay, a botanist with the Greenland Botanical Survey, had visited Frigg Fjord in 1985 and was impressed with the relative richness of the flora at this high latitude. He considered it to be a high arctic oasis. He also visited many other Peary Land localities including Kap Morris Jesup (Fredskild *et al.* 1986, 1987).

British Floras, e.g. Clapham, Tutin & Warburg (1952), Sell & Murrell (1996), continue to quote the same north latitude figures for several of the species found in North Peary Land. I have therefore

TABLE 1. THE NORTHERN LIMITS ATTAINED BY THE 25 NATIVE BRITISH PLANTS IN NORTH PEARY LAND, GREENLAND

Species	Site name	Northern limit
<i>Alopecurus borealis</i>	Kap Morris Jesup	83°39'N
<i>Cardamine pratensis</i>	Brainard Sund	82°58'N
* <i>Carex atrofusca</i>	Frigg Fjord	83°12'N
<i>Carex maritima</i>	Frigg Fjord	83°16'N
<i>Carex rupestris</i>	Brainard Sund	82°58'N
* <i>Carex saxatilis</i>	Frigg Fjord	83°16'N
<i>Cerastium arcticum</i> s.l.	Kap Morris Jesup	83°39'N
<i>Cystopteris fragilis</i> s.l.	Frigg Fjord	83°12'N
<i>Equisetum arvense</i>	Frigg Fjord	83°12'N
<i>Equisetum variegatum</i>	Frigg Fjord	83°16'N
<i>Juncus biglumis</i>	Kap Morris Jesup	83°39'N
* <i>Juncus castaneus</i>	Frigg Fjord	83°12'N
<i>Juncus triglumis</i>	Frigg Fjord	83°16'N
* <i>Kobresia simpliciuscula</i>	Frigg Fjord	83°12'N
<i>Koenigia islandica</i>	Frigg Fjord	83°12'N
<i>Minuartia rubella</i>	Kap Morris Jesup	83°39'N
<i>Oxyria digyna</i>	Constable Bugt	83°34'N
<i>Poa glauca</i>	Frigg Fjord	83°11'N
<i>Persicaria vivipara</i>	Constable Bugt	83°34'N
<i>Sagina nivalis</i>	Frigg Fjord	83°12'N
<i>Saxifraga cernua</i>	Kap Morris Jesup	83°39'N
<i>Saxifraga cespitosa</i>	Kap Morris Jesup	83°39'N
<i>Saxifraga nivalis</i>	Kap Morris Jesup	83°39'N
<i>Saxifraga oppositifolia</i>	Kap Morris Jesup	83°39'N
<i>Silene acaulis</i> (leg. O. Bennike 1984)	Nansen Land	83°09'N

The nomenclature of the species follows Stace (1991).

*New northern limit 1995.

documented updated information on these hardy members of the British flora found at the most northern botanical localities on earth. The information given in Table 1 is based on Bay (1992), Bay (pers. comm. 1997) and the 1995 field work at Frigg Fjord.

Not surprisingly 21 of the 25 species listed are members of the arctic-alpine or arctic-subarctic element of the British flora (Matthews 1955). *Equisetum variegatum* is a representative of the northern montane element and *Cardamine pratensis*, *Cystopteris fragilis* and *Equisetum arvense* are widespread (Birks 1973). Seventeen of the species are designated rare or scarce (Perring & Farrell 1983; Stewart *et al.* 1994). In addition to the three widespread species only *Juncus triglumis*, *Oxyria digyna*, *Persicaria vivipara*, *Saxifraga oppositifolia* and *Silene acaulis* are relatively common and widespread in the Scottish Highlands but much scarcer elsewhere in the British Isles being rare to very rare in Ireland from which *Juncus triglumis* is absent (Webb 1977).

All the species are well distributed throughout most of the Arctic with *Juncus triglumis* being represented by the closely related *Juncus albescens* in the Canadian arctic (Polunin 1959). They are all common and widespread in Greenland with the following exceptions: *Alopecurus borealis* is absent from the southern half and *Cardamine pratensis*, *Carex atrofusca*, *C. rupestris*, *C. saxatilis*, *Juncus castaneus* and *Kobresia simpliciuscula* show disjunct patterns of distribution. This may be related to areas which have undergone little or no glacial erosion during the Weichselian (Devensian) glaciation (Bay 1992).

The reported increase in the northward range of these species is due to fieldwork conducted in new areas rather than new colonisation from possible climatic amelioration. The four species seen at a new northern limit in 1995 gave the appearance of being long established. The favourable south facing *Carex stans* mires irrigated by snow beds and melt from the underlying permafrost were in stark contrast to the areas of dry stony high arctic desert virtually devoid of plant life.

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POPULATION SIZES OF *GENTIANELLA ULIGINOSA* (WILLD.) BOERNER, DUNE GENTIAN, ON COLONSAY (V.C. 102) IN 1996

Gentianella uliginosa (Willd.) Boerner, Dune Gentian, has been recorded from five sites in South Wales (Lousley 1950; Abell 1954; Pritchard 1959; Kay 1972; Ellis 1983), three sites on Colonsay (Rose 1998) and two old sites in England (Rich 1996). In July and August 1996, a detailed survey of two of the three sites on Colonsay was undertaken as part of the Scottish Rare Plant Project (Lusby 1992) of the Royal Botanic Garden, Edinburgh.

At Balnahard Dunes seven populations were found, with a maximum separation of c. 300 m. 1709 plants were counted in the largest population by R. L. Gulliver and P. Lusby using a grid. Each plant had a dried chick pea placed beside it to avoid counting it twice. Individuals were assigned to *G. uliginosa* rather than *G. amarella* if the pedicel length was well above 50% of the plant height (Pritchard 1959; Stace 1991; cf. Pritchard & Tutin 1972). Most *G. uliginosa* and some *G. amarella* and *G. campestris* plants were single flowered and less than 8 cm tall. Occasionally specimens of *G. uliginosa* with only a single leaf at the base of the pedicel were encountered. (In one case a plant had a single leaf at the base of one of its pedicels and two leaves at the base of the other two, thus confirming the status of the single structures as leaves.)

The size of the other six populations was estimated, with values ranging between 200 and 1000. The total estimate for the site was 4509.

In 1994 the sizes of the two largest populations in South Wales, where numbers are known to vary greatly from year-to-year (Q. O. N. Kay, pers. comm., 1997) were 4000–8000 at Oxwich and 600–1000 at Whiteford (Kay & John 1995). Colonsay therefore contains one of the largest known populations of *G. uliginosa* in the British Isles.

The number of plants of all three species of *Gentianella* with fully developed corollas (in terms of length) and/or with capsules was recorded on 24 July, 9 August and 23 August 1996 from a fixed 2 × 2 m quadrat (Table 1). The values in Table 1 can increase in time as small flower buds grow to their full length; or decrease due to grazing. On 24 July none of the *G. uliginosa* plants recorded were in fruit, by 9 August half were completely in fruit and a further nine had capsules plus either closed or open corollas. By 23 August the majority of plants were in fruit. *G. campestris* was the latest flowering of the three species, with *G. amarella* occupying an intermediate position, though the number of plants present was small.

At Balnahard in 1996 sheep, cattle and rabbits were present and grazing levels were high in July and August. This seemed to act "preferentially" on the taller *G. amarella* thereby reducing the

TABLE 1. THE NUMBER OF PLANTS WITH FULLY DEVELOPED COROLLAS AND/OR CAPSULES OF *GENTIANELLA ULIGINOSA* IN A FIXED 2 × 2 M QUADRAT IN JULY AND AUGUST 1996 AT LEAC BHUIDHE, BALNAHARD DUNES, COLONSAY, V.C. 102, TOGETHER WITH NUMBERS OF *GENTIANELLA AMARELLA* AND *GENTIANELLA CAMPESTRIS* (SEE ALSO TEXT)

	24 July	9 August	23 August
<i>Gentianella uliginosa</i>			
Corolla(s) closed (fully expanded but not open), no capsules	22	8	0
Corolla(s) open, no capsules	0	0	4
Corolla(s) closed, capsules also present	0	8	0
Corolla(s) open, capsules also present	0	1	0
Total number of plants, flowering or about to flower	22	17	5
Capsules (only)	0	17	28
Total number of <i>Gentianella uliginosa</i> plants with fully expanded corolla(s)	22	34	33
<i>Gentianella amarella</i>			
Corolla(s) present	+	4	5
<i>Gentianella campestris</i>			
Corolla(s) present	+	25	62

Note + indicates present, no count undertaken.

possibility of introgression between the two species, which is reported to be affecting *G. uliginosa* populations in South Wales (Pritchard 1959, 1972). On the other hand Kay & John (1995) report more or less pure stands of *G. uliginosa* from South Wales with little or no signs of introgression, even when surrounded by *G. amarella*. Grazed examples of *G. uliginosa* were noted on all three visits.

In 1996 the locations of the Balnahard populations (slopes, mini-plateaux and dry hollows) were all very dry. They frequently contained small gaps in the dune turf in which annuals could establish. In South Wales the plants usually grow in dune slacks with *Salix repens* present, though the water table is often well below the surface all the year round (Q. O. N. Kay, pers. comm., 1997). Lousley (1950) reported some plants on dry dune grassland at Oxwich Burrows.

On Colonsay no *G. uliginosa* was found at the second site, Traigh nam Barc, where it was reported in 1981 by Rose (1998); though *G. amarella*, *G. campestris* and *Coeloglossum viride* which are associated with it at Balnahard Dunes were present.

Kilaran Bay (Traigh Ban), the third site with a 1981 record by Rose (1998), has been examined repeatedly between 1991 and 1996. Neither *G. uliginosa*, *G. amarella* nor *Coeloglossum viride* have been located. However *G. campestris* has recently (1997) been found (A. Skrimshire, pers. comm., 1997).

G. uliginosa is a British *Red data book* species which has been included on the list of species to receive special conservation attention as part of the United Kingdom's contribution to the United Nations Convention on Biological Diversity. More information on year-to-year fluctuations in population numbers, the precise habitat/management requirements of the species, and on the extent of hybridization with *G. amarella* are urgently needed, especially as Colonsay represents the only known station for this rare and elusive plant in Scotland, where it is at the most north west edge of its global distribution (Hulten & Fries 1986).

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× AGROPOGON ROBINSONII (DRUCE) MELDERIS & D. C. MCCLINT.

The southern European and Mediterranean grass *Polypogon viridis* (Gouan) Breistr. (Poaceae) is now locally frequent as an established plant of damp rough ground in the Channel Islands, and is sporadic in Britain on rubbish tips and similar places as a casual from wool, cotton, grain and probably other sources. There is a good drawing of it in Hubbard (1984, p. 304). It is distinct from other species of *Polypogon* in its entire (not 2-lobed), awnless (not awned) glumes, and was formerly included in *Agrostis* (as *A. semiverticillata* (Forssk.) C. Chr.). It is placed in *Polypogon* mainly on account of its spikelet disarticulation, which is well below the glumes rather than at the base of the floret. The species is readily recognized by its distinctive, rigid, dense, much-branched panicles, and by the minutely rough (i.e. strongly papillate) glumes.

Sometimes it is accompanied on rubbish tips in Britain by another grass with a very similar habit and similarly papillate glumes, but with slightly notched glumes each with an awn up to 2 mm long. This is the hybrid *Agrostis stolonifera* L. × *Polypogon monspeliensis* (L.) Desf. (= × *Agropogon littoralis* (Sm.) C. E. Hubb.), which is also found as a rare native in southern Britain within the range of *P. monspeliensis*.

The hybrid *Agrostis stolonifera* × *P. viridis* (= × *Agropogon robinsonii* (Druce) Melderis & D. C. McClint.) is a very rare grass, having been reported on only three previous occasions, all in Guernsey (McClintock 1975, 1987). It was discovered by F. Robinson in 1924 at St Sampson (N. E. Guernsey) and determined and named as *Agrostis × robinsonii* (but written in error as × *F. robinsonii*) by Druce (1925), confirmed by J. Fraser and E. D. Marquand. The specimen is in BM, seen by C.A.S. The second record was made in 1953 at Vazon (W. Guernsey) (not at Grandes Rocques as stated by McClintock (1975)) by C. E. Hubbard (specimen in K, seen by C.A.S.), and the third in 1958 at Grandes Rocques (N.W. Guernsey) by D. McClintock, confirmed by A. Melderis (specimen in STP, seen by C.A.S.).

In July 1994 P.M. discovered a single plant of a grass (**herb. P.M.**) that closely resembles *P. viridis* in habit in a long-abandoned industrial site in Shieldhall, Glasgow, Lanarks, v.c. 77. It grew 20 m from the edge of a lorry park in current use and c. 750 m from the nearest dock on the River Clyde. The habitat was scrubby grassland dominated by *Holcus lanatus* with a few plants of *Agrostis stolonifera* and very few of *A. capillaris*. No other grasses were present in the immediate vicinity. Other associates, one to a few plants in each case, were *Artemisia vulgaris*, *Cirsium arvense*, *Chamerion angustifolium*, *Dactylorhiza fuchsii*, *D. × venusta*, *Epilobium montanum*, *Equisetum arvense*, *Luzula multiflora*, *Senecio jacobaea*, *Trifolium hybridum* and *Tussilago farfara*. Scattered in the area were *Salix caprea*, *S. cinerea* subsp. *oleifolia* and *S. × reichardtii*, ranging in height approximately 1–3 m.

The plant differs from *P. viridis* in its scarcely papillate glumes, lemma entire (not minutely toothed) at apex, palea c. 3/4 as long as lemma (not nearly as long) and anthers c. 1·2 mm (not c. 0·6 mm) long. The pollen grains are empty, and the plant is clearly a hybrid between *P. viridis* and a grass with non-papillate glumes, lemma entire at apex and much longer than palea, and anthers >1 mm long. *Agrostis stolonifera* fits this perfectly: glumes not papillate; lemma entire at apex; palea c. 2/3 as long as lemma; anthers 1–1·5 mm long.

The Scottish plant closely resembles the 1924 and 1953 Guernsey specimens of × *A. robinsonii*. The glumes are not bifid and awned as stated by Sell & Murrell (1996) in any of these specimens. The 1958 Guernsey plant, on the other hand, is obviously a slightly unusual specimen of *Agrostis stolonifera*, being fertile and having all the diagnostic spikelet characters of that species.

The Glasgow plant is therefore only the third known record of × *A. robinsonii* (Stace 1997). It must be considered a casual, having arrived at the site presumably as hybrid seed, unlike the native Guernsey records. An intensive search of the site and surrounds was carried out by P.M. in 1996, but no further plants were found. Although the hybrid is endemic to the British Isles as far as is

TABLE 1. DIAGNOSTIC CHARACTERS OF *× AGROPOGON ROBINSONII* (TAKEN FROM THE 1953 GUERNSEY AND 1994 SCOTTISH MATERIAL) AND ITS PARENTS

	<i>Agrostis stolonifera</i>	<i>× Agropogon robinsonii</i>	<i>Polypogon viridis</i>
Spikelet disarticulation	below floret	none	near pedicel base
Spikelet length (mm)	1.8–3	1.8–2.3	1.5–2.2
Glumes	± smooth	scarcely papillate	conspicuously papillate
Lemma length (mm)	1.3–1.8, c. 0.6–0.8 × as long as glumes	1.2–1.5, c. 0.6–0.7 × as long as glumes	0.7–1.0, c. 0.5–0.6 × as long as glumes
Lemma apex	± entire, sometimes awned	entire, awnless	denticulate, awnless
Palea length (mm)	0.8–1.2, c. 0.6–0.7 × as long as lemma	0.9–1.1, c. 0.7–0.8 × as long as lemma	0.6–0.9, c. 0.8–0.9 × as long as lemma
Anther length (mm)	1–1.5	0.9–1.2	0.5–0.7
Pollen grains	full	empty	full
Caryopsis	c. 1 mm	not formed	c. 1 mm

known, it probably occurs in southern Europe where *P. viridis* is native, and whence the Glasgow plant might have been introduced.

The diagnostic characters are listed in Table 1; see also Bradshaw (1975).

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GENTIANELLA ULIGINOSA (WILLD.) BOERNER (GENTIANACEAE) FOUND IN COLONSAY (V.C. 102), NEW TO SCOTLAND

On 4 September 1978 the late E. C. Wallace and I were surveying various sites on Colonsay (v.c. 102) for a week. We found *Gentianella uliginosa* (Willd.) Boerner, new to Scotland, in the flushed "machair" on the south facing slopes of Leac Bhuidhe, NW of Balnahard Bay, NM/426.004 on 4 September 1978. We were both quite convinced of its identity, but we sent specimens to the *Gentianella* specialist Dr Noel Pritchard who provisionally agreed with the identification but expressed a desire to see living material before fully confirming its identity. I was not able to revisit Colonsay until 1981, when I collected more material and sent it to him, and he has recently agreed that the Colonsay plants were good *G. uliginosa*. When I visited Colonsay in 1981 I also found *G. uliginosa* in machair type grassland at Traigh nam Barc (NR/355.909), and possible plants of it at Traigh Ban [Kiloran Bay] (NR/404.982) with much *G. amarella*.

In 1978 we estimated that there were 30–40 plants at Leac Bhuidhe; in 1981 I counted 36 plants in the part of the site I studied. On 15 June 1989 I was surprised to see many plants coming into flower, but as most were not yet out, no proper count could be made, especially as rabbit grazing was then

TABLE 1. PLANT SPECIES OCCURRING IN A 1 M² QUADRAT WITH *GENTIANELLA ULIGINOSA*
IN COLONSAY (V.C. 102)

The first figure indicates cover and the second indicates sociability on the Braun-Blanquet scale (Shimwell 1971)

Vascular plants	Bryophytes		
<i>Gentianella uliginosa</i>	5 plants	<i>Ditrichum flexicaule</i> agg.	2-2
<i>Schoenus nigricans</i>	3-2	<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	2-2
<i>Festuca ovina</i> agg.	2-2	<i>Entodon concinnus</i>	1-2
<i>Lotus corniculatus</i>	2-2	<i>Pseudoscleropodium purum</i>	1-2
<i>Thymus polytrichus</i>	2-2	<i>Ctenidium molluscum</i>	+-2
<i>Pilosella officinarum</i>	1-2	<i>Rhytidadelphus triquetrus</i>	+-2
<i>Bellis perennis</i>	1-1	<i>Trichostomum crispulum</i>	+-2
<i>Euphrasia</i> sp.	1-1		
<i>Linum catharticum</i>	1-1		
<i>Plantago lanceolata</i>	1-1		
<i>Ammophila arenaria</i>	+-2		
<i>Campanula rotundifolia</i>	+-2		
<i>Plantago maritima</i>	+-2		
<i>Polygala vulgaris</i>	+-2		
<i>Centaurium erythraea</i>	+		
<i>Prunella vulgaris</i>	+		

Species recorded outside the quadrat, but in the same community, included: *Anagallis arvensis*, *Carex flacca*, *Galium verum*, *Gentianella campestris*, *Pinguicula vulgaris*, *Plantago coronopus*, *Selaginella selaginoides*; with the bryophytes (in a wetter hollow): *Cratoneuron commutatum* subsp. *falcatum* and *Drepanocladus revolvens*; and the lichens: *Diploschistes muscorum* and *Squamaria cartilaginea*.

Nomenclature follows Stace (1991) for vascular plants, Corley & Hill (1981) for bryophytes and Purvis, Coppins & James (1993) for lichens.

severe, and many were bitten off. At Traigh nam Barc on 28 August 1981 B. J. Coppins, P. Wormell and I estimated that there were at least 40 plants.

COMMUNITIES

At Leac Bhuidhe on 26 August 1981, we noted that the *G. uliginosa* grew mostly on and around *Schoenus nigricans* tussocks in sloping flushes on blown sand on a south to south-east facing slope. A 1 m² quadrat was recorded on this date, Table 1. This vegetation probably equates to the *Festuca rubra* – *Galium verum* fixed dune grassland *Prunella vulgaris* sub community of the N.V.C. (Rodwell 1998, in press) but is more flushed and damper than the above community, with *Schoenus nigricans*, *Selaginella selaginoides*, etc., and approaches the character of dune slack vegetation in places.

At Traigh nam Barc in 1981, the communities were rather similar but less flushed, and *Schoenus nigricans* was not seen at this exact location; however, *Selaginella selaginoides*, *Antennaria dioica*, and a rich bryophyte and lichen flora occurred on the damp calcareous machair, which at the time was a quite open community. It is worth noting here that, at the time of our visit, the machair areas of Colonsay were very fine, some of the best I have seen in western Scotland, and little disturbed by any human factors for a long time.

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Book Reviews

Welsh ferns, clubmosses, quillworts and horsetails, 7th ed. G. Hutchinson & B. A. Thomas. Pp. 265. National Museums & Galleries of Wales, Cardiff. 1996. Price £11.00. ISBN 07200-04-35-7.

Welsh ferns is one of those books which has become a familiar old friend, parochially titled but broad in scope and which has developed and for the most part improved with the passing of each of its many editions. The latest, seventh, edition marks perhaps the most radical change, resulting in a book nearly half as long again as its predecessor. Gone are the hard cover and all mention of herbarium records. The major innovation, which I welcome, is the inclusion of maps giving Welsh distribution at the hectad (10-km square) level and thumbnail sketches of broader European ranges. The latter, while somewhat small, convey a useful impression. However the use of a mid-tone for uncertain occurrence is poorly reproduced and unclear.

The introductory preamble on biology and morphology has been split, the morphological section moved until after the fern allies and now relating to the true ferns alone. I think this is a mistake and would have preferred an all-embracing section prior to the species accounts. The many nomenclatural changes made in the 18 years since the last edition have been taken on board, although *Asplenium trichomanes-ramosum* L. should be called *A. ramosum* L., a name itself proposed for rejection. In some contentious areas, e.g. the taxonomy of *Pteridium*, the authors give an overview without explicitly expressing an opinion. The treatment of all British taxa, which always made a nonsense of the volume's title, has been taken to an extreme, with all taxa, however briefly naturalised, getting a mention and a token Welsh name. The manufacture of vernacular names attracts strongly polarised views; I dislike it and it adds here to an already cumbersome and less than easy to use index! The original half-tone plates have been re-photographed and are deplorable. There are niggling errors aplenty. *Cystopteris alpina*, an extinct(?) native, is curiously completely omitted. *Asplenium viride* is given as L., not Huds., throughout. *A. × badense* was convincingly shown to be an aberrant, possibly octoploid, *A. ceterach* and not of hybrid origin in 1989. Herbarium specimens of reputedly British *A. fontanum* do exist, etc. The world distributions for some taxa have been retained from earlier editions although taxonomic changes have occurred in the meantime, e.g. we have the near cosmopolitan distribution of *Trichomanes radicans* given instead of the true Macaronesian-European endemic range for *T. speciosum*. Similarly *Huperzia selago* does not occur as stated in Macaronesia where it is replaced by *H. suberecta*.

In spite of these criticisms there is much to recommend this inexpensive and useful guide, which like its antecedents deserves a place on the bookshelf.

F. J. RUMSEY

The botanists and guides of Snowdonia. D. Jones. Pp. 174. Gwasg Carreg Gwalch, Llanrwst. 1996. Price £6.95. ISBN 0-86381-383-6. Obtainable for £7.50 (incl. p. & p.) from Gwasg Carreg Gwalch, 12 Yard yr Orsaf, Llanrwst, LL26 0EH.

This small softback book is described as “an account of the botanical exploration of Snowdonia from the earlier period when the Herbalists and Apothecaries conducted ‘simplicy voyages’ into the countryside to gather plants for medicinal uses, up until the Victorian era by which time botany had developed into a separate science”. Having written comparable accounts in Floras of Shropshire and Montgomeryshire (including tracing different activities of many of the same botanists), I well understand the difficulties of providing readers with a satisfying balance between biographical information, anecdotal material and sometimes long lists of the species found and of maintaining some thematic unity in the work as a whole.

Dewi Jones breaks up his account into 19 chapters, but the guides who led visiting botanists up Snowdon and some of the local botanists, as well as the routes they followed, often serve to link these together. On the historical side (as Gwynn Ellis mentions in his foreword), particularly enlightening is the underlying theme of the contrast between the life style of the English gentry who wished to see the sights and plants of Snowdonia and that of the local peasantry who guided them. I found that the botanical information did not always come to life quite as vividly, but a full index to plant names enables one to trace the story of individual species, sometimes over nearly three centuries. I tried this with *Lloydia serotina* (18 entries, from Edward Lhwyd's discovery of it, published in 1696, to the splendid story of the 19th century Oxford Professor in smooth-soled leather boots who never saw the Snowdon lily in situ on the Glyder cliffs because he was too terrified to open his eyes), *Saxifraga nivalis* (eleven entries) and the two *Woodsia* species (nine entries jointly) and gained a perspective on them which I had not obtained when first reading the book. However, the result was far less satisfying with *Saxifraga cespitosa* (four entries).

I can scarcely fault the botanical index, but too many people mentioned in the text do not appear in the general index. Twelve Robertses and ten Joneses are indexed, but I have found two more of each in the text! The choice of works in the bibliography seems arbitrary, and some of the authors of works mentioned in the text but not in the bibliography are in the index, some not. The twelve colour photographs of plants are satisfactory, but some of the 28 black-and-white illustrations much less so. I wish I knew the sources of the coloured print of the busy summit of Snowdon in the 1850s on the cover and of the monochrome print on the title page.

Jones does not stick strictly to Snowdonia in this book. The first chapter, on the 16th century manuscript herbal of William Salesbury (whom I prefer to spell Salusbury), is included on the grounds that its author "spent the greater part of his life at Plas Isa, Llanrwst", and another chapter is about Hugh Davies's *Welsh botanology* (1813), essentially a Flora of Anglesey with an alphabetical list of Welsh plant names with their Latin and English equivalents. My editorial fingers itched at the erratic punctuation and misspellings; some of the Latin is faulty too. But in the end I was prepared to follow a few byways and to tolerate some bumps along the road. This is a book packed with fascinating information about North Wales, historical, social and botanical.

P. H. OSWALD

The introduction of Chinese plants into Europe. L. A. Lauener, edited by D. A. Ferguson. Pp. xii + 269. S.P.B. Academic Publishing, Amsterdam. 1996. Price Dfl. 140.00/US \$87.50. ISBN 90-5103-130-0.

When Andrew Lauener died in 1991, he left a virtually complete manuscript of this book, the fruits of many years' experience of working with Chinese collections in the Herbarium of the Royal Botanic Garden, Edinburgh. David Ferguson, with the help of some colleagues, prepared it for publication, which was facilitated by friends in The Netherlands.

The author approaches his subject mainly from a systematic angle, unlike Emil Bretschneider's monumental *History of European botanical discoveries in China* (1898), E. H. M. Cox's *Plant hunting in China* (1945) and Roy Lancaster's *Travels in China: a plantsman's paradise* (1989), the longest chapter by far being that entitled "The plants". This consists of an alphabetical account by genus of how some Chinese plants reached our gardens. The factual details (often fascinating) of collecting and introducing them into cultivation are accompanied by comments about botanists who have worked on the genus and their publications, about the names, nomenclatural history and botanical features of certain species, and about their uses both in their native region and in cultivation. All this information is provided in a personal way, reflecting the author's experience and including remarks on who is working on what and what is due to be published soon (data that are inevitably sometimes out of date). Each genus is illustrated by one or more bold line drawings that give a good impression of the plant in question but may on occasion strike some readers as being rather dark, even fuzzy. The book also includes small chapters on China, Chinese place names and plant collectors (alphabetically), a selective bibliography, a useful gazeteer of most place names mentioned (with co-ordinates) and indexes.

Readers interested in the activities of botanical collectors in China will find little in this book that

has not been treated in more detail in the three works mentioned above (only the first two are in the bibliography). What it will do is answer such questions as "Who introduced that species into cultivation?" and, for some species, "Has it always been grown under that name?" A certain amount of apparently irrelevant information, a comment about *Rubus chamaemorus*, *R. idaeus* and *R. fruticosus*, for example, would seem to be aimed at gardeners who are more familiar with European members of the genus than with Chinese ones. In general, however, the information given is usually accurate, though sometimes incomplete. If you know that a garden plant is Chinese in origin, you are likely to find some interesting and/or useful background data about it in this book.

N. K. B. ROBSON

Aquatic plants in Britain and Ireland. C. D. Preston & J. M. Croft. Pp. 365. Harley Books, Colchester. 1997. Price £25.00. ISBN 0-946589-55-0.

The introduction clearly states that this book summarises the distribution, habitat and reproductive biology of the vascular plants which grow in freshwater in Britain and Ireland. For the purposes of identification one is referred to Stace's *New Flora of the British Isles* (1991) or to special literature. I find it a pity that there are no keys or "important diagnostic characters"; there is rather a lot of unprinted paper in the book and it would not have been longer or more expensive with, at least, some information on critical taxonomic features. In some cases this is important because new introductions such as *Cabomba caroliniana* and *Hydrocotyle ranunculoides* are not described in Stace's *Flora*. Granted, both species are illustrated but the illustrations are without scales and are not much more than habit sketches; they do not allow critical determination. It is no doubt unfair to criticise something which is clearly stated not to be an aim of the book but its title and very attractive cover may lead some people to believe it is a "popular" work. This is a serious scientific work written for experienced botanists.

The authors discuss the problems concerning the definition of what an aquatic plant is. They attempt to include those species which "characteristically" grow in water which persists throughout the year. In the Apiaceae some species which are deliberately excluded are listed including *Sium latifolium*; this species germinates under water and develops finely divided submerged leaves and it overwinters under water. This book is for summer botanists. *Apium repens* and its hybrid with *A. nodiflorum* are not even mentioned; in my experience the hybrid is rather more aquatic than, for example, *Calla palustris* and *Myosotis scorpioides* which are included. *Hypericum elodes*, at least in Ireland, may grow in water the whole year but it is not even mentioned, neither are *Cotula coronopifolia*, *Lycopus europaeus*, *Teucrium scordium* and *Samolus valerandi*. The choice of species is a problem of personal experience and is not important – all the "real" aquatics are included – but it would be useful to know which "aquatic" species were intentionally excluded. Each genus but not each species is illustrated. The purpose of the illustrations in an important scientific book like this is not quite clear; some of them, such as *Cabomba caroliniana* and *Lagarosiphon major*, are poor.

Each species has an updated distribution map clearly showing changes in the distribution. Distinct symbols are used for pre-1950, 1950 to 1969, and 1970 and later records. It is very depressing to see the changes since 1950. The introduced species have different symbols and, on the whole, they seem to be doing rather better than the natives. An interesting case is *Sagittaria latifolia* which seems to be slowly taking hold in the south. *Sagittaria sagittifolia* is a very distinct plant: everyone knows what it looks like and it is rarely gathered. Nobody needs to poke into its flowers or put its fruits under a lens. However, if you do it may turn out to be *S. latifolia*. Around Zürich it seems to have virtually replaced *S. sagittifolia* and nobody saw it happen! For this reason it would have been valuable to have some diagnostic characters; the authors do, at least, say it may be overlooked because of its similarity to *S. sagittifolia*.

The habitat descriptions are very concise and clearly presented, also they are well documented. The bibliography runs to 24 pages! The part on reproductive biology is rather mixed: for some species it is excellent but for others almost no information is given. It would have been valuable to know more about which species are self-incompatible and the vectors for pollen transfer among insect-pollinated plants. The nature of the effective disseminules and their dispersal could have

been expanded; the authors have considerable experience with these plants and should, perhaps, have more often added their own observations rather than relying on published work. Conservation designations of the rare species are presented at the end of the book.

I have devoted most of my life to the biology of aquatic plants. This book has delighted me and I have learnt a lot of new information. What more can one wish? This is an essential work for all people concerned with the ecology and management of freshwater. The standard of production is very high – I failed to find any serious mistakes. For a book of this quality and length the price is remarkably low.

C. D. K. Cook

The making of the Cretan landscape. O. Rackham & J. Moody. Pp. 237. Manchester University Press, Manchester. 1997. Hardback £50.00, ISBN 0-7190-3646-1. Paperback £19.99, ISBN 0-7190-3647-X.

Crete is the most southerly region of Greece and the largest, most mountainous Greek island. The native flora is of enormous national and global importance, and one of the choicest in the plant-rich Mediterranean region. Of some 1650 higher plant species, 10% are endemic or shared only with Karpathos and Kasos to the east. This unique and ancient flora, as significant as that of most tropical islands, is also irresistible to the hundreds of British botanists and naturalists who flock there each spring. Now a book is available to supplement their field guides.

In *The making of the Cretan landscape*, English botanist and landscape historian Oliver Rackham and American archaeologist Jennifer Moody present the fascinating and complex story of the vegetation and landscape of this beautiful island. They dedicate just one chapter directly to the flora and two to the vegetation, but their holistic approach is essential to a full understanding of the processes that have influenced, and continue to influence, the varied plant life of Crete. The book is beautifully written, scholarly but never losing its humour or lightness of touch.

This exciting work, which pursues themes familiar from Oliver Rackham's 1986 classic, *The history of the countryside*, will guide the curious visitor, whether botanist, conservationist or bemused tourist, through the complexities of Cretan vegetation and landscape. The authors break away from the conventional philosophy and restrictive practices of contemporary biology and ecology to combine their field observations, trawls through Venetian archives and broad perspective of geography and history. They take the reader from the earliest geological and prehistoric beginnings, through the "Golden Ages" under the Minoans and the Byzantine Empire, superseded by long Venetian and Turkish occupations, to the modern Crete of E.U. subsidies.

On Crete, links with the past are real and tangible. Agriculture has long been the basic occupation of the people, and the prosperous market town of Archanes near Iraklion has remains of a Minoan farm, complete with olive press. Rackham & Moody cite the observation of a visitor from Renaissance Venice who recorded "Iusgriano con fior d'oro" (Golden Henbane, *Hyoscyamus aureus*) on a bastion of Iraklion's huge 16th century city walls. This predominantly south-west Asian plant survives today at the site.

The opening chapters, on geology, physical geography, climate and animal life past and present, include a useful account of how the famous flower-rich gorges and the distinctive flat mountain-plains like Lassithi and Omalos may have formed. The simple, elegant map of gorges and mountain-plains in the preface is the only one of its kind in published form. Oliver Rackham is a fine cartographer and calligrapher and his diagrams and maps embellish the text throughout. He provides valuable distribution maps of major endemics, such as Cretan Wall-lettuce (*Petromarula pinnata*), Cretan Sainfoin (*Ebenus cretica*) and Cretan Dittany (*Origanum dictamnus*), and the principal trees, among them the endemic Ambelitsiá (*Zelkova cretica*) and Cretan Date-palm (*Phoenix theophrasti*), the latter now known also from the Dodekanisos and adjacent Turkish coast. The maps illustrate new data, notably Hungarian Oak (*Quercus frainetto*), otherwise not recorded from Crete. Another oak, *Q. brachyphylla*, is usually recorded as *Q. pubescens*. One should note that Rackham & Moody eschew (probably wisely) recent taxonomic progress, including the revised *Flora Europaea Volume 1*!

Above all, Rackham & Moody endeavour to dismantle the simplistic but widespread notion that Crete, and much of the Mediterranean region, is merely a ruined landscape or "Lost Eden". The

conventional view is that grazing by goats and other domestic stock is the culprit. The authors refute this, stating (their italics) that “*There can be no doubt that in Crete, ‘excessive’ browsing is not an artefact, but is the natural state to which the flora, and especially the endemics, are adapted.*” While native vegetation has certainly been profoundly modified by more than five millennia of human activity, the authors argue that today’s vegetation, notably the scrublands and woodlands, may actually be in better condition than for centuries. This has immense implications for nature conservation in Crete, the rest of Greece and perhaps all the lands around the Mediterranean.

The authors pursue their radical hypothesis with reference to flora, vegetation and landscape history in the context of the socio-economic and historical background of human settlement, trade, rural industry, roads and tracks, animal husbandry and vernacular architecture. The Cretan flora itself remains a dynamic, living resource, with wild plants still being utilised by the local population. The authors argue that, despite often considerable fluctuations in tree cover and agricultural priorities, basic ecological patterns and processes remain the same. Indeed the ancient Minoans and Mycenaeans may well have known similar vegetation to what we see today. Overgrazing and bulldozing of new olive terraces is certainly a problem in many areas, but once the visitor starts to look around, it is remarkable how much land is covered by impenetrable scrub and stands of woodland, wood-pasture and what the authors rightly call savanna. Rackham & Moody are undoubtedly closer to the mark than the Greek pundits who see Crete’s apparent lack of forest cover as another calamity of Turkish rule!

Rackham & Moody demonstrate convincingly that most of the woody vegetation has either persisted or regenerated over the last 150 years. Landscape drawings of 19th century visitors such as Edward Lear in 1864 show this clearly. Pines, cypresses, maples and oaks have invaded former fields and terraces, both in the lowlands and the mountains. In western Crete, high maquis dominated by Strawberry Tree (*Arbutus unedo*) and Tree Heather (*Erica arborea*) has developed into dense woodland. This echoes a trend seen over the rest of Europe in the late 20th century, as people drift away from the countryside and land falls out of cultivation.

In the final chapter, “Conservation and the future”, the authors are more optimistic than most commentators. Nevertheless, they are concerned about current trends in the Cretan landscape. They note especially ribbon development on the coast, destructive bulldozing for new roads and olive terraces, and “the idea that the irrigation of olives is a necessity rather than a bonus. The search for water has dried up rivers and springs . . . All this is for a subsidized monoculture unlikely to last long.” Certainly, arable weed communities such as those in small upland fields dominated by bulbous or tuberous-rooted, arable weeds like wild tulips and *Geranium tuberosum*, are threatened by progress. As all over Europe, wetlands have disappeared or diminished, although coastal lagoons and marshes survive here and there. Fortunately, apart from plants of coastal sands such as *Androcymbium rechingeri* and *Centaurea pumilio*, relatively few endemic plants are threatened by habitat destruction. Many are under threat due to their natural rarity, but they grow in remote places with few or no visitors. Most occur on remote rocks and scree, high up on the sides of gorges or precipitous cliffs; several, like Cretan Wall-lettuce and *Verbascum arcturoides*, thrive on walls.

The authors rightly conclude that the way forward must lie in education, and are cheered by the fact that younger people in Greece are waking up to the interest, value and fragility of their native environment. They stress the contribution of ecotourism, since increasingly people visit Crete for its natural history. It is certainly a way to restore prosperity and people to village communities in the mountains. The island has breathtaking, dramatic scenery, fine antiquities and excellent tourism facilities, and not least traditional Greek *xenophilia* or hospitality to travellers (these days, alas, tempered by a canny, sometimes aggressive commercial streak). Even ecotourism can damage fragile plant, animal and human communities, but it is much less a threat than outright habitat destruction through uncontrolled development.

Oliver Rackham and Jennifer Moody provide much food for thought, and a good read on the long flight to Chania or Iraklion. Their splendid book will provide the thinking naturalist – why do so many amateur botanists merely want *names* for plants? – with the indispensable background information to appreciate the Cretan flora. One hopes too that at least the odd copy of *The making of the Cretan landscape* finds its way on to the desks of decision makers and politicians in Greece. The book is a triumph, a milestone in the study of the Mediterranean world and its ecology.

Flora of Great Britain and Ireland. Volume 5. Butomaceae–Orchidaceae. P. D. Sell & G. Murrell. Pp. xxi + 410. Cambridge University Press, Cambridge. 1996. Price £60.00. ISBN 0-521-55339-3.

In the light of destruction of forests for paper, one has to ask with the publication of the third major Flora of the British Isles by Cambridge University Press in ten years, is it worth having? My feeling is an emphatic yes! Chop down those forests – this is a landmark in British botany. The Clapham, Tutin & Warburg era can now be laid to rest with the highest honours and affection.

The *Flora of Great Britain and Ireland* has largely been written by Peter Sell with the assistance of Gina Murrell and Potamogetonaceae and Ruppiaceae contributed by C. D. Preston. The aim of the Flora is to supply full descriptions of all the species in Stace's (1991) *New Flora of the British Isles*, to include all the large apomictic genera and many infraspecific variants, and to add more information about hybrids. It is thus a detailed desk-top reference work complementary to Stace, the latter concise and portable.

The Flora follows the classification used in Stace's *New Flora* (1991) and Kent's *List of vascular plants of the British Isles* (1992), resulting in a degree of harmony between the three, with the genera and species sometimes in a different order (Pontederiaceae is listed under Bromeliales in the Conspectus but in the correct place in the text). There are some taxonomic differences from Stace and Kent such as the plant hitherto called *Zostera angustifolia* included under *Z. marina*, *Carex viridula* under *C. flava*, and *Dactylorhiza lapponica* under *D. traunsteineri*. As a result of the extensive nomenclatural work done on the British flora in recent years there are few changes in names, and there is no difficulty in relating the three due to the extensive synonymy.

As the Flora aims to provide full descriptions I checked those for the first species on or after pages 1, 90, 180, 270 and 360 against our herbarium material in the National Museum and Gallery of Wales (NMW). In general the accounts all worked well though there were the few usual specimens and measurements exceeding the stated limits, perhaps because we grow larger and better plants in Wales than in Cambridge. The bracteole-like structures present in the inflorescence of *Butomus umbellatus* were not mentioned. Our plants of *Carex diandra* are significantly larger with stems to 75 cm and leaves to 60 cm × 4 mm. The account of *Deschampsia flexuosa* is very good. We have no material of *Chionodoxa luciliae* and I wonder if it really merited inclusion as it has only been recorded from lawns of Cambridge Botanic Garden. I was surprised to find *Ophrys insectifera* has leaves up to 8 cm wide – ours are rarely more than 2 cm. Overall there was a refreshing feeling that the measurements and descriptions had been looked at afresh and not copied from elsewhere.

The keys to species include infraspecific taxa as well as the species, and those to *Juncus*, *Luzula* and *Puccinellia* I checked worked well. A few literature references such as the Biological Floras or taxonomic papers are cited. Summary distribution data for all taxa are provided. Inevitably a few are out of date (e.g. *Cyperus fuscus* has been known in Berkshire since the early 1980s) and later volumes will no doubt draw on *Atlas 2000*.

Judgement on treatment of critical groups will really have to wait for the *Hieracium* treatment in volume 4, and the only really critical genus dealt with is *Dactylorhiza*. The genus has a novel treatment, probably the most complex in the Flora, with numerous subspecies, varieties and forms, and useful details of the hybrids. I found it difficult to apply to herbarium material due to the necessary emphasis on flower features, but the detailed accounts will help interpret variation present in the field. The drawings of the labella will help, and I would have liked colour photographs.

A substantial amount of the book is dedicated to the intraspecific taxa, and this Flora provides the first recent serious attempt to summarise the information available. This was my only disappointment, not because of what was included but because I was left wanting to know more. There is no means of tracing any infraspecific taxon not included in the Flora, even if they are no longer worthy of recognition. For instance, we have many specimens of *Deschampsia flexuosa* in NMW named as var. *montana* (L.) Hook. f., a variety mentioned in Hubbard's *Grasses* (1984), and I was left wondering if it existed or not, and similarly what has become of *Carex diandra* var. *major* Koch? Perhaps these are our big Welsh plants?

Many infraspecific taxonomic problems remain to be investigated. Are there Norfolk plants of *Alisma gramineum* subsp. *wahlenbergii* or not? There are specimens of *Juncus maritimus* var. *atlanticus* from Cornwall and Hampshire in BM (and possibly elsewhere), and a similar plant occurs down the west coast of Europe to at least northern Spain where it appears to have been described as

var. *longipedicellatus* Sen. & Elias. Similarly, a form of *Juncus maritimus* visually identical with var. *congestus* occurs in Spain where it has been named as var. *compactus* Elias. Jan Kirschner and I do not accept *Luzula multiflora* subsp. *frigida* as a British plant, though the material of *Luzula multiflora* from Scotland would repay further study (our 1996 subsp. *hibernica* was published too late for inclusion). I am uneasy about the way infraspecific taxa in many genera have been strait-jacketed into one infraspecific rank, but thankful that there are few new combinations as a result. These problems simply point to the huge amount of work which remains to be done on infraspecific taxa, and this Flora gives an excellent baseline from which to direct further work.

The full descriptions of aliens will be helpful to botanists without ready access to literature or herbaria. An alien in the hand can now be checked in detail against the description – all too often the brief accounts in some Floras result in an assumption that the plant in the hand is the one in the book. Deciding which aliens to include and which to exclude presents its usual difficulties; the approach taken is to include as many as possible. Some species have been given fuller treatment than others (compare on the same page the full account of *Chionodoxa luciliae*, with the briefly mentioned *Muscari azureum*, apparently naturalised in derelict parkland in Somerset). On the basis of the information available to date, both *Serapias lingua* and *S. parviflora* merited full treatment as native species.

The book has a laminated hardback cover with a picture of bluebells. It contains an introduction, a conspectus of families for the whole work and a key to the monocotyledonous families included, the systematic accounts, a separate list of new taxa and combinations, a glossary and an index. The typeface and layout is that of the third edition of Clapham *et al.*, *Flora of the British Isles* (1987) and is not distinctive, and the illustrations are somewhat functional. There are a few minor formatting and typographical errors.

To sum up, the two key features of the Flora are the full descriptions of British plants with updated nomenclature, and the treatment of the infraspecific taxa. It is an essential reference work for academic and serious amateur botanists in the British Isles, and probably for all in north-west Europe. This is a taste of Peter Sell's outstanding, detailed knowledge of the British flora after a lifetime of study, and I sincerely wish Peter and Gina the best of luck with its completion.

T. C. G. RICH

New Flora of the British Isles, 2nd ed. C. A. Stace. Pp. xxx + 1130. Cambridge University Press, Cambridge. 1997. Price £28.95. ISBN 0-521-58935-5.

It is five years since Arthur Chater reviewed the first edition of this book in *Watsonia* 19: 161–163. As predicted it has become the standard Flora for taxonomy, nomenclature and identification within the British Isles. The limited and idiosyncratic typeface and skeletal index of the first edition have now been thoroughly remedied. The index now occupies 131 pages and the new typeface is clear, more varied and less wasteful of space. As a consequence, on roughly the same number of very slightly enlarged pages, a more generous margin is provided at the foot of each page and an additional 320 taxa are included.

The book is bound in similar flexible plastic covers to the first edition. Despite its weight, just exceeding 1.5 kg, the bindings appear to be adequately robust. I have received but one report of the binding of the first edition failing. Although the plastic cover is clearly designed to improve its durability in the field, the weight and bulk of the book are a severe drawback to it becoming a regular companion. As an aid to its use in the field, a centimetre and millimetre scale is provided on the inside front cover. In this edition its length has been usefully extended but it has been placed so close to the edge that the millimetre scale is barely visible on my copy.

Taxonomic and nomenclatural changes between editions have been mercifully few. I am particularly pleased that the name *Asplenium viride* has been restored to us, together with *Drosera anglica* and *Fragaria moschata*. On the other hand *Helianthemum canum* becomes *H. oelandicum*, to join a select band of half a dozen taxa or so now sporting new names. *Huperzia selago* has been split into two subspecies, whilst *Arctium* has been completely revised, following H. Duistermaat, to now recognise three species only. This latter genus is still described as "difficult", which on first use of the key and new descriptions cannot be disputed. Other minor changes have been made to the

treatment of subspecies, e.g. within *Luzula multiflora*. Elsewhere many of the larger keys have been subject to minor changes to improve their performance and take in additional taxa. *Cotoneaster*, for example, has been extended from 45 to 68 species.

The treatment of hybrids is still very uneven. Few generic keys (the most notable exception being *Potamogeton*) include hybrids. Some are described in detail whilst only the British distribution of others is mentioned. The generally sparing treatment of intraspecific taxa may also still not suit all tastes. No attempt has been made to extend the ecological notes which are still far more brief than those of Clapham, Tutin & Moore (1987) in their *Flora of the British Isles*. Nor is any information provided on world distribution except for introduced taxa. Chromosome numbers have, however, been added to the second edition and distribution information mostly brought up to date. Technical terms have, according to the preface, been further reduced. This is to be welcomed and should be carried further in future editions, perhaps also considering an expansion of the glossary. In this, as in the first edition, no doubt to save space, users of the glossary are referred back to the generic texts for an explanation of some terms. This is not helpful when the latter description has forced reference to the glossary in the first place.

Improvements have been made to the illustrations. The small unsatisfactory silhouettes of *Euphrasia* have been replaced with excellent line drawings. Examples of species from the major sections of *Hieracium*, *Taraxacum* and *Rubus* are now included as line drawings for the first time, as are illustrations of *Polypodium* sporangia. Unfortunately no changes have been made to the illustrations of *Odontites*, *Veronica hederifolia* and *Ranunculus omiophyllus* criticised by Chater in his review of the first edition. In compensation other numerous small improvements include the addition of numbers to the family and generic names on the page headers, making recourse to the now formidable index largely unnecessary when moving from one key to another.

Taken together, the typeface change and large number of other small changes and improvements render this new edition so much more pleasant to use that, even if you already have a first edition, I strongly recommend that it is worth purchasing the second edition. It is still excellent value for money and whilst the native flora may not be covered in such depth as in other Floras, this is more than made up for by the large number of non-native taxa not covered elsewhere so conveniently. As undoubtedly the standard Flora for the British Isles for years to come, it is to be hoped the publishers will consider the investment worthwhile to ensure that the quality of the illustrations in future editions matches the quality of the text.

R. G. Woods

A dictionary of plant-lore. R. Vickery. Pp. 437. Oxford University Press, Oxford. 1995. Price £14.99. ISBN 0-19-866183-5.

Anyone accustomed to the orderly, cut-and-dried world of field botany is likely to experience a series of shocks on any extended acquaintance with the literature of the study of folklore. For a start, there is no consensus on where that subject begins and ends. Many folklore collectors, for example, ignore medicinal uses of herbs, apparently regarding these as too mundanely practical to count for their purposes and perhaps better left to their kinsmen, the students of folk life. Then there is the lack of large-scale compendia, on the lines of *Topographical botany* or the *Biological Flora of the British Isles*, which would enable one to tell what is known already. In the absence of such works much energy is wasted in recording the same things over and over again. Only rarely, moreover, is information quantitative or spatial, making it impossible to tell how many people in any one locality or area follow the belief or practice in question or how widely it is to be met with in terms of geography. Newcomers will further find to their horror that few books on folklore are indexed, so there is usually no alternative but to search through them page by page.

For having the persistence to operate on such a dauntingly unsatisfactory front the author of a volume like the one under review deserves both sympathy and admiration. To a large extent, though, Vickery has sidestepped the worst of the problems by restricting his concerns in this particular case mainly to items recorded in the period 1981–94, just to the British Isles and just to plants (wild and cultivated alike). Essentially the book is the fruit of information provided, unsystematically, by some 700 informants. There is no means of knowing how far the reports

received were representative of the present-day pattern of behaviour overall, and all that could be done was to select some of the reports for quoting, simply as illustrations of the variety of beliefs and practices attached today to a great range of plants even in such a comparatively sophisticated set of cultures as those to be found in these islands. Many of the quotations are quite lengthy and make colourful reading. Within these limitations the coverage is comprehensive, and the average reader should find his or her curiosity satisfied on just about every matter likely to raise a query. The fact that the author is an experienced botanist in addition to being one of Britain's leading folklorists gives this work a special authority, and the punctilious way in which the source is cited for every particularised piece of information is assurance enough of the scholarly standard that obtains throughout.

Handy in size, attractively produced and very reasonably priced, this is a work which many readers of this journal will want to have not only on their shelves for reference, but also on their bedside tables for occasional dipping into – worthy successor as it is to those long-prized Victorian standbys, Mrs Lankester and the evergreen Anne Pratt.

D. E. ALLEN

Obituaries

DOREEN SYLVIA LAMBERT M.B.E. (1915–1996)

Doreen Lambert died unexpectedly in July 1996. She had been for many years the B.S.B.I. Recorder for both Co. Londonderry (v.c. H40) and Co. Tyrone (v.c. H36), a job which she pursued with characteristic vigour and attention to detail. Originating from Co. Galway, from an old Anglo-Irish family of the sort which at times seems more English than the English, despite generations spent in Ireland, Doreen claimed her family was connected with Colonel Lambert, one of Oliver Cromwell's notable lieutenants who settled in Ireland during the Commonwealth. The Lambert clan became well established in the Oughterard district of Galway, but Doreen and her parents moved to Garvagh in Co. Londonderry in the 1930s, where Doreen used to "shoot the hills" with her father. During World War II she characteristically volunteered for service in the British Forces, becoming an officer in the Royal Air Force, attached to the newly developing Radar arm. During part of the war she was stationed at a Radar station atop the Great Orme at Llandudno, an excellent posting for a field botanist as she fondly remembered! She was awarded the M.B.E. for her wartime services. Later she pursued a successful career as a civil servant in Northern Ireland, latterly working in the Ancient Monuments section of the Department of the Environment, Northern Ireland.

After retirement in the 1970s she and her mother (an astonishing lady in her own right who died at the age of 102 with a mind as clear as a bell to the end; like many of the Irish she had a great fondness for horses) moved to the small seaside resort of Castlerock on the windy north coast of Co. Londonderry (Doreen always, incidentally, referred to it as "Derry"), to a large bungalow with magnificent views of the Atlantic Ocean from the picture windows. There she settled down in earnest to pursue her hobby of field botany which had begun before the War; she had gone out botanising in the 1930s with Robert Lloyd Praeger, and had become very friendly with the late Miss Pat ("Paddy") Kertland of Queen's University, Belfast, who was the leading light in field botany in Northern Ireland in the 1950s and 1960s, and with Maura Scannell, of the Botany Dept at the National Museum in Dublin, later of Glasnevin. I first met her in the very early 1970s at Miss Kertland's home, and from about 1973 we developed a mutual passion for dandelions inspired by John Richards' *Taraxacum Flora* published in 1972. Many of the first Irish county records of various *Taraxacum* species are Doreen's. She collected assiduously, not only in the northern counties, but also in her native west of Ireland, where she was able to show that *Taraxacum palustre* and its allies were nowhere near so rare as had been hitherto thought. 1972 was also the year that Miss Kertland produced a *Supplement* to Praeger's 1938 edition of the *Flora of the north-east of Ireland*, helped considerably, as the title page states, by Doreen.

From about 1976, by which time Doreen had settled down at Castlerock and had become the Recorder for Cos Londonderry (H40) and Tyrone (H36), we worked together on producing a revision of the *Flora of the north-east of Ireland*. Doreen, with her collaborators in Co. Londonderry, notably Ian and David McNeill, John Harron, David Riley and Mrs Jo Newbould, provided me with a steady, and at times almost overwhelming, stream of records, sightings and queries. At the same time she was vigorously opposing the spoilation of the countryside of her adopted county, especially of its beautiful coast. A keen golfer, she used to botanise on the links at the same time as golfing, but she vociferously opposed the damage done to the north coast dunes by extensions of local golf courses at Castlerock and Portstewart and was instrumental in averting the worst consequences that might have followed without intervention. Her golfing activities included membership of the Castlerock Golf Club, on which course she had seen what she considered to be *Campanula gieseckiana*. Determined to show this to me one day, she took me on to the course and walked past and through small armies of irate golfers who kept shouting warnings at us. I expected any moment to be struck down by a golf ball, but Doreen placidly ignored the shouts, said "I'm a member!" and leisurely proceeded on her way.

She was a careful and meticulous observer and was quite an accomplished botanical artist – she recorded many of her more notable finds as watercolours in a series of loose-leaf albums. It includes carefully observed drawings of most of the *Taraxacum* microspecies that she had found and collected; together with her herbarium material the collection of drawings is housed in the Ulster Museum, Belfast. Doreen's contribution to our botanical knowledge of the north of Ireland is considerable, as any glance through our 3rd edition of the *Flora of the north-east of Ireland*, which appeared in 1992, will show; her name appears with the other principal collaborators on the title page. (Whilst engaged on the *Flora of the north-east*, she was simultaneously preparing a typescript draft Flora of Tyrone.)

It was my privilege to know Doreen as a friend for nearly 25 years, and I was saddened by her unexpected death, but whenever I visit the north coast dunes I will half close my eyes and remember her stocky, jovial figure, the upper class accent, and long talks about hybrids and subspecies over gin-and-tonic with the majestic waters of the Atlantic in the background.

P. HACKNEY

EDGAR W. B. H. MILNE-REDHEAD M.B.E, I.S.O., T.D.
(1906—1996)

Edgar Wolston Bertram Handsley Milne-Redhead, who died on 29 June 1996 in his 91st year, was a professional systematic botanist but better simply described as an all-round naturalist; field work had more appeal for him than writing monographs in the herbarium. He will be best remembered as an ardent and successful conservationist, a collector of superb specimens, for his editorial work but perhaps above all for firing the enthusiasm of many amateur botanists, particularly in Africa, to



emulate his own magnificent results. He had at first sight an austere military air caught to perfection by his Belgian colleague Prof. J. Léonard (a co-founder of Association pour l'Étude Taxonomique de la Flore d'Afrique Tropicale) – to translate his comments would spoil them – “comme c'était ma première visite à Kew il eut la délicate attention de venir me chercher à la gare de Victoria à Londres. Je vis un homme sérieux très droit que me fit immédiatement penser à un officier anglais de l'armée britannique des Indes. Mais sous cet aspect un peu sévère je découvris rapidement un caractère particulièrement aimable.”

Edgar was born near Frome in Somerset on 24 May 1906. His father George Bertram Milne-Redhead was a keen gardener and his grandfather Richard, a great traveller, seed collector and Fellow of the Linnean Society, had established a fine garden at Holden Clough near Clitheroe. His mother Agnes was interested in classical music and croquet and after the death of Edgar's elder sister Rosamund at only 16 developed a strongly protective manner towards him. Edgar's early schooling was at The Old Ryde preparatory school in Bournemouth. In 1920 the family moved to Cheltenham enabling him to attend the college as a day boy and to enjoy the fine countryside. He went up to Gonville and Caius College, Cambridge in 1925 and read Natural Sciences, taking a particular interest in botany after meeting the legendary Humphrey Gilbert-Carter and gaining a half-blue for rifle shooting. Examinations, however, were not his forte and rather than take Part II of the Tripos he applied for a post at Kew. No posts being available he accepted an unpaid position for several months. A terse announcement in the *Bulletin of miscellaneous information*, Kew records that in 1929 C. E. Hubbard and E. Milne-Redhead had been appointed Temporary Subassistants in the Herbarium – there were no flattering titles for the lower ranks in those days! For a year he worked successively on plants of Europe, Canada, Fiji and elsewhere; then a remarkable opportunity occurred in March 1930. The then Director of Kew, Sir Arthur Hill, was asked by the Colonial Office to suggest a botanist to assist with an aerial survey of what is now Zambia and offered to second Edgar to the scheme. The offer was eagerly accepted and he spent four and half months in Mwinilunga District when he prepared some of the most elegant herbarium specimens ever to have come out of Africa. His unpublished report on the interpretation of vegetation by aerial surveys is in the library at Kew.

In 1933 he married Olive, the sister of a senior colleague Kenneth Airy Shaw. She became an excellent botanical artist and her drawings of African plants grace the work of many botanists (including one of my earliest papers). Their golden wedding was celebrated with friends at Great Horkesley. She survived him until September 1997.

For some years the Empire Marketing Board had funded several posts at Kew including Edgar's but in 1935 the Board came to an end and Edgar and others joined the official Kew staff. In 1936 he succeeded John Hutchinson as head of the tropical African Section, a position he held until 1959. Leading a University Travel Club expedition to the Austrian Tyrol he gained some insight into the European mountain flora. A return to Mwinilunga was possible in 1937, thanks mostly to the hospitality of his friends Capt. and Mrs K. R. Patterson but after four and half months his request to stay longer in order to encompass the second half of the rainy season was refused for no obvious reason. Edgar was embittered by this ill-considered decision typical of the attitude of half-witted administrators to scientists everywhere. The second collection was even better than the first and it is a great pity it was not written up as a whole. Nevertheless many of the more striking new species Edgar were described in a series of contributions to *Hooker's Icones Plantarum* and in a series entitled African Plants in the *Bulletin of miscellaneous information*, Kew. The collection was kept in the basement and often missed by visiting researchers, in fact frequently hidden from them; only people judged to be good workers were given access. In my opinion it would have been preferable if the whole collection had been named up even if only to genus and the duplicates distributed. In the end decades were to pass before it was all dealt with and accessible to everyone. This collection has been one of the main sources of information for Mwinilunga District for *Flora Zambesiaca*. Before the war Edgar gave up quite a lot of time (unlike most of his colleagues) encouraging the student gardeners by giving talks and taking them out on botanical excursions.

Work at Kew was of course totally disrupted by the war. Edgar who had been commissioned as a Second Lieutenant in the Territorial Army in 1929 and served for ten years with the 30th (Surrey) Searchlight Battalion, Royal Engineers was called up when the Air Defence services were mobilised in August 1939. He became a gunner in 1940 when the searchlight units were transferred to the Royal Artillery and in November were drafted to West Africa and attached to the Royal West

African Frontier Force. Edgar rose from the rank of Captain to Temporary Major and managed to collect a few plants and make some observations in Nigeria, Sierra Leone and the Gold Coast (now Ghana). On his return to England in early 1942 he became a Sector Searchlight Control Officer working with R.A.F. Fighter Command stationed at the R.A.F. Radar Station at East Hill near Houghton Regis on night interception of German bombers. Daylight hours were spent exploring on a bicycle around Dunstable and the nearby chalk hill flora. He also collected Hemiptera-Heteroptera, at that time very poorly known in Bedfordshire, and the results were written up by Airy Shaw. He soon made friends with local naturalists, particularly John Dony and Vic Chambers and also with two youngsters, myself and Peter Taylor who both owe him a great deal. Peter was later to leave his engineering job to join him at Kew and Edgar was instrumental in obtaining a job for me with Peter Greenway in what was then Tanganyika. At the request of James Fisher, Edgar undertook the rook census for South Bedfordshire in 1944. Luton Hoo was rich in rookeries but was the local testing ground for tanks by Commer Cars in Luton. It was definitely off limits to everyone. Edgar decided that if he wrote to the War Office for permission, by the time it had arrived the rooks would have left so he put on his uniform and walked smartly in, receiving a salute from the sentry who did not ask him his business. Once in he was free to wander all over the area counting nests, with tanks charging about the drives and tracks. He completed the task in about two hours and walked out past the sentry with no questions asked. It resulted in a very big count, more nests per hectare than anywhere else in his allotted area.

When he returned to Kew after the war he soon gained the rank of Principal Scientific Officer and set out to build up the African section. He encouraged many local amateur collectors (mostly but not all colonial government officers) in Tropical Africa to send in material and most responded to his request to collect only high quality material with meticulous notes. His great success is immediately apparent to anyone working at Kew who has to compare African plants with those from other areas. His standard slowly spread to all collectors on expeditions from Kew. Nothing annoyed him more than a poor specimen with scrappy notes.

The *Flora of West Tropical Africa* had long been completed and in fact work on a new edition was shortly to begin. A Flora for the other side of the continent was mooted some years before the war and Edgar was instrumental in 1949 in initiating the Colonial Office programme for such a project with provisions built in for a number of major expeditions. This vast undertaking was supposed to be finished in 20 years but is still far from completion. Edgar was the main editor until his retirement. His first co-editor was the Keeper of the Herbarium, W. B. Turrill, who thought a species could be written up in 20 minutes whereas a week is nearer the mark. Hubbard followed Turrill and in 1965 Roger Polhill, who continued alone after Edgar's retirement.

It is equally true of both professional and amateur botanists that they are associations of friends and the founding of A.E.T.F.A.T. in 1949 by Edgar, together with Arthur Exell of the British Museum and Jean Léonard of Brussels, was from the first an informal organisation of friends which has been of immense importance to students of African botany. It still flourishes and membership has grown over twenty fold but the informality of the small band of original friends still to some extent prevails.

In 1956 Edgar and Peter Taylor undertook an eight month collecting expedition to East Africa spending most of their time in Songea District in southernmost Tanzania, an area where only a very few small collections had been made. Their collaboration resulted in 5000 quite perfectly prepared gatherings of plants, mostly with many duplicates, which added immensely to the knowledge of East African plants.

In 1959 Edgar became Deputy Keeper of the Herbarium and editor of the *Kew bulletin* (the channel for publication of most scientific work at Kew), posts he retained until his retirement in 1971. He was very disappointed not to get the post of Keeper (for which he was ideally suited) – it went instead to C. E. Hubbard who had come into scientific work from the gardens and was academically unqualified. One must not forget of course that Hubbard had become one of the world's foremost grass experts and was much better known worldwide than Edgar and to reward him with such a post was only just, but Hubbard was a poor administrator. Edgar worked well at his new posts and despite his authoritarian manner was intensely loyal to his staff.

Edgar had long been deeply involved in various aspects of conservation, being an Associate of the Royal Society for Nature Conservation from 1948 and on the Standing Committee of "The Countryside in 1970" the third of a series of conferences, supported by the Duke of Edinburgh and

the then Prime Minister Edward Heath, to assess land use and environmental responsibilities. One of his last successes at Kew was to persuade the new Director, Prof. Heslop-Harrison, to set up a conservation unit at Kew. This was achieved in 1972 in time for Kew to participate in the first meeting of the Convention for International Trade in Endangered Species (CITES) (in Washington 1973). Kew has been concerned with conservation ever since.

The retirement dinner for Edgar was a very well attended affair with hand-painted menus by Pat Halliday. I think he was pleased to be going and looking forward to having time for other interests, which was fortunately vouchsafed him.

He had of course always been deeply interested in British botany and participated fully in the mapping schemes which resulted in the *Atlas of the British flora* in 1962. He joined the B.S.B.I. in 1929 and was on the Council as early as 1939 and at various other times, 1946–1950, 1951–1955 and again in 1957. He served on the Development Committee (later Development and Rules) from 1947–1967 being secretary in 1950, also on the Field Work Committee (from 1947), Maps Committee (1952–1965), Records Committee (1966–1967) and Conservation Committee (1952–1985), serving as its Chairman for over 10 years. This committee was very involved with the "Conservation of wild creatures and wild plants" Bill completed in 1975. Edgar represented the B.S.B.I. on the Council for Nature (1960–1969) of which he was a founder member and on the Wild Plant Protection Working Party in 1965 formed to promote legislation for wild plants in Britain. The publication and wide distribution to the public of the Code of Conduct for the Conservation of Wild Plants and the "Save our endangered wild flowers" poster were mainly due to him. He became President in 1970–1971 and was eventually awarded with honorary membership; at the end he was the Society's oldest living member.

In 1964–1967 he was a leading campaigner on the Teesdale Appeal Committee to save the wonderful relict flora of Cow Green from being destroyed by a reservoir, and representing B.S.B.I. he founded the *Cypripedium* Committee in 1970 to look after the single remaining specimen of the Lady's slipper orchid. Edgar used to tell how he persuaded the rather suspicious local naturalists to a first meeting held in a Grassington pub after a good lunch. The policy agreed differed from that of the locals who had previously believed in total secrecy, but now with co-operation and wider resources available the single remaining plant was saved, the seed collected and after many years seedlings successfully raised and now planted out at the original and new sites. Edgar also helped organise the annual scrub clearance on the Goring Scarp to preserve other scheduled orchids. He also encouraged one of the first County Wildlife Roadside Verge Schemes. He was also instrumental in setting up the smallest nature reserve in the world to conserve *Ranunculus ophioglossifolius* in Gloucestershire at Badgworth, designated an S.S.S.I. in 1949. It was leased by the Society for the Promotion of Nature Reserves to the Gloucestershire Trust for Nature Conservation in 1962 when Edgar was Chairman of the Management Committee of that Trust (of which he was a founder member). Its success was due to him noticing that the species responded well to trampling and recommending that cattle should be allowed to disturb the ground.

His well known survey of the native black poplar occupied him for many years and was his chief interest – in fact he was identifying specimens until a few weeks before his death. His fondness for this tree he attributed to Gilbert-Carter (reports that Edgar searched for it as a schoolboy are incorrect but he and his father certainly made special records of it for the *Flora of Gloucestershire*). He published many reports on the progress of the survey which grew to national dimensions when it was taken up by *The Daily Telegraph*.

His involvement with societies on various aspects of conservation was endless – he seemed to collect societies like some collect stamps (in fact he did that also). They include the Bedfordshire Natural History Society, B.B.O.N.T., Cotteswold Naturalists' Field Club (Vice-President), Essex Naturalists' Trust, Gloucestershire Naturalists' Trust, The Kew Guild (President 1968–1969), Kew Lawn Tennis Club 1930–1970 (of which he was secretary for many years) (Olive was ladies' champion on many occasions), Linnean Society (Vice-President 1953–54), London Natural History Society (Chairman of Nature Conservation Committee), his own local Nayland with Wissington Conservation Society (President), Norfolk Naturalists' Trust, North Gloucestershire Naturalists' Society (President), Ray Society (President, 1968–1971), Richmond Society, Société Royale de Botanique de Belgique (Honorary Member), Somerset Naturalists' Trust, Suffolk Naturalists' Trust (Hon. Vice-President), Surrey Naturalists' Trust (Regional Representative for Western Boroughs of Greater London, Regional Secretary for Richmond, Representative on the County

Naturalists' Trust Committee of the Society for the Promotion of Nature Reserves, later the Royal Society for Nature Conservation and now the Wildlife Trust).

Edgar certainly had his faults (who of any value does not), a short temper being one of them but it soon passed and he bore no grudge to its recipient, and to counter it his sense of humour was pronounced. He could be a most annoying editor both to authors and printers, suddenly deciding to alter something in page proof and not doing it properly so that a paper initially consistent in some recurring feature had some items half one way and half another; adding a last minute triviality could result in a real error and I and many authors were livid at the gratuitous mistakes in our work due to last minute fiddling, but he did bring new standards into the editing of the *Kew bulletin*. Little foibles could irritate – his habit of using the unit decimetre which was confusing to most people and his insistence that orbicular meant round and disk-like whereas I (and the Queen) used it for something spherical. He could be impractical; Peter Taylor was saddled with all the chores during their African trip and Edgar who was a poor linguist learnt no Swahili and was unable to communicate with their local staff.

He did not write a great deal himself and was I believe temperamentally incapable of spending the immense time needed to revise a large group or write a long floristic account when no matter how long one spends errors and omissions are inevitable. Edgar was scathing about large works produced quickly by J. Hutchinson, W. Robyns and others, rather forgetting that one just had to have these practical works. He liked to attack more circumscribed problems thoroughly and excelled at producing published accounts of small groups – that on Montiniaceae for example is a typical gem. This sort of work gave full scope for his meticulous nature. This did not prevent him being interested in large groups. His long term work on *Crotalaria* and the *Acanthaceae* involved putting the herbarium material in order, sorting out the new species which needed describing but not actually doing much of the writing. Roger Polhill who joined Edgar at Kew in 1962 (following a collecting expedition arranged by Edgar in 1961 and after working with me in Nairobi for about a year) brought the revision of African *Crotalaria* (some 500 species) to fruition but would be the first to acknowledge Edgar's considerable spade work.

MR (as we all knew him) was awarded the Imperial Service Order in the 1967 New Year's Honours List in recognition of his distinguished service at Kew and an M.B.E. in 1996 for his conservation work (it should have been more). Although he did not reach what a career pusher would consider any position of importance and is not mentioned in the recent history of Kew his work on Tropical African botany assures him of an honoured place in its history and 25 species have epithets commemorating him (list below). His beautifully prepared material will be valued by workers for as long as they last. His handwriting, exceedingly elegant and completely unmistakable will join those which when found on a label pronounce the determination as reliable. We at Kew are constantly and pleasantly reminded of our old friends since we use their determinations daily. His last months were spent at Nayland near his daughter Annette and her husband Basil Harley (well known for their natural history publishing) and later living with them at Martins, Gt Horkestone. Annette's interest in entomology had been aroused by her uncle Kenneth Airy Shaw who was at Daglingworth (where much of Kew's material was sent during the war) when she and her mother were at Cirencester during Edgar's wartime absence. Edgar's funeral at All Saints Church, Gt Horkestone was a joyous beautifully conducted celebration of a full life devoted to natural history. The church was decorated and his coffin strewn with branches from the Black Poplar he had planted at Martins.

LIST OF PUBLICATIONS OF E. MILNE-REDHEAD

- Campanula orphanidea* Boiss. *Bulletin of miscellaneous information*, Kew 1929: 142 (1929) (with W. B. Turrill)
 Variation in *Anemone nemorosa*. *Journal of botany* 70: 325–328 (1932) (with W. B. Turrill)
Begonia plagiomeura [sp. nov.]. *Bulletin of miscellaneous information*, Kew 1930: 269–271 (1930)
Aporrhiza nitida Gilg in Tropical African plants: VII. *Bulletin of miscellaneous information*, Kew 1931: 272–273 (1931)
 The genus *Strobilanthesopsis*. *Bulletin of miscellaneous information*, Kew 1932: 344–347 (1932)
Campanulata spathulata S. et S. var. *Giuseppii* Milne-Redhead et Turrill [in Turrill, W. B. On the flora of the nearer east: XIII]. *Bulletin of miscellaneous information*, Kew 1932: 453 (1932)
 Tropical African plants: X. *Bulletin of miscellaneous information*, Kew 1933: 142–151 (1933). Contributions by

- E.M.R. *Oxygonum fruticosum*: 142; *Acacia (Vulgares-Ataxacantheae) chariessa*: 143–144; *Albizia (Eualbizia-Microphyllae) struthiophylla*: 144
- Tropical African plants: XI. *Bulletin of miscellaneous information, Kew* 1933: 467–479 (1933). Contributions by E.M.R. *Crotalaria (Simplicifoliae) vialis*: 469; *Disperma crenatum*: 477; *Aloë (Eualoë) ortholopha*: 478–479, pl. 18 (with H. B. Christian)
- Hooker's Icones Plantarum* 33:
- t. 3213 *Vigna nuda* N.E.Br.
 - t. 3214 *Physostigma mesopotamicum* Taub.
 - t. 3215 *Oxygonum pachybasis* Milne-Redhead
 - t. 3216 *Oxygonum tenerum* Milne-Redhead (1933)
- Hooker's Icones Plantarum* 33:
- t. 3243 *Crotalaria annua* Milne-Redhead
 - t. 3244 *Crotalaria praecox* Milne-Redhead
 - t. 3245 *Crotalaria streptorrhyncha* Milne-Redhead
 - t. 3246 *Bolusia resupinata* Milne-Redhead (1934)
- A buttercup. *Gloucestershire countryside* 1 (12): 187–188 (1934)
- The type of *Ornocarpum kirkii*. *Bulletin of miscellaneous information, Kew* 1934: 42–43 (1934) (with T. A. Sprague)
- Notes on the flora of Southern Africa V. The genus *Ruellia* in Thunberg's Herbarium. *Bulletin of miscellaneous information, Kew* 1934: 264–265 (with R. A. Dyer)
- Tropical African plants: XII. *Bulletin of miscellaneous information, Kew* 1934: 301–307 (1934). Contributions by E.M.R. *Albizia sericocephala*: 301; *Vigna juncea major*: 301–302; *Disperma nudanthera*: 304; *Dyschoriste procumbens*: 304; *Monechma ciliatum*: 304–305; *Lapeyrouseia schimperi*: 307
- New Combinations under *Copaifera*. *Bulletin of miscellaneous information, Kew* 1934: 400 (1934)
- Curtis's botanical magazine* 157:
- 9345 *Hypericum kouytchense* Léveillé
 - 9349 *Campanula propinqua* var. *grandiflora* Milne-Redhead
 - 9361 *Verbena corymbosa* Ruiz & Pavon
 - 9373 *Viburnum alnifolium* Marshall (1934)
- Hooker's Icones Plantarum* 33:
- t. 3266 *Blepharis hornbyae* Milne-Redhead
 - t. 3267 *Anisotes umbrosus* Milne-Redhead
 - t. 3268 *Anisotes bracteatus* Milne-Redhead
 - t. 3291 *Barleria tetraglochin* Milne-Redhead
 - t. 3292 *Barleria proxima* Lindau
 - t. 3293 *Barleria quadrispina* Lindau (1935)
- Tropical African plants: XIII. *Bulletin of miscellaneous information, Kew* 1935: 271–285 (1935). Contributions by E.M.R. *Triplochiton zambesiacus*: 271–272; *Hibiscus mastersianus*: 272–273; *Crotalaria (Eucrotalaria) lotiformis*: 274–276; *Clausenopsis hildebrandtii*: 278–279; *Crossandra thomensis*: 280–281; *Disperma eremophilum*: 282–283; *Rhinacanthus pulcher*: 283–284
- Curtis's botanical magazine* 158:
- 9385 *Choananthus cyrtanthiflorus* (C.H. Wright) Rendle
 - 9412 *Rhodohypoxis baurii* (Bak.) Nel (1935)
- Curtis's botanical magazine* 159:
- 9436 *Campanula formanekiana* Degan & Dörfler
 - 9444 *Adenophora morrisonensis* Hayata
- Eranthemum* of the "Flora of tropical Africa". *Bulletin of miscellaneous information, Kew* 1936: 255–274 (1936)
- Tropical African plants: XIV. *Bulletin of miscellaneous information, Kew* 1936: 469–489 (1936). Contributions by E.M.R. *Indigofera annua*: 470; *Indigofera shiyangensis*: 471; *Vigna macrorrhyncha*: 473; *Salix subserrata*: 474; *Fagaropsis hildebrandtii*: 475; *Turraea fischeri*: 475; *Anisotes dumosus*: 487; *Justicia salviooides*: 488; *Kniphofia (Laxiflorae) rogersii*: 488; *Anthericum suffruticosum*: 489
- Curtis's botanical magazine* 159:
- 9452 *Sutera grandiflora* (Galpin) Hiern (1936)
- Curtis's botanical magazine* 160:
- 9470 *Chasmanthe caffra* (Bak.) N.E.Br.
 - 9487 *Homeria collina* (Thunb.) Salisb. (1937)
- Tropical African plants: XVII. *Bulletin of miscellaneous information, Kew* 1937: 411–432 (1937). Contributions by E.M.R. *Euphorbia eranthes* (with R. A. Dyer): 413; *Phyllanthus holostylus*: 414; *Dialium orientale*: 415; *Isoberlinia densiflora* & *magnistipulata*: 415; *Acacia eggelingii*, *hebeclada* & *nigrescens*: 416–417; *Desmodium setigerum*: 417; *Mundulea sericea*: 417; *Pleiotaxis arenaria*: 424; *Dicliptera arenaria*: 427; *Dicliptera capitata*: 428; *Dicliptera nemorum*: 429; *Justicia (Rostellularia) syncollotheca*: 429; *Monechma praecox*: 430; *Phaylopsis hispida*: 431

- The genus *Cordyla* Loureiro. *Repertorium Specierum Regni vegetabilis* 41: 227–235 (1937)
- Curtis's botanical magazine* 159: 9510 *Homoglossum merianella* (Thunb.) Bak. (1938)
- Choice between epithets of the same date. *Bulletin of miscellaneous information, Kew* 1939: 34–35 (1939)
- The correct name for *Sesbania aculeata*. *Bulletin of miscellaneous information, Kew* 1939: 159 (1939) (with T. A. Sprague)
- A new conception of the genus *Ammocharis* Herb. *Journal of the Linnean Society (botany)* 52 (342): 159–197 pl. 2, 3, 4 (1939) (with H. G. Schweickerdt)
- Hooker's Icones Plantarum* 34:
- t. 3388 *Eriocaulon strictum* Milne-Redhead
 - t. 3389 *Eriocaulon annuum* Milne-Redhead
 - t. 3390 *Gerardina eylesiana* Milne-Redhead (1939)
- Curtis's botanical magazine* 161:
- 9556 *Campanula incurva* Auch. ex DC. (1939)
- Curtis's botanical magazine* 162:
- 9568 *Campanula affinis* Roem. & Schultes (1939)
- Tropical African plants: XVIII. *Bulletin of miscellaneous information, Kew* 1940: 49–66 (1940). Contributions by E.M.R. *Crotalaria diloloensis*: 52; *Crotalaria elisabethae*: 52; *Hypoestes rosea*: 64; *Barleria (Somalia) phaylopsis*: 65
- Hooker's Icones Plantarum* 35: t. 3417 *Buchnera prorepens* Engl. & Gilg (1940)
- Curtis's botanical magazine* 164: 9676 *Erica pillansii* Bolus (1946)
- Hooker's Icones Plantarum* 35:
- t. 3459 *Fadogia spectabilis* Milne-Redhead
 - t. 3460 *Piliostigma thonningii* (Hochst.) Milne-Redhead (1947)
- Tropical African plants: XIX. *Kew bulletin* 2: 23–35 (1947). Contributions by E.M.R. *Gomphrena celosioides*: 23; *Impatiens niamniamensis*: 23; *Syzygium huillense*: 24; *Baphia pyrifolia*: 26; *Crotalaria unicaulis*: 26; *Vigna paludosa*: 27; *Morinda morindoides*: 31; *Pavetta coriacea*: 31; *Pentas zanzibarica*: 31; *Aloe zanzibarica*: 33; *Anthericum dimorphum*: 33; *Crinum minimum*: 33; *Juncus dregeanus*: 35
- A probably [sic] natural hybrid in *Hymenocardia* Tul. *Kew bulletin* 2: 46 (1947)
- Cerastium brachypetalum* Pers: in Britain. *The naturalist* 1947 [822]: 95–96 (1947)
- Ferdinandia* Welw. ex Seem [Bignoniacae], an unintentional orthographic error. *Kew bulletin* 3: 170–171 (1948)
- Tropical African plants: XX. *Kew bulletin* 3: 449–473 (1949). Contributions by E.M.R. *Cladostemon kirkii*: 449–450; *Bergia capensis*: 450; *Polycarpon prostratum*: 451–452; *Robbairea delileana*: 452; *Philocerus vermicularis*: 452–453; *Geranium ocellatum* var. *sublaeve*: 453; *Geranium yemensc*: 453–454; *Hypericum oligandrum*: 454; *Hypericum stolzii*: 455–456; *Corchorus hochstetteri*: 456; *Oldfieldia somalensis*: 456; *Euphorbia geniculata*: 457–458; *Vigna juncea*: 458; *Nauclea latifolia*: 459; *Ceropegia yorubana*: 465; *Chrysanthellum americanum*: 466; *Solanum bifurcatum*: 467; *Dopatrium luteum*: 467; *Crocosmia pauciflora*: 469; *Urginea glaucescens*: 470–471; *Paepalanthus lamarckii*: 472
- The positions of Kew in relation to taxonomic and ecological researches in Africa. Communication No. B (h) 22 at African Regional Scientific Conference, Johannesburg 4 pp. (1949)
- Hooker's Icones Plantarum* 35:
- t. 3477 *Loranthus dependens* Engl.
 - t. 3478 *Petamenes vaginifer* Milne-Redhead
 - t. 3479 A et B *Ensete homblei* (Bequaert ex DeWild.) E. E. Cheesm.
 - t. 3480 *Euphorbia erythrocyclala* Bally et Milne-Redhead
 - t. 3481 *Euphorbia asclepiadea* Milne-Redhead (1950)
- Curtis's botanical magazine* 167:
- 111 *Crotalaria raffillii* Milne-Redhead (1950)
- Clef pratique des Marantacées Congolaises. *Bulletin de la Société royale de Botanique de Belgique* 83: 5–32 (1950) (with J. Léonard & W. Mullenders)
- Notes on African Marantaceae: 1. *Kew bulletin* 5: 157–163 (1950)
- Variation in leaf-shape within a species: some examples from the Gold Coast. *Kew bulletin* 5: 261 (1950)
- Tropical African plants: XXI. *Kew bulletin* 5: 335–384 (1951). Contributions by E.M.R. *Spergula fallax*: 338; *Robbairea delileana*: 340; *Geranium purpureum*: 341; *Hypericum scioanum* & *humbertii*: 343–344 (with J. B. Gillett); *Pterygota macrocarpa*: 348; *Adenocline acuta*: 349; *Crotalaria grandistipulata*: 349–351; *Neorautanea pseudopachyrhiza*: 355; *Eriosema burkei*, *cryptanthum*, *velutinum*, *molle* & *andohui*: 355–363; *Lasiodesmus zenkeri*: 366; *Emilia praetermissa*: 375–376; *Crassocephalum bauchiense*, *montuosum*, *baoulense* & *mannii*: 376–377; *Exochaenium pygmaeum*: 377–378; *Cyphia erecta*: 378–379; *Englerastrum gracillimum*: 380; *Monechma ciliatum*: 381; *Vellozia schnitzleinia* var. *occidentalis*: 381–382; *Amorphophallus abyssinicus*: 382–384
- Tropical African plants: XXII. Ranunculaceae. *Kew bulletin* 5: 389 (1951) (with W. B. Turrill)
- A new species of *Ranunculus* from East Africa. *Kew bulletin* 6: 147 (1951) (with W. B. Turrill)

- The identity of *Polygala phylicoides* Thunb. *Kew bulletin* 6: 148 (1951)
 Les espèces africaines du genre *Clematopsis* Boj. ex Hutch. *Bulletin de la Société royale de Botanique de Belgique* 83: 407–427 (1951) (with A. W. Exell & J. Léonard)
- Field Meeting to Taunton. *B.S.B.I. Year Book* 1951: 37–39 (1951)
 Field Meeting to Isle of Man. *B.S.B.I. Year Book* 1952: 32–34 (1952)
 Notes on African Marantaceae. *Kew bulletin* 7: 167–170 (1952)
Flora of Tropical East Africa. Ranunculaceae, pp. 23 (1952) (with W. B. Turrill)
Flora of Tropical East Africa. Marantaceae, pp. 11 (1952)
 The vegetation of the Solwezi and Mwinilunga Districts of Northern Rhodesia. Symposium 1 of A.E.T.F.A.T., *Flora and vegetation of Tropical Africa:* 125 (1953) (reprinted from *Lejeunia* 16)
Lepidagathis collina in Tropical African plants XXIII. *Kew bulletin* 8: 119 (1953)
 Tropical African plants XXIV. *Kew bulletin* 8: 431–445 (1953). Contributions by E.M.R. *Ranunculus oligocarpus:* 431; *Hypericum keniense* & *annulatum:* 434–437; *Vismia pauciflora:* 437; *Justicia praecox:* 444
Flora of Tropical East Africa. Hypericaceae, p. 23 (1953)
Zornia in tropical Africa. *Boletim da sociedade broteriana* 28: 79–104 (1954)
 Distributional ranges of flowering plants in tropical Africa. *Proceedings of the Linnean Society* 165: 25–35 (1954)
 Hooker's Icones Plantarum 36:
 t. 3541 A & B *Montinia caryophyllacea* Thunb.
 t. 3542 *Montinia caryophyllacea* Thunb.
 t. 3543 *Grevea eggelingii* Milne-Redhead
 t. 3544 *Grevea eggelingii* Milne-Redhead [pp. 1–16] Montiniaceae (1956)
 Flora of Tropical East Africa. *Memórias da Sociedade broteriana* 13: 57–59 (1958)
 Ranunculaceae in *Flora Zambesiaca* 1: 89–102 (1960) (with A. W. Exell)
 Miscellaneous notes on African species of *Crotalaria:* 1. *Kew bulletin* 15: 157–167 (1961)
 The typification of *Hedysarum diphyllym* L. *Kew bulletin* 17: 73–74 (1963) (with J. E. Dandy)
Dioscorea (Borderea) gilletii. Contribution to Tropical African plants XXVII. *Kew bulletin* 17: 177–179 (1963)
 B.S.B.I. Conference Reports No. 8. *The conservation of the British flora,* pp. 90, 1963 [editor]
 Birds in Richmond during the Winter of 1962–63. *The Surrey naturalist.* Annual Report. April 1965: 25–27 (1965)
Curtis's botanical magazine 175: 474 *Arisaema schimperianum* Schott (1965)
 Progress of the Flora of Tropical East Africa (Proceedings of 5th meeting of A.E.T.F.A.T.). *Webbia* 19: 891–892 (1965)
 The firearms act and Conservation. *The Surrey naturalist.* Annual Report for 1966: 41–42 (1967)
 Flora of Tropical East Africa (Proceedings of 6th meeting of A.E.T.F.A.T.). *Acta phytogeographica suecia* 54: 291 (1968)
 The London Nature Conservation Committee. *The Surrey naturalist.* Annual Report for 1969: 36–38 (1970)
 Progress of the Flora of Tropical East Africa (Proceedings of 7th meeting of A.E.T.F.A.T.) *Mitteilungen aus der botanischen Staatssammlung München* 10: 66–67 (1971)
 Leguminosae – *Zornia.* Contribution to Tropical African plants XXXI. *Kew bulletin* 25: 178–180 (1971)
 Presidential address 1970. Botanical conservation in Britain, past, present and future. *Watsonia* 8: 195–203 (1971)
 Notes on African *Dioscorea.* *Kew bulletin* 26: 573–576 (1972)
 Flora of Tropical East Africa. Leguminosae-Papilionoideae (1971). Contributed *Zornia*, pp. 442–450;
Gamwellia, Rothia & Lotononis, pp. 808–817; *Adenocarpus*, pp. 1009–1011
 Ranunculaceae in *Flora de Moçambique* 4, p. 16 (1973) (with A. W. Exell & M. L. Gonçalves)
Orchis militaris. *B.S.B.I. news* 3 (1): 11–12 (1974)
 Reserves for arable weeds. *B.S.B.I. news* 3 (2): 10 (1974)
 Obituary. Dr H. Milne-Redhead. *B.S.B.I. news* 3 (2): 15–16 (1974)
 Letter to Mr Beckett. *B.S.B.I. news* 3 (2): 21 (1974) (with F. H. Perring)
 Report. B.S.B.I. Black Poplar survey. *Watsonia* 10: 299 (1974)
 Obituary. Humphrey Milne-Redhead (1906–1974). *Watsonia* 10: 449–450 (1975)
 Flora of Tropical East Africa. Dioscoreaceae, p. 25 (1975)
Pholeus [sic] *phalangioides* at Walberswick [Pholcus]. *Suffolk natural history* 17: 67 (1975)
 Black Poplar survey. *Watsonia* 10: 295–296 (1975)
 Rex Graham Reserve. *B.S.B.I. news* 9: 9 (1975)
 Black Poplar survey. *B.S.B.I. news* 9: 10–12 (1975)
 A remarkable population of *Ophioglossum vulgatum* L. in Suffolk. *Watsonia* 10: 415–416 (1975) (with P. J. O. Trist)
 Another Suffolk record for *Balea perversa* (L.). *Suffolk natural history* 17: 66–67 (1975)
 Rex Graham Reserve. *B.S.B.I. news* 14: 8–9 (1976)
 Obituary. Victor Samuel Summerhayes (1887–1974). *Watsonia* 11: 90–92 (1976)
 Report. B.S.B.I. Black Poplar survey. *Watsonia* 11: 180–181 (1976)

- Populus nigra* Linn. – a rare Essex tree. *Essex naturalist* 33: 155–156 (1976)
 A cosmopolitan psocid in Suffolk. *Suffolk natural history* 17: 141 (1976)
 The Black Poplar survey – a progress report. *B.S.B.I. news* 15: 9 (1977)
 More about the Black Poplar survey. *B.S.B.I. news* 16: 13–14 (1977)
 An appreciation from an absentee member. *Bedfordshire Natural History Society newsletter* 26: 1 (1977)
Chelostoma campanularum Kirby, Hymenoptera. *Suffolk natural history* 17: 379–380 (1978)
 Obituary. Mary Alice Eleanor Richards (1885–1977). *Watsonia* 12: 187–190 (1978)
 Field Meeting Report. Tewkesbury, Glouc. May 8th. *Watsonia* 12: 66 (1978)
Lapsana intermedia. *B.S.B.I. news* 20: 24 (1978)
 John Dony at 80. *B.S.B.I. news* 22: 6 (1979)
 An under-recorded millipede from Suffolk. *Suffolk natural history* 18: 148 (1980)
 Orchids at Waltham Abbey – Essex. *B.S.B.I. news* 25: 22–23 (1980)
 Notes on some Suffolk sawflies. *Suffolk natural history* 18: 293–295 (1982)
 The Black Poplar survey. *B.S.B.I. news* 33: 6 (1983) [errata in 34: 38 (1983)]
 Autumn Lady's Tresses. *B.S.B.I. news* 36: 27 (1984)
 In pursuit of the poplar. *Natural world* 10: 26–28 (1984)
 Obituary. Maybud [May] Sherwood Campbell (1903–1982). *Watsonia* 15: 157–160 (1984) (correction: 419 (1985))
 The not so hardy British Oak. *B.S.B.I. news* 39: 19 (1985)
 Where my caravan has rested. *B.S.B.I. news* 40: 8 (1985)
 More hosts of *Orobanche*. *B.S.B.I. news* 41: 29 (1985)
 Field Meeting Report. Vale of Aylesbury, Buckinghamshire, 26th–27th May 1984. *Watsonia* 16: 113 (1986)
 Cotton tree in Lancashire. *B.S.B.I. news* 45: 32 (1987)
 Conservation of *Muscaria atlanticum* Boiss. & Reuter in Suffolk. *B.S.B.I. news* 47: 32–33 (1987)
 An uncommon orchid hybrid, *Dactylorhiza × transiens*. *Suffolk natural history* 24: 82–83 (1988)
 An unusual gall. *Suffolk natural history* 24: 100 (1988)
 Where are Suffolk's earwigs? *Suffolk natural history* 25: 44 (1989)
 The B.S.B.I. Black Poplar survey, 1973–88. *Watsonia* 18: 1–5 (1990)
 More about white flowers. *B.S.B.I. news* 58: 12–13 (1991)
 Cutting roadside verges. *B.S.B.I. news* 60: 31 (1992)
 Mega-Mustard (*Sinapis alba* L.). *B.S.B.I. news* 60: 65 (1992)
 Protected roadside verges. *White Admiral* 22: 13 (1992)
 B.S.B.I. Black Poplar survey, 1973–8. *White Admiral* 25: 35 (1993)
 Reminiscences of a naturalist nearly 50 years ago. *The Muntjac* 90: 1 (1993)
 Edgar reflects: His first African expedition in 1930. *White Admiral* 26: 8–9 (1993)
 Edgar Milne-Redhead – a correction. *White Admiral* 27: 39 (1994)
 Obituary. Sonia C. Holland (1912–1993). *Watsonia* 20: 171–173 (1994)
Viola pensylvanica – a mystery solved? *Transactions of the Suffolk Naturalists' Society* 28: 59 (1992)
 B.S.B.I. Black Poplar survey. *B.S.B.I. news* 67: 22–23 (1994)
 Black Poplar hunt. *White Admiral* 29: 27–28 (1994)
 Ticking them off. *White Admiral* 30: 38 (1995)
Tragopogon in Suffolk. *B.S.B.I. news* 70: 21 (1995)
 Recollections of the early years 1. *The Muntjac* 103: 3 (1996)
 He also made numerous contributions particularly of birds to various parts of "Additions to the wild fauna and flora of the Royal Botanic Gardens Kew" published in the *Kew bulletin*.

Eponymous epithets

Aloe milne-redheadii Christian, *Amphiasma redheadii* Brem., *Ascolepis erythrocephala* S. S. Hooper, *Cissus milnei* Verdc., *Clerodendrum milne-redheadii* Moldenke, *Crotalaria milneana* Wilczek, *Digitaria redheadii* (C. E. Hubbard) Clayton, *Helichrysum milne-redheadii* Brenan, *Hypericum milne-redheadii* Gilli, *Indigofera milne-redheadii* J. B. Gillett, *Ipomoea milnei* Verdc., *Lantana milne-redheadii* Moldenke, *Lobelia milneana* E. Wimmer, *Monotes redheadii* Duvign., *Nymphoides milnei* A. Raynal, *Pandika milnei* Suesseng & Overk., *Pavetta redheadii* Bremek., *Polystachya erythrocephala* Summerhayes, *Rotala milne-redheadii* A. Fernandes & Diniz, *Spermacoce milnei* Verdc., *Strychnos milne-redheadii* Duvign. & Staquet, *Stylochaeton milneanus* Mayo, *Triglochin milnei* H. Horn, *Vernonia milne-redheadii* H. Wild. There is also a *Euphorbia erythrocephala* Bally & Milne-Redhead which has red cyathia but was probably meant as a bit of a joke!

ACKNOWLEDGMENTS

I am grateful to the writers of several previous obituaries, to Mary Briggs for information on British connections, to Annette and Basil Harley for vetting the manuscript, to Rosemary Davies for the list of eponyms many of which I would otherwise have missed and to Suzy Dickerson for some of his publications. E.M.R. kept no list and I have doubtless missed a great many.

B. VERDCOURT

JOHN GRANT ROGER
(1909—1997)

Grant Roger was an Aberdonian whose youthful passion for botany led him first to the tropics as a tea planter on Sumatra. Disillusioned with colonial ways, he returned to Aberdeen University to study botany under Professor J. R. Matthews. After graduating with distinction, he joined the Regional Museum in Aberdeen, but in 1944 became Assistant Keeper in charge of Botany in the Manchester Museum. When the Nature Conservancy was set up in 1949, a career in wildlife conservation beckoned, and the next year he joined the Edinburgh headquarters staff, to participate in developing the Scottish programme.

Grant's botanical expertise led to field survey and assessment widely over Scotland, developing a valuable network of contacts and spreading the message as an ambassador for conservation. His later role as Regional Officer for north-east Scotland gave him jurisdiction over the magnificent Cairngorms and other parts of his home territory. He helped to set up the National Nature Reserves over the Cairngorms, and other famous areas, including Glens Clova and Caenlochan, Muir of Dinnet, Sands of Forvie, St Cyrus and the Morrone Birchwood at Braemar, his spiritual home.

These reserves and the more numerous Sites of Special Scientific Interest were his most enduring achievement in conservation, and their management and monitoring became a major part of his work. The administrative side was a necessary but less appealing part of the job, and Grant was happiest in the field, keeping an eye on reality in nature and discussing the flora and fauna with Wardens and other people on the ground. He was a brilliant photographer, and formed a unique pictorial record of his field experiences, which he drew upon in his many and much acclaimed lectures about botanical conservation.

Grant knew the Scottish flora inside out, and especially the mountain plants, but had a wide knowledge of British botany and its history besides. His own searches expanded knowledge of plant distribution considerably. A revered figure in the Botanical Society of Edinburgh (now Scotland), he became its President from 1966–68. After retirement from the Nature Conservancy in 1970, he was honoured with the Queen's Jubilee Medal for his work on wildlife conservation in Scotland. For long afterwards, he gave annual courses in field botany at Kindrogan Field Studies Centre, where students continued to absorb his knowledge and wisdom.

Amongst those who knew him, it is Grant Roger the person who is remembered above all. He had an endearing modesty, gentleness and old-world courtesy, and a total lack of conceit or pretence, yet a keen sense of fun, that won him a great many friends. A delightful companion, his priceless anecdotes, aphorisms and wry comments on the human condition, enlivened his learned discourses on matters botanical. His heroes were the self-taught Victorian naturalists of humble origin such as Russel Wallace, Richard Spruce and Hugh Miller whose selfless dedication to the pursuit of knowledge he so much admired. His wide interests were to be seen in his home full of books, covering not only natural history, but also art, music, literature, philosophy, history, castles, heraldry, ships and railways.

Grant was blessed with a long and happy married life of 55 years, to Jean, who supported him devotedly throughout, including nursing him through a final difficult period of heart problems. Their warm hospitality to their many friends and visitors was legendary. Home life with Jean and children Neil, Lindsay, David and John meant a great deal to Grant, and annual family holidays in interesting places were a great event. Their lives were, sadly, clouded by John's tragic death in a

climbing accident in 1975. The company of his grandsons Ben and Sam became a great delight to Grant in later life.

Grant Roger was a lovable person, whose integrity, high ideals and generosity of spirit will remain an abiding memory and inspiration to those fortunate to have known him.

D. A. RATCLIFFE

Report

THE ANNUAL GENERAL MEETING, 17 MAY 1997

The Annual General Meeting of the Society was held at the Dorset County Museum, High West Street, Dorchester, by kind invitation of the Curator, Mr Richard de Peyer, at 11.00 a.m. The President, Mr D. A. Pearman took the Chair in the presence of 112 members.

Apologies for absence were read and Minutes of the 1996 Annual General Meeting, published in *Watsonia* 21: 301–303 (1997), were accepted as correct, approved and signed by the President.

REPORT OF COUNCIL

The President took members through the Report of the Council, which had been previously circulated to members, commenting on the main achievements of the Society during the year, including the progress of Atlas 2000 and the computerisation of vice-county recorders. Mr R. G. Ellis was congratulated on producing his first Annual Report and Mr M. Walpole on his 26th and final Treasurer's Report and Accounts. The adoption of both Reports was proposed by R. M. Burton, seconded by R. M. Walls and accepted unanimously.

RULE CHANGES

The President explained the reasoning behind the proposed amendment to Rule 9 where Council had proposed a change from: "*The President shall be elected to serve for a term of two years and shall not be eligible for immediate re-election . . .*" to "*The President shall be elected to serve for a term of two or three years, according to the wishes of Council and the nominee on taking office, and shall not then be eligible for immediate re-election . . .*" After some discussion this amendment was proposed by C. A. Stace, seconded by A. O. Chater and carried with one opposing vote and some abstentions. As a result of this rule change, R. G. Ellis proposed and T. G. Evans seconded that D. A. Pearman be re-elected President for a further year and this was carried unanimously.

In introducing the proposed amendment to Rule 22, the President mentioned the outstanding contribution Messrs Grant Thornton had made to the successful running of the Society in auditing our accounts for the past 25 years. The proposal by Council to change Rule 22 was to give the Society flexibility when selecting a replacement for Messrs Grant Thornton. Council had proposed a change from: "*An auditor shall be appointed by the members at the Annual General Meeting and the accounts, having been audited by him, shall be approved by the Council before presentation to the next Annual General Meeting.*" to "*An Auditor or Independent Examiner shall be appointed by the members at the Annual General Meeting to report on the Financial Statements and Accounts which shall then be approved by Council before presentation to the next Annual General Meeting.*" The amendment was proposed by D. E. Allen, seconded by M. Walpole and carried unanimously.

ELECTION OF VICE-PRESIDENT

The President commented on the importance to the Society of having experienced members as Vice-Presidents who could assist the Chair when necessary. He paid tribute to Mr M. Walpole who had done so much for the Society as Hon. Treasurer and Chairman of Publications Committee for over a quarter of a century. Mrs M. Briggs then gave an appreciation of Mr Walpole with whom she had worked so closely as Hon. General Secretary for almost the same quarter of a century. The election of Mr M. Walpole was proposed by the President, seconded by Dr S. L. Jury and carried

with acclamation. Mr Walpole then gave a short address in which he expressed his gratitude for being allowed to serve the Society for so many years.

ELECTION OF HON. GENERAL SECRETARY

Council had nominated Mr R. G. Ellis. His election was proposed by Mr T. G. Evans, seconded by Mr R. G. Woods and carried unanimously.

ELECTION OF HON. TREASURER

With the resignation of Mr M. Walpole there was a vacancy for the post of Hon. Treasurer. Council had nominated Mr M. E. Braithwaite. His election was proposed by Mr A. O. Chater, seconded by Miss E. Young and carried unanimously.

The President then warmly thanked the Editors of *Watsonia* and *B.S.B.I. news*, the compiler of *B.S.B.I. abstracts*, and all representatives on Council and other Committees for the hard work they carried out, voluntarily, on behalf of the Society. This was greeted by applause.

ELECTION OF COUNCIL MEMBERS

In accordance with Rule 11 nominations had been received for Mr C. R. Boon, Prof. M. Crawley and Dr S. J. Whild. Profiles had been published with proposers and seconds, and election of these members was approved unanimously.

ELECTION OF HONORARY MEMBERS

The President mentioned that there was a slight break with tradition in that no fewer than five members had been nominated for Honorary Membership of the Society this year. All had made outstanding contributions to the Society and to field botany in general. Sponsors for all five gave short appreciations of their respective candidates (to be published in *B.S.B.I. news*) and their election was carried unanimously with warm applause.

The five new Honorary Members (and sponsors) were: Mr A. C. Jermy (Mr D. A. Pearman), Mr J. Ounsted (Miss A. Burns), Dr F. H. Perring (Mr M. Walpole), Dr F. Rose (Mr D. Streeter) and Mr P. D. Sell (Dr C. D. Preston & Dr S. M. Walters).

PRESIDENT'S AWARD

David Bellamy (President Wild Flower Society) and David Pearman (President B.S.B.I.) had both unhesitatingly recommended Richard Mabey for his *Flora Britannica*. Both Presidents thought this book quite superb and it had opened up botany to many people who would not otherwise have had an interest in the subject.

ELECTION OF HONORARY AUDITOR OR INDEPENDENT EXAMINER

The President again warmly thanked Grant Thornton, West Walk, Leicester for their exemplary auditing of our accounts. Their decision not to seek re-election resulted in a vacancy. The new Hon. Treasurer Mr M. E. Braithwaite had approached one of his local "competitors", Mr John Coates, of Greaves West & Ayre, Chartered Accountants, Berwick upon Tweed, who had agreed to stand for

election. He was proposed by Mr D. A. Pearman, seconded by Mr J. Ounsted and carried unanimously.

There being no other business, the meeting closed at 12.40 p.m.

GWYNN ELLIS

FIELD EXCURSIONS HELD IN CONJUNCTION WITH THE A.G.M.

Four field meetings were held over the weekend; all were very well attended, and we have to thank our leaders, Dr Sue Eden, Miss Anne Horsfall and Dr Humphrey Bowen for their sterling work.

FRIDAY 16 MAY, KINGCOMBE

This was meant to be a foretaste for early arrivals, yet over 50 members assembled for the walk, which was by courtesy of the Dorset Wildlife Trust, who own and farm the 158 ha reserve. Kingcombe is certainly one of the largest blocks of unimproved neutral grassland in southern England, and has very good numbers of plants, once common, but now rare outside reserves. The party saw *Genista anglica* (Petty Whin), *Pedicularis sylvatica* (Lousewort), *Ophioglossum vulgatum* (Adder's-tongue), the leaves of *Serratula tinctoria* (Saw-wort), *Succisa pratensis* (Devil's-bit Scabious) and *Oenanthe pimpinelloides* (Corky-fruited Water-dropwort), and a huge quantity of sedges, of which over 20 species occur here. There are good populations of Marsh and Small Pearl-bordered Fritillaries too. The highlight of the meeting was the discovery of a small patch of *Botrychium lunaria* (Moonwort) which, in Dorset, has only been seen once in the last 20 years. Sixty three members then found their way through the lanes to Frome St Quintin and tea and obligatory garden tours.

SATURDAY 17 MAY, WINFRITH HEATH

A coach load and some private cars met here for an early season heathland visit. The best area was a closely rabbit-grazed "village green", where *Cerastium semidecandrum* (Little Mouse-ear), *Crassula tillaea* (Mossy Stonecrop) (very frequent), *Ranunculus parviflorus* (Small-flowered Buttercup), *Trifolium micranthum* (Slender Trefoil), *T. ornithopodioides* (Bird's-foot Clover), *T. scabrum* (Rough Clover), *T. striatum* (Knotted Clover) and *T. subterraneum* (Subterranean Clover) were all found. Growing with them was a small patch of *Chamaemelum nobile* (Chamomile), now confined to three sites in Dorset. A little further on was *Eleocharis quinqueflora* (Few-flowered Spike-rush), but it was too early for *Radiola linoides* (Allseed) and *Anagallis minima* (Chaffweed).

On the heath itself there was little flowering, except some bushes of *Genista anglica* (Petty Whin), but the verges had *Geum rivale* (Water Avens), *Carex disticha* (Brown Sedge) and *Genista tinctoria* (Dyer's Greenweed). Some energetic members ventured into a bog to look at vegetative *Deschampsia setacea* (Bog Hair-grass), but again the heathland specialities such as *Gentiana pneumonanthe* (Marsh Gentian) and *Rhynchospora fusca* (Brown Beak-sedge) were not yet visible. A flush had *Carex pulicaris* (Flea Sedge), *Cirsium dissectum* × *palustre*, *Dactylorhiza praetermissa* (Southern Marsh-orchid), *Ophioglossum vulgatum* (Adder's-tongue) and *Sanguisorba officinalis* (Great Burnet).

The return to Dorchester was by way of Oakers Wood where there was still a good show of *Pulmonaria longifolia* (Narrow-leaved Lungwort) along the roadside verge.

Another smaller party of members met at West Bexington, at the westward end of Chesil Beach. *Crambe maritima* (Sea Kale) was in full flower, along with some *Glaucium flavum* (Yellow-horned Poppy).

The party was then invited to tea by Mr and Dr Eden, who have an extremely interesting Mediterranean shingle garden (with a good reptile fauna too). Many scarce plants such as *Lathyrus aphaca* (Yellow Vetchling), *Vicia parviflora* (Slender Tare) and *Petroselinum segetum* (Corn Parsley) are garden weeds here, and are well looked after.

SUNDAY 18 MAY, PORTLAND AND FERRYBRIDGE

A very large group, augmented by a few members of the Dorset Natural History and Archaeological Society, who had been our hosts the day before, met at Portland Heights. With the overnight mist

clearing one party went to St George's Reforme, where there is a large churchyard with *Arum italicum* subsp. *neglectum* (Italian Lords-and-Ladies); many naturalised plants including *Narcissus tazetta* (Bunch-flowered Daffodil), *Scilla peruviana* (Portuguese Squill) and *Gladiolus communis* (Eastern Gladiolus) were seen. Across the road is one of the quarry faces that holds *Adiantum capillus-veneris* (Maidenhair Fern). This party then proceeded to Church Ope Cove, a well-known botanical site. Here *Valerianella eriocarpa* (Hairy-fruited Cornsalad), *Polypodium cambricum* (Southern Polypody), *Linum bienne* (Pale Flax) and *Orobanche hederae* (Ivy Broomrape) were seen along with some small patches of *Limonium recurvum* (Portland Sea-lavender). No *Gentianella anglica* (Early Gentian) plants were found, but on the way back a native site for *Adiantum capillus-veneris* (Maidenhair Fern) was shown.

The other party drove to Portland Bill. *Parapholis incurva* (Curved Hard-grass) grows on bare ground by the lighthouse and nearby is a long established clump of *Borago officinalis* (Borage). Walking eastwards along the coast there was much *Crithmum maritimum* (Rock Samphire), *Inula crithmoides* (Golden Samphire) and a magnificent stand of *Salvia verbenaca* (Wild Clary). The locus classicus of *Limonium recurvum* (Portland Sea-lavender) was admired, and then the party turned into one of the arable strips, where *Medicago polymorpha* (Toothed Medick) was found and *Trifolium squamosum* (Sea Clover). In the next field there was a mass of *Lathyrus aphaca* (Yellow Vetchling) and *Ranunculus parviflorus* (Small-flowered Buttercup). A walk behind the Pulpit Inn to find *Gentianella anglica* (Early Gentian) was unsuccessful, but here there was much *Thesium humifusum* (Bastard Toadflax) and a rich calcareous flora.

Lunch was held back at Portland Heights, where *Valerianella eriocarpa* (Hairy-fruited Cornsalad) was seen again. Then the group descended to Ferrybridge, where Chesil Beach joins the Isle of Portland. Despite roads, railways, car parks, visitors and windsurfers this is still an extremely rich site and the mass of *Armeria maritima* (Thrift) in flower made it extremely colourful. Here the party saw *Polycarpon tetraphyllum* (Four-leaved Allseed), first recorded here in 1770, with *Phleum arenarium* (Sand Cat's-tail), *Trifolium scabrum* (Rough Clover) and *Vulpia fasciculata* (Dune Fescue). The car park held *Anthriscus caucalis* (Bur Chervil). Across the road, by the old railway line, was what looked like *Limonium recurvum* with *L. dodartiforme*, *Calystegia soldanella* (Sea Bindweed) and *Eryngium maritimum* (Sea Holly). Further on was a newly discovered very large patch of *Asparagus officinalis* subsp. *prostratus* (Wild Asparagus), which, like the *Polycarpon tetraphyllum*, has been known in the area for over 200 years. *Euphorbia portlandica* (Portland Spurge) and *Suaeda vera* (Shrubby Sea-blite) were also frequent here, along with a few plants of *Papaver dubium* subsp. *lecoqii* (Long-headed Poppy). Further on there were found huge drifts of *Anisantha madritensis* (Compact Brome), looking very fresh and reddish-green, and finally many plants of *Geranium purpureum* (Little Robin) and *G. rotundifolium* (Round-leaved Crane's-bill). Ice creams and tea rewarded those not already surfeited!

DAVID PEARMAN

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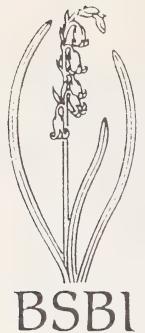
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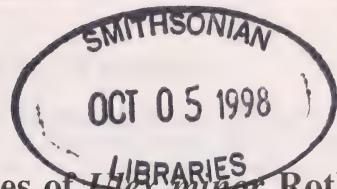
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The cover illustration of *Meconopsis cambrica* (L.) Viguer (Welsh Poppy) was drawn by Rosemary Wise.



Chromosome numbers and flower sizes of *Ulex minor* Roth. and *Ulex gallii* Planch. in Dorset

J. M. BULLOCK, J. CONNOR, S. CARRINGTON and R. J. EDWARDS

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ABSTRACT

This study was carried out to address the continuing uncertainty concerning the identification and chromosome numbers of the closely-related species *Ulex minor* Roth. and *U. gallii* Planch. (Fabaceae). The species co-occur in Dorset and chromosome counts from mixed and single-species populations gave results of $n = 16$ for all 52 *U. minor* plants sampled and of $n = 32$ for 52 *U. gallii* plants. The *U. minor* count is uncontroversial. The *U. gallii* count has been reported in other studies, but some studies in Great Britain, Ireland, France and Spain have reported $n = 48$. One plant, found in a mixed population of the two species and identified as *U. gallii*, had a count of $n = 24$. This number has never been reported before for a European *Ulex* and the plant may be a *U. gallii* \times *U. minor* hybrid. It had an intermediate flower size.

Although the two species are best distinguished by flower size, a survey over Dorset showed appreciable overlap in flower standard and calyx lengths. However, use of a suite of characters (flower size, spine length and bush size) always gave correct identification when tested against chromosome number. A search for hybrids – based on the hypothesis that mixed populations will contain more intermediate plants (because of hybridization) than single-species populations – suggested that *U. gallii* \times *U. minor* hybrids are rare.

KEYWORDS: *Ulex gallii* \times *U. minor*, *U. gallii* \times *U. europaeus*, gorse, morphometrics, ploidy levels.

INTRODUCTION

Ulex minor Roth. and *U. gallii* Planch. (Fabaceae) have caused problems to British and European botanists since *U. gallii* was first described by Planchon in 1849. Before its description, *U. gallii* was taken to be a large form of *U. minor*, and there are still problems in distinguishing the two species (Castroviejo & Valdés-Bermejo 1990; Gloaguen 1986; Proctor 1967). This is because the species show substantial overlap in many characters, e.g. bush height, spine length, flower colour and pod size (Proctor 1965). Although flower size (standard and calyx lengths) is the most reliable character for species identification, even this character is not completely distinct between the species (Proctor 1965). Chromosome counts might be expected to provide a method for separating the species; indeed, they do have different chromosome numbers (see below). However, cytological studies over the past decade have opened up a new area of controversy and debate.

Several studies of *U. minor* in France and Spain have all arrived at a count of $2n = 32$ (e.g. Alvarez Martinez *et al.* 1988; Castroviejo & Valdés-Bermejo 1983, 1990; de Castro 1941; Fernandez Prieto *et al.* 1993; Misset 1990; Misset & Gourret 1996). The same results were obtained from a site in Dorset by Fernandez Prieto *et al.* (1993) and from a site in Surrey listed in the B.S.B.I. database. However, chromosome counts for *U. gallii* have been more varied. The first count, by de Castro (1943), suggested $2n = 80$. This was probably wrong, and the debate over the last 15 years has revolved around the fact that studies of *U. gallii* in Europe have found both $2n = 96$ and $2n = 64$. Castroviejo & Valdés-Bermejo (1983, 1990) counted both $2n = 64$ and 96 in Spain. Alvarez Martinez and co-workers (Alvarez Martinez *et al.* 1988; Fernandez Prieto *et al.* 1993) found $2n = 64$ in Spain and France, $2n = 96$ in Spain and one plant with $2n = 32$ in Spain. Misset (1990; Misset & Gourret 1996) found $2n = 96$ in north-west France, although she had one example of $2n = 64$. In the British Isles, Fernandez Prieto *et al.* (1993) studied eight *U. gallii* sites in Devon and Cornwall and found only plants with $2n = 64$. However the B.S.B.I. database contains counts of $2n = 96$ from three *U. gallii* sites, on Alderney, in Derbyshire and in County Dublin. Where methods have been given, all these studies distinguished species in the field using the differences of flower calyx and standard lengths, spine length and bush size reported by Proctor (1965).

This confusion has prompted suggestions for changes in the taxonomy of the two species, involving splitting *U. gallii* Planch according to chromosome numbers. Castroviejo & Valdés-Bermejo (1983, 1990) suggested that plants with $2n = 64$ should be named *U. minor* subsp. *breoganii* and those with $2n = 96$ become *U. minor* subsp. *gallii* (with *U. minor* becoming *U. minor* subsp. *minor*). Conversely, Alvarez Martinez *et al.* (1988) suggested $2n = 64$ plants should remain *U. gallii* while $2n = 96$ plants become *U. cantabricus*. However, neither suggestion has been accepted generally. Clearly, more data are needed on the chromosome numbers of *U. gallii* and *U. minor*.

Another unresolved question concerns the occurrence of *U. gallii* \times *U. minor* hybrids. While *U. gallii* \times *U. europaeus* hybrids are commonly described (Benoit 1962; Gloaguen 1986; Misset & Fontenelle 1992; Stace 1975) (interestingly, no *U. minor* \times *U. europaeus* hybrids have been suggested), the evidence for *U. gallii* \times *U. minor* hybrids is weak (see Stace 1975). Millener (1952) failed to produce



FIGURE 1. The distributions of *Ulex minor* and *U. gallii* in Britain. *U. minor* occurs east of the line and *U. gallii* occurs west of the line - - - - and in East Anglia in the region marked *.

TABLE 1. CHARACTERS OF TWO *ULEX* SPECIES IN BRITAIN, AS DESCRIBED BY PROCTOR (1965)

<i>Ulex minor</i>	<i>Ulex gallii</i>
Flowering season: July–September	Flowering season: as <i>U. minor</i>
Flowers	Flowers
Standard: 6–12 mm (mode 9·5 mm)	Standard: 10·5–18 mm (mode 15 mm)
Calyx: 6–9 mm	Calyx: 9·5–12·5 mm
Wings: variable	Wings: strongly curved, c. 1 mm longer than keel
Pedicels: 3–5 mm, appressed hairs	Pedicels: as <i>U. minor</i>
Flower colour – mostly aureolin and lemon yellow	Flower colour – mostly buttercup and Indian yellow
Bracteoles: 0·5–0·8 × 0·6–0·8 mm	Bracteoles: as <i>U. minor</i>
Pod: 6–11 mm	Pod: 6–12 mm
Spines: 6–25 mm	Spines: 8–34 mm
Bush height: 5–150 cm	Bush height: 10–200 cm
	Other: flower opens more widely than <i>U. minor</i> after pollination. Possible red veining of standard.

pods or seeds in an attempted cross between *U. minor* (♂) and *U. gallii* (♀). All suggestions of *U. gallii* × *U. minor* hybrids in the field derive from notes by Corillion (1950) and Lambinon (1962) on plants with vegetative and floral characteristics intermediate between the two species. Given the overlap in characteristics of the described species (e.g. Proctor 1965), it is extremely tenuous to call intermediate plants hybrids. Chromosome counts would provide more solid evidence of hybrids, if plants of intermediate chromosome numbers were found in mixed populations of *U. gallii* and *U. minor*.

U. gallii occurs in the west of Britain and *U. minor* is in the south-east, and their distributions only overlap substantially in Dorset (Fig. 1). Within Dorset most heaths contain only one of the two *Ulex* species (single-species populations), although there are several heaths (mixed populations) with both species (unpublished data J. M. Bullock & R. J. Edwards); this suggests competitive separation of the two species. It is therefore likely that any British *U. gallii* × *U. minor* hybrids would be found in Dorset. In this study we carried out chromosome counts of a large sample of plants from a mixed population of *U. gallii* and *U. minor* and from single-species populations in Dorset in order to answer the following questions.

1. What are the chromosome numbers of *U. gallii* and *U. minor* in Dorset?
2. Is field identification of *U. gallii* and *U. minor* using Proctor's (1965) criteria reliable, as tested by chromosome counts?
3. Is there any chromosomal evidence for *U. gallii* × *U. minor* hybrids in mixed populations?

Questions 2 and 3 were explored further by taking measurements of floral standard and calyx lengths from *U. gallii* and *U. minor* plants in mixed and single-species populations throughout Dorset in order: 1. to assess the overlap in flower size (an extension of Proctor's 1965 work); and 2. to determine whether mixed populations have a greater proportion of plants with flower sizes intermediate between the two species; this would provide indirect evidence of hybrids, which (if they exist) should be more prevalent in mixed populations. Proctor (1965) showed that standard and calyx lengths were the best characters with which to separate the species (Table 1). Therefore, if hybrids have intermediate characters, then standard and calyx lengths should be the best characters with which to identify hybrids. It should be noted that this hypothesis does not assume that all intermediate plants are hybrids, but does assume that the presence of hybrids will change the frequency distribution of flower sizes. The third distinguishing character by Proctor (1965) was flower colour, but we did not use this because it is a discontinuous variable and would be difficult to use to identify intermediates.

METHODS

CHROMOSOME COUNTS

A survey of the occurrence of both species in each heath in Dorset had been carried out in 1995 (R. J. Edwards, unpublished data), and this was used to select three heaths from which to sample. Gore Heath

TABLE 2. THE DORSET HEATHS (WITH GRID REFERENCE) FROM WHICH SAMPLES OF *ULEX* spp.
FLOWER SIZES WERE TAKEN

<i>U. minor</i> only heaths	Arne Heath Bovington Heath Hurn Common Winfrith Heath	SY/964.878 SY/838.916 SZ/136.960 SY/380.876
<i>U. gallii</i> only heaths	Canford Heath Cripplestyle Common Puddletown Forest Upton Heath	SZ/021.962 SU/092.118 SY/728.920 SY/974.956
Mixed heaths	Ferndown Common Godlingston Heath Gore Heath Ham Common Holt Heath Parley Common Stoborough Heath Studland Heath	SZ/064.994 SZ/015.820 SY/924.900 SY/976.908 SU/054.030 SZ/084.986 SY/936.848 SZ/022.844

(SY/924.900) contained both species and the populations were intermingled. This was judged to be the best example of a mixed population in Dorset. Plants were sampled at random over the whole heath. Each plant was identified in the field as *U. minor* or *U. gallii* using Proctor's (1965) characters; the most useful characters were flower size (i.e. standard length), spine length and bush size. These characters were generally larger in *U. gallii* than in *U. minor* and we used field measurement of all three characters to distinguish the species (we did not make notes of these measurements). Every plant encountered was sampled, even those which were difficult to identify. Buds were taken from 50 *U. minor* bushes and the same number of *U. gallii* bushes. To provide baseline chromosome counts for both species, *Ulex* plants were sampled in heaths containing single-species populations. Ten *U. gallii* bushes were sampled from Canford Heath (SZ/021.962) and ten *U. minor* bushes were sampled from Winfrith Heath (SY/380.876). All sampling was done on 12–13 August 1996.

The methods used for counting chromosomes were the same as those given by Misset (1990) and Fernandez Prieto *et al.* (1993) (see also Gurr 1965). Flower buds of c. 2 mm length were fixed in the field in Carnoy's fixative (3:1 Glacial acetic acid-Ethanol) and then kept refrigerated for at least 48 hours. The anthers were then dissected out on a microscope slide in a drop of aceto-carmine and squashed under a coverslip. Counts were made of stained chromosomes in pollen cells at metaphase 1. Counts were made from at least two buds from each plant.

FLOWER SIZES

The 1995 survey was used to select four heaths which contained only *U. minor*, another four heaths which contained only *U. gallii*, and eight heaths with mixed populations (Table 2). In each heath 20 bushes of each of the gorse species present (identified using Proctor's characters) were chosen at random over the entire extent of the heath. As with the chromosome counts, difficult bushes were not avoided. Five fully opened flowers were picked from each bush and stored in an ice-box. Within 24 hours of collection the floral standard and calyx lengths of each flower was measured to the nearest 0.5 mm. The five measures for each bush were used to calculate mean standard and calyx lengths for each of the 320 bushes sampled. Sampling was carried out over August 1995.

RESULTS

CHROMOSOME COUNTS

The ten *U. minor* plants from Winfrith Heath all gave chromosome counts of $n = 16$ and the ten *U. gallii* plants from Canford Heath had counts of $n = 32$. Of the plants from the mixed population on Gore Heath,

all those identified in the field as *U. minor* gave counts of $n = 16$ (counts were taken from 42 plants; we were unable to obtain adequate preparations from the remaining eight plants), but of those identified as *U. gallii* 42 gave counts of $n = 32$ and one gave a count of $n = 24$ (Fig. 2). To assess the consistency of this last unusual chromosome number, counts were made from ten buds on the plant and all gave $n = 24$. Several preparations were made of pollen grains, and the pollen for the $n = 24$ plant appeared normal and similar to that of the $n = 16$ and $n = 32$ plants. A single flower preserved with the buds of the $n = 24$ plant had a standard and a calyx length of 11.5 mm and 8.5 mm respectively. This plant had been identified in the field as *U. gallii* on the basis of its standard and spine lengths and bush size. However, we were not able to relocate this plant in the field in order to make detailed measurements of its floral and vegetative characters.

FLOWER SIZES

T-tests showed that the average floral standard and calyx lengths of the *U. minor* and *U. gallii* were significantly different (single-species populations, standard length, $t = 19.4$, $p < 0.001$, calyx length, $t = 16.3$, $p < 0.001$; mixed populations, standard length, $t = 28.6$, $p < 0.001$, calyx length, $t = 25.8$, $p < 0.001$), and most of the *U. gallii* plants had longer standards and calyces than any *U. minor* plant (Figs 3 & 4). However there was an overlap in flower sizes, with both species having bushes with mean standard lengths of 11–12.5 mm and mean calyx lengths of 8–10 mm. The distribution of flower sizes of each species did not differ between the single-species populations and the mixed populations (standard length, *U. minor* $\chi^2 = 12.3$, $df = 7$, nsd; *U. gallii* $\chi^2 = 6.6$, $df = 8$, nsd; calyx length, *U. minor* $\chi^2 = 10.7$, $df = 6$, nsd; *U. gallii* $\chi^2 = 11.5$, $df = 8$, nsd).

The hypothesis that mixed populations would have a greater proportion of bushes with intermediate flower sizes (suggesting the presence of *U. gallii* \times *U. minor* hybrids) was tested by comparing the proportions of three categories of bushes between the single-species and mixed populations. These categories were: bushes with intermediate flower sizes, bushes with smaller than intermediate flower sizes and bushes with larger than intermediate flower sizes. Two definitions of intermediate standard size were tested: a. 11.5–12 mm, b. 11–12.5 mm. Definition a gave no significant differences between the population types ($\chi^2 = 4.3$, $df = 2$, nsd). Definition b resulted in a significant difference ($\chi^2 = 6.5$, $df = 2$, $p < 0.05$), but this was because there was a smaller rather than greater proportion of intermediate plants in the mixed (16%) than in the single-species population (25%).

Similarly, two definitions of intermediate calyx size were tested: a. 8.5–9.5 mm, b. 8–10 mm. Neither definition gave a significant difference between the population types (a, $\chi^2 = 3.1$, $df = 2$, nsd; b, $\chi^2 = 3.8$, $df = 2$, nsd).

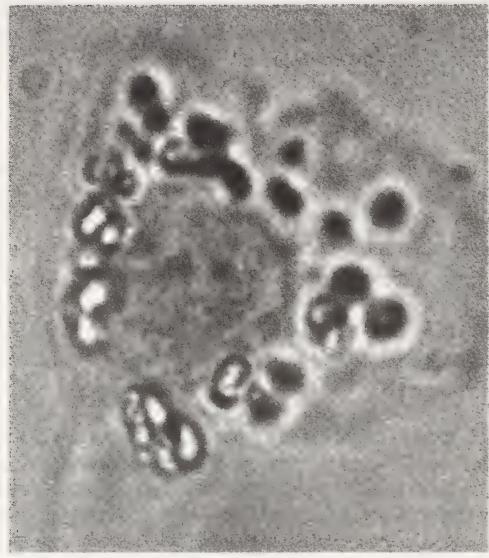
DISCUSSION

CHROMOSOME NUMBERS OF *U. GALLII* AND *U. MINOR*

Despite the overlap in flower sizes of the two *Ulex* species (Figs 3 & 4), the suite of character differences (we found the most useful to be flower size, bush height and spine length) between the two species allow accurate field identification of the species. There was complete agreement between the field identification of the plants and the chromosome counts obtained, $n = 32$ for *U. gallii* and $n = 16$ for *U. minor* (the single unusual count of $n = 24$ is discussed below), even for plants in an extensively mixed population.

While there is no controversy about the chromosome numbers of *U. minor* ($2n = 32$), this paper contributes to the debate in France and Spain on the chromosome numbers of *U. gallii* ($2n = 64$ in this paper). Misset (1990; Misset & Gourret 1996) contended that *U. gallii* has $2n = 96$ and called her single example of *U. gallii* with $2n = 64$ a "ploidy accident" (Misset & Gourret 1996). Castroviejo & Valdés-Bermejo (1990) also asserted that $2n = 96$ for *U. gallii* and suggested that the counts by Alvarez Martinez *et al.* (1988) of $2n = 64$ were mistakes. Alvarez Martinez and co-workers (Alvarez Martinez *et al.* 1988; Fernandez Prieto *et al.* 1993) however suggested that the two ploidy levels for *U. gallii* are common (even suggesting that *U. gallii* with $2n = 32$ may occur).

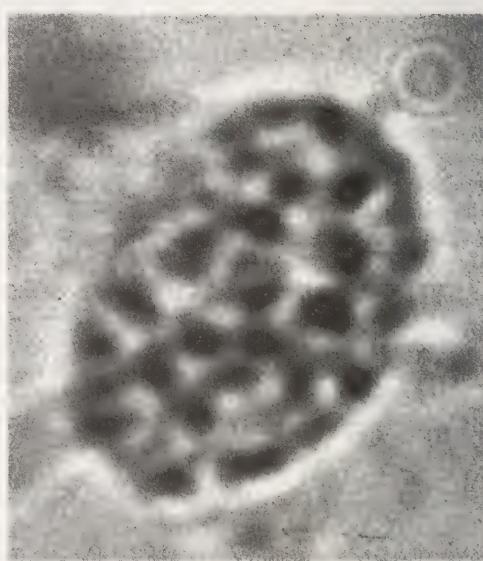
These workers have all identified their specimens using standard and calyx lengths (and sometimes other characters such as spine lengths), although most are not clear about the criteria used to distinguish the species. We assume that they have used the size range of flower sizes for each species reported by



b)



a)



c)

30µm

FIGURE 2. Cells at metaphase I with stained chromosomes. a. *Ulex minor*, n = 16; b. *U. gallii*, n = 32; and c. plant identified as *U. gallii*, n = 24.

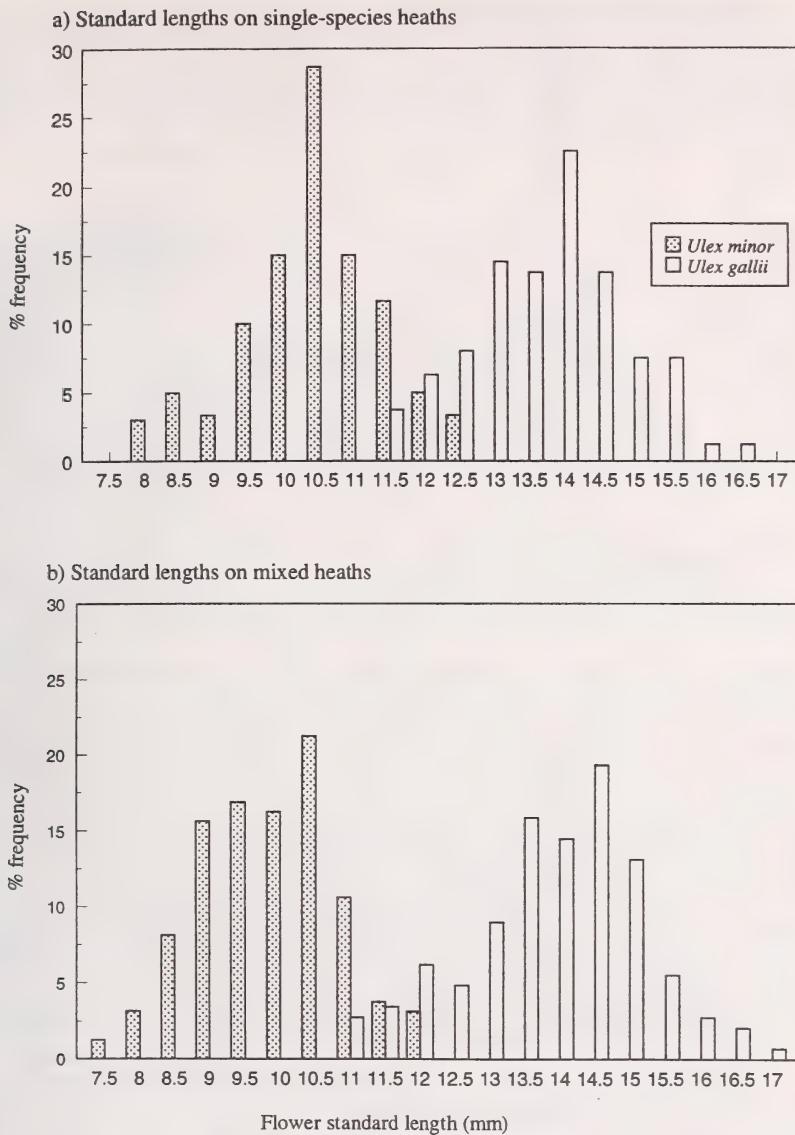
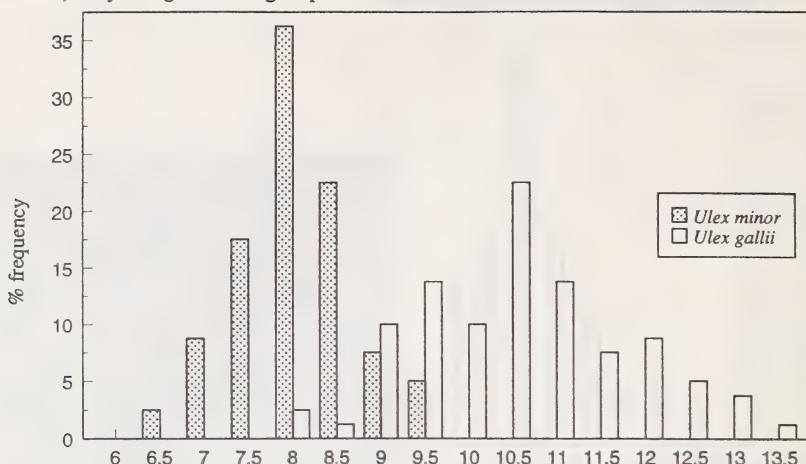


FIGURE 3. Histograms of the frequency distributions of flower standard length (using plant means) for the two *Ulex* species in single species populations (80 plants sampled for each species) and in mixed populations (160 plants sampled for each species).

Proctor (1965) (*U. minor* standard = 6–12.5 mm, calyx = 5.5–10.5 mm; *U. gallii* standard = 10.5–18 mm, calyx = 8.5–14.5 mm), which are similar to those found in this study (*U. minor* standard = 7.5–12.5 mm, calyx = 6–10 mm; *U. gallii* standard = 11–17 mm, calyx = 8–13.5 mm).

However, where measurements have been reported, they do not help to clarify the taxonomic problems concerning *U. gallii* ploidy levels. Alvarez Martinez *et al.* (1988) reported standard and calyx lengths of 8.7–15.8 mm and 6.8–14.5 mm respectively for plants with $2n = 64$ identified as *U. gallii* and of 10.3–14.3 mm and 8.7–12.4 mm for plants with $2n = 96$ named as *U. cantabricus*. These are curious results because the minimum lengths for *U. gallii* are very low in comparison to those in this

a) Calyx lengths on single-species heaths



b) Calyx lengths on mixed heaths

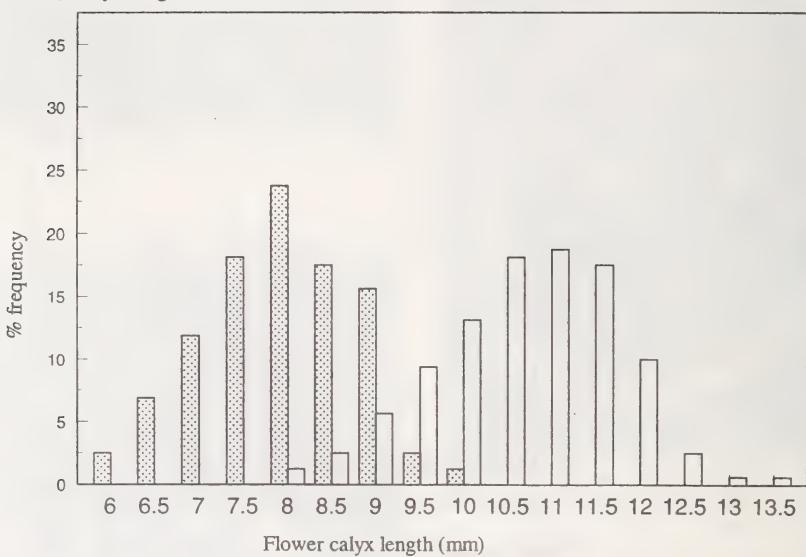


FIGURE 4. Histograms of the frequency distributions of flower calyx length (using plant means) for the two *Ulex* species in single species populations (80 plants sampled for each species) and in mixed populations (160 plants sampled for each species).

and Proctor's studies, and the *U. cantabricus* measurements fall within the range of the putative *U. gallii* plants in these other studies. Castroviejo & Valdés-Bermejo (1990) gave calyx lengths of 7–9.5 mm for plants identified as *U. minor* with $2n = 32$, 9.5–14 mm for plants identified as *U. gallii* with $2n = 96$, and 8.5–11 mm for plants named as *U. minor* subsp. *breoganii* with $2n = 64$. Therefore, the plants named as *U. minor* subsp. *breoganii* have calyx lengths intermediate between those given for *U. minor* and *U. gallii* and Castroviejo & Valdés-Bermejo (1990) describe this putative subspecies as having a generally intermediate morphology.

It seems likely that *U. gallii* has two ploidy levels on the European mainland and – given the three

examples with $2n = 96$ on the B.S.B.I. database and the populations with $2n = 64$ found by Fernandez Prieto *et al.* (1993) and in this study – possibly in the British Isles. However, taxonomic and morphological confusion means that it is unclear whether it is possible to distinguish these ploidy levels morphologically or what their taxonomic standing should be. Clearly, there is a need to address these issues by extensive morphological and cytological studies in Britain and Europe. It would seem premature to adopt the names *U. cantabricus* or *U. minor* subsp. *breoganii* for one or other of the ploidy levels.

U. GALLII × *U. MINOR* HYBRIDS

The mechanism that produced the single *Ulex* bush with a count of $n = 24$ ($2n = 48$) can only be guessed at. One possible explanation is that it was a *U. gallii* × *U. minor* hybrid, and indeed it did have an exactly intermediate chromosome number. Other supporting evidence (although tenuous) is that the single flower retrieved from the specimen was of intermediate size. It is usually stated or implied that the base chromosome number (x) for the genus *Ulex* is 16, and that *U. minor* is diploid, *U. gallii* is tetraploid ($2n = 64$) or hexaploid ($2n = 96$) and that *U. europaeus* is hexaploid (Castroviejo & Valdés-Bermejo 1990; Fernandez Prieto *et al.* 1993; Misson & Gourret 1996). If $x = 16$ then a plant (whether hybrid or not) with $2n = 48$ would be a triploid, and would usually be infertile (Felber & Bever 1997). However, microscopic examination of pollen grains from this plant suggested that they were fertile. If the base number of *Ulex* was $x = 8$ (as suggested by de Castro 1941, 1943) then the putative hybrid would be hexaploid (*U. minor*) and octoploid (*U. gallii*) parents.

If the $n = 24$ plant was a *U. gallii* × *U. minor* hybrid, then such hybrids are extremely uncommon. This chromosome count has never before been reported for *U. minor*, *U. gallii* or *U. europaeus*, or any other European *Ulex*. Only one such plant was found in a sample of 85 bushes from Gore Heath; a heath where the intimate mixing of the two species should provide ideal conditions for hybridisation.

The fact that mixed heaths did not have a greater proportion of bushes with intermediate flower sizes (standard and calyx lengths) than single-species heaths also provides indirect evidence against there being any great abundance of hybrids. While not all intermediate plants are necessarily hybrids (given the morphological overlap between the species), the presence of hybrids should increase the proportion of plants with intermediate characters. However, such a conclusion assumes that hybrids will have intermediate characters. This assumption has been shown to be only partly true for plant hybrids; certain characters may be indistinguishable from those of one parent or the other (Stace 1975; Riesberg & Ellstrand 1993). However, without better information, this assumption is acceptable and these data will be of use until there are more detailed studies which link morphological characters with allozyme or DNA markers in populations over a wide geographical area.

The possibility that there are few *U. gallii* × *U. minor* hybrids may be useful for British botanists, as it suggests that separation of the two species will not be complicated by the presence of hybrids. However, it raises the question of why such similar species with identical flowering seasons do not hybridise. Investigations of cross-compatibility and pollinator behaviour may suggest solutions.

U. GALLII × *U. EUROPAEUS* HYBRIDS

Although they were not looked for explicitly, our study of summer-flowering *Ulex* plants did not provide any evidence of *U. gallii* × *U. europaeus* hybrids. Such hybrids are commonly described, but evidence is usually based on intermediate vegetative and floral characters (Gloaguen 1986; Millener 1952; Stace 1975). Only Misson & Fontenelle (1992) give reliable evidence which is based on differing isoenzyme systems of *U. gallii* and *U. europaeus*, and shows that putative hybrids have elements of both isoenzyme systems. *U. europaeus* is usually described as $2n = 96$ (de Castro 1941, 1943; Castroviejo & Valdés-Bermejo 1983; Misson 1990), and counts from four bushes sampled on Gore Heath on 14 January 1997 gave the same number (V. Herrera, unpublished data). The only chromosome counts for *U. gallii* × *U. europaeus* hybrids have given $2n = 96$, and these are in papers which give the count for *U. gallii* of $2n = 96$ (Misson 1990; Misson & Gourret 1996). Where the count for *U. gallii* is $2n = 64$, the count for hybrids should be $2n = 80$ (interestingly, the count originally given by de Castro (1943) for *U. gallii*). The flowering season of *U. gallii* × *U. europaeus* hybrids is described as extending over the seasons for both the parent species (Gloaguen 1986; Millener 1952; Stace 1975), so samples spread over a longer period than covered in this study may provide more solid evidence of hybridization.

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Alan Raybould gave valuable advice on chromosome staining and Ralph Clarke advised on statistics. Alan Gray, Roger Daniels and an anonymous referee kindly commented on earlier drafts.

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Morphometric variation in Irish *Sorbus* L. (Rosaceae)

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ABSTRACT

Sorbus aria (L.) Crantz and *S. hibernica* E. F. Warb. are shown to differ from one another in a number of characteristics not previously noted, in particular, *S. aria* has a longer petiole, longer leaf blade with a more sharply pointed apex, greater number of leaf teeth and more widely spreading veins than *S. hibernica*. It does not appear that *S. aria* is more variable than *S. hibernica* in Ireland as is suggested generally by the literature. In addition, despite the very limited number of *Sorbus devoniensis* specimens available for study in Ireland, this species appears readily distinguishable from other, vegetatively similar, species of *Sorbus* on the basis of its longer petioles, higher number of leaf-teeth, more acutely pointed leaves and widely spaced veins.

KEYWORDS: *Sorbus aria*, *Sorbus hibernica*, *Sorbus devoniensis*, multivariate analysis.

INTRODUCTION

Sorbus is a critical genus represented in Ireland by seven species (Webb, Parnell & Doogue 1996). Two species, *Sorbus aucuparia* L. (Rowan) and *Sorbus intermedia* (Pers.) Ehrh., are readily separable from the rest purely on vegetative characteristics (their leaves are, respectively, pinnate or deeply lobed rather than more or less entire or shallowly lobed); these two species will not be considered in detail further. The other five species – *Sorbus anglica* Hedl., *S. aria* (L.) Crantz, *S. devoniensis* E. F. Warb, *S. hibernica* E. F. Warb. and *Sorbus rupicola* (Syme) Hedl. are usually each placed in one of three aggregate species groups – *S. anglica* in *S. intermedia* agg., *S. aria*, *S. hibernica* and *S. rupicola* in *S. aria* agg. and *S. devoniensis* in *S. latifolia* agg. (Stace 1997). Like *S. aucuparia*, *S. aria* is a diploid; all other species are polyploids and probably apomictic (Proctor, Proctor & Groenhof 1989). Species in the *S. intermedia* agg. and *S. latifolia* agg. probably originated as hybrids of *S. aria* and *S. aucuparia* and the non-Irish *S. terminalis* (L.) Crantz (Clapham, Tutin & Moore 1987).

Undoubtedly the most problematic distinction in this group of species in Ireland is between *S. aria* and *S. hibernica*. When writing the key to *Sorbus* for Webb, Parnell & Doogue (1996) Parnell indicated that the most obvious vegetative distinction between these two species lies in the upswept leaf-teeth of *S. aria* (where the outer margin of each tooth is longer than the inner) whereas the leaf-teeth of *S. hibernica* are straight and symmetrical. Additionally it is clear that the density of the white indumentum on the undersurface of the leaves of *S. hibernica* is usually greater than in *S. aria*. Stace (1997) indicates that while the leaves of *S. hibernica* may have 10 or fewer pairs of lateral veins, *S. aria* always has at least 10 pairs of veins. However he rightly points out both leaves and fruits are required for identification by beginners. These criteria are often difficult to meet; very many specimens in herbaria or in the field and also many brought in for identification are sterile or lack fruit. Whilst the key in Webb, Parnell & Doogue (1996), which relies on vegetative characters only, does allow most Irish material to be keyed out accurately and consistently it is clear that it could be improved; however, any improvement can only come about through a systematic description of the variation in leaf form in *S. hibernica* which currently does not exist. The aforementioned difficulties are compounded by the

view of most authors (e.g. Clapham, Tutin & Moore 1987) that *S. aria* is a relatively variable species in comparison to its polyploid relatives.

The present data-set was collected with the object of attempting to ascertain the differences, if any, in quantifiable leaf characters between the five species of *Sorbus* listed above, with special reference to the distinctions between *S. aria* and *S. hibernica* and to discover if there are any new distinctions between these species.

MATERIALS AND METHODS

In order to make a comprehensive survey, all material (146 sheets) of the genus *Sorbus* from the two largest Irish herbaria (**DBN** & **TCD**) was examined. In addition two extensive collections of new material were made from large populations of *S. hibernica* (20 trees from Coolbawn, County North Tipperary, Grid. ref. R/831.923; v.c. H10 and 44 trees from Kilbeggan, County Westmeath, Grid. ref. N/366.371; v.c. H23). The material of all taxa was from wild populations. The number of populations sampled in total was 148 (each herbarium sheet represented materials from a single plant and, as far as it was possible to determine, population). As a minimum, rarely two, and more usually six mature leaves were measured from each plant. Consequently the 148 populations were represented by 672 sets of leaf character measurements. The 672 measurements were then averaged so as to provide a mean value for each of the 148 populations. Of these only four plants assigned to *S. anglica*, another four of *S. devoniensis* and seven of *S. rupicola* were located. Characters (Table 1) were measured on each leaf (measurements were either in degrees or in mm or cm as appropriate).

Unfortunately, as can be seen from Table 1 it proved impossible to effectively measure or code for the degree of upsweptness of the leaf teeth or the density of the indumentum. However it was essential to have some *a priori* means of assigning names to specimens and these two characters were used as the primary method whereby *S. aria* and *S. hibernica* were initially identified. The other taxa were assigned names on the basis of the key in Webb, Parnell & Doogue (1996). A number of authors refer to pairs of veins in the leaf (vide Stace 1997); however our experience suggests that veins are not always strictly

TABLE 1. CHARACTERS OF *SORBUS* TAXA CODED FOR ANALYSIS IN PCA

Character number and its abbreviation

1. The angle made between the left-hand side of the base of the leaf blade and the petiole (Angbotlf)
2. The angle made between the right-hand side of the base of the leaf blade and the petiole (Angbothr)
3. The angle made between the third lateral vein from the base of the leaf blade and the midrib (Angof3ve)
4. The angle made between the fourth lateral vein from the base of the leaf blade and the midrib (Angof4ve)
5. The angle made between the margin of the left-hand side of the top of the leaf blade and the midrib (Angtoplflf)
6. The angle made between the margin of the right-hand side of the top of the leaf blade and the midrib (Angtoprphr)
7. The distance between the excursion points of the third and fourth lateral veins at the midrib (Distbet34)
8. The distance from the third lateral vein from the base of the leaf blade to the base of the leaf blade (Distbot3v)
9. The distance from the third lateral vein from the base of the leaf blade to the top of the leaf blade (Distfrm3v)
10. The distance from the insertion point of first tooth on left-hand side of base of the leaf blade to the base of the leaf blade (Distteel)
11. The distance from the insertion point of the first tooth on left-hand side of the base of the leaf blade to the base of the leaf blade (Distteer)
12. The length of the leaf blade, measured along its midrib (Leaflen)
13. The breadth of the leaf blade, measured at its point of maximal width (Leafwid)
14. The length of the leaf blade, measured along its midrib, to the widest point of the leaf blade (Leaflentwp)
15. The number of secondary veins on the leaf blade (Noveins)
16. The number of teeth present in the top centimetre of the leaf blade (Noteeto)
17. The number of teeth on the left-hand side of the leaf blade (Notnlhs)
18. The number of teeth on the right-hand side of the leaf blade (Notnrrhs)
19. The length of the petiole (Petlen)
20. The width of the petiole (Petwid)

paired and therefore we counted individual veins rather than pairs. With the sole exception of character number 20, the width of the petiole (Petwid), all characters were more or less normally distributed (r^2 values of $\geq 90\%$ after regression of their normal probability plot values and with values for kurtosis and skewness usually ≤ 1). In a few cases (except Petwid) where the latter values were > 1 , r^2 remained $\geq 90\%$ and transformation to attain normality was therefore not attempted. Petwid had large values for kurtosis and skewness (9.5 and 2.8 respectively) and a r^2 for regression of its normal probability plot values of 50%. A very large number of transformations were attempted for Petwid in an attempt to normalise its distribution; however no significant increase in normality could be obtained. Trial and error showed that exclusion of Petwid from the analyses undertaken had a minimal effect and therefore it was included in an untransformed state.

A number of different types of analysis were undertaken on these data, and two fundamentally different techniques were used. Firstly the data were ordinated. The ordination technique chosen was Principal Components Analysis (PCA) as produced by Datadesk 5.0.1 (cf. Data Description Inc., Ithaca, New York).

With all biological data sets PCA will extract as many summary axes as there are original variables in the data. However, only the first few of these axes represent effective summaries of the data and are non-trivial. The key question is – which axes are these? Unfortunately, this vital question is virtually ignored in the taxonomic literature. Many, if not most, workers use the heuristic Kaiser-Guttman criterion to determine which PCA axes are of significance (Jackson 1993). Simply put, this translates into consideration being given only to those axes whose eigenvalues are greater than unity (1), all other lesser scoring axes being ignored. Jackson (1993) argues that this criterion is too lax and permits consideration of components which are trivial explicators of the total variation pattern and which should really be ignored. However, others disagree and some standard ecological texts suggest that where the pattern of the data is weak, where the data-set is exceptionally large or where the investigator is concerned with the preservation of inter-object distances (i.e. pattern) it is possible to obtain perfectly valid plots associated with weak eigenvalues (Legendre & Legendre 1983). Obviously there is no universally accepted solution to this problem. However some, which are non-arbitrary, are discussed by Jackson (1993). According to him the best available single test for the importance of specific eigenvalues in PCA is that of Frontier (1976) who showed that the decrease in the eigenvalues of sequentially extracted axes in PCA generally follows a "broken-stick" distribution-type, where a fixed length is broken at random into a number of segments. Jackson (1993) uses this distribution to argue that any axis with an eigenvalue less than that predicted to occur from the appropriate "broken-stick" distribution could be ignored as insignificant. Comparison of eigenvalues with those in Frontier's table of "broken-stick" values was undertaken: in all cases discussed in this paper the first four axes proved significant.

A second technique, Discriminant Analysis (DSC), was used to test whether pre-defined groups of species visualised on PCA were or were not statistically distinguishable. This multivariate extension of analysis of variance (Marriott 1974) was performed in both a non-stepwise and stepwise manner (all default options, i.e. minimisation of Wilks λ , auto F-to-enter and F-to-remove) using SPSS 6.1 (cf. Norusis & SPSS Inc. 1993).

95% confidence limits are used throughout where appropriate.

RESULTS

The very low number of samples obtained of three taxa (*S. anglica*, *S. devoniensis* and *S. rupicola*) meant that it was not possible to draw firm conclusions relating to any of them. Nevertheless it is worth noting that an initial analysis which included all taxa was useful and that coefficients of variation for characters measured on these species were in the normal range of 10–20%. The four PCA axes which met Frontier's (1976) criteria had eigenvalues (expressed as percentages of the variance) of 28.4%, 17.9%, 11.7% and 9.3% respectively; there were therefore six biaxial plots of potential significance which required examination. Examination of these six plots together with initial DSC analysis showed that *S. devoniensis* was easily and consistently distinguishable from the other species of *Sorbus* measured on the basis of a combination of:

- i. character 1 – its longer petioles (> 2 cm \pm 0.2 cm as opposed to always c. 1.4(–1.9) cm \pm 0.06);

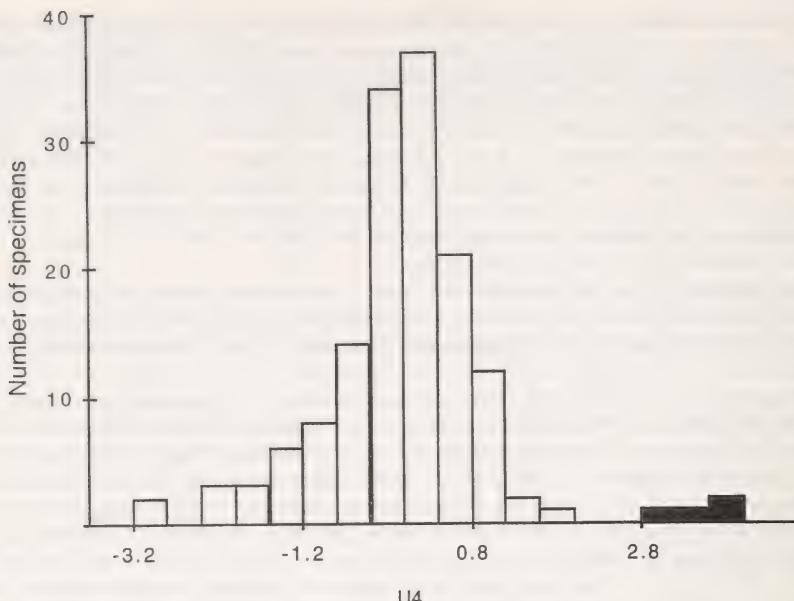


FIGURE 1. Plant scores for *Sorbus* taxa along Axis 4 (U4) which accounts for 9·4% of the total variance in the initial PCA analysis. Scores for *S. devoniensis* plants are indicated in black.

- ii. characters 17 & 18 – the number of teeth on the left and right-hand side of the leaf blade (c. 68 ± 12 as opposed to c. $45(-53) \pm 2$);
- iii. characters 5 & 6 – its more acutely pointed leaves forming an angle of c. $92^\circ \pm 10^\circ$ at the apex (as opposed to $\geq 106^\circ \pm 1.8^\circ$);
- iv. character 8 – the greater distance from the third lateral vein to the base of the leaf ($2.2 \text{ cm} \pm 0.42$ as opposed to $1.7 \text{ cm} \pm 0.07$); and
- v. character 7 – the more widely spaced third and fourth lateral veins $1.4 \text{ cm} \pm 0.10$ as opposed to $0.93 \text{ cm} \pm 0.04$) for the other species taken together.

Fig. 1 shows the distribution of scores along Axis 4 of this initial PCA which, for *S. devoniensis* is dominated by characters 7, 8 & 15 (the distance between the excursion points of the third and fourth lateral veins at the midrib, the distance from the third lateral vein from the base of the leaf blade to the base of the leaf blade and the number of secondary veins on the leaf blade respectively). Table 2 gives the eigenvector scores for this axis for all characters. Evidently at least these strong scoring characters must be further examined with a more comprehensive data set based on British material as it appears that further biometric work on these taxa will allow sufficiently robust algorithms to be calculated so allowing clear distinctions to be made.

Further analysis concentrated on the distinction between *S. aria* and *S. hibernica*. As can be seen from Fig. 2 a–c, PCA offered some support for separation of *S. aria* from *S. hibernica*; however it is clear that this support is limited and that considerable overlap of the taxa occurs. In part this is because the plots in Fig. 2 are simple biaxial plots which maximally account for 47% of the variance. A more accurate picture of the separation between these taxa can be obtained by DSC which gave good separation between these two species. Indeed non-stepwise DSC, the more conservative option, gave an overall misclassification rate of only 5·3% and stepwise DSC a highly significant intergroup F-ratio of 26·9 (d.f. 5, 126; $p \leq 0.001$). Further discussion will be confined to non-stepwise DSC. In general DSC was more successful at correctly classifying *S. hibernica* (97% success) than *S. aria* (86% success). The univariate F-ratios for differences between the groups for particular characters highlighted a number of the latter as being of particular differential importance (Table 3). Table 4 lists these characters in decreasing differential order together with their means and 95% confidence limits.

As can be seen from these two tables the single most important differential characteristic between

TABLE 2. EIGENVECTOR SCORES FOR AXIS 4 OF THE INITIAL PCA

OF *SORBUS* TAXA

Characters are numbered and abbreviated as in Table 1 above.

Character number and its abbreviation	Eigenvector
1. Angbotlf	0·018
2. Angbotrh	0·122
3. Angof3ve	-0·260
4. Angof4ve	-0·262
5. Angtoplfl	-0·125
6. Angtoprh	-0·084
7. Distbet34	0·472
8. Distbot3v	0·401
9. Distfrm3v	-0·134
10. Distteel	-0·148
11. Distteer	-0·162
12. Leafflen	-0·010
13. Leafwid	0·031
14. Leaflentwp	-0·039
15. Noveins	-0·448
16. Noteeto	0·273
17. Notthlhs	0·201
18. Notthrhs	0·233
19. Petlen	-0·031
20. Petwid	-0·040

S. hibernica and *S. aria* is the number of secondary veins (character 15); there being an average 22 secondary veins in *S. aria* and 18 in *S. hibernica*. As the distance between the third and fourth veins is not significantly different between the two groups (character 7, Table 3) and therefore the vein spacing over the whole leaf is likely to be similar, then it is unsurprising to find that the leaves are significantly smaller (on average over 1 cm shorter) in *S. hibernica* than *S. aria* and that the third vein from the base is closer to the apex in *S. hibernica* than *S. aria*. Table 4 also shows that the smaller leaves of *S. hibernica* are borne on significantly shorter petioles (character 19), have rather more steeply rising veins (characters 3 & 4) but fewer leaf teeth (character 17).

So far this analysis has been concerned with differences between individual *Sorbus* plants and implicitly populations. As *S. hibernica* is reputedly apomictic it might be expected that the most morphologically similar trees would be in closest physical proximity to one another. Equally if apomixis in *S. hibernica* is not obligate it might also be expected that a regional analysis would show greater similarity between *S. aria* and *S. hibernica* and possibly intermediates where the ranges of the species overlap. The above data were therefore amalgamated on a vice-county basis and vice-county means used to calculate a PCA. Plots of plants against the four significant axes whose eigenvalues exceeded Frontier's criteria are shown in Fig. 3.

As can be seen from Fig. 3 there is almost complete separation between *S. aria* and *S. hibernica* in most plots – examination of these makes it clear that this is largely due to the scores for these species on Axis 1. Indeed the separation between *S. aria* and *S. hibernica* would be perfect if it were not for a single *S. hibernica* point. The data from which this point are derived relate to the only collection available of *S. hibernica* from County Meath. Further examination of this specimen (DBN), which is sterile, shows that there has been doubt expressed about its status, with D. Synnott, the original collector identifying it as *S. aria* and D. A. Webb as *S. hibernica*. The specimen is undoubtedly unusual with a mixture of characters of *S. hibernica* and *S. aria* – the somewhat upswung leaf-teeth, very dense indumentum, with the leaf veins rising at a steep angle (c. 43°) of *S. hibernica*, combine with a leaf blade of c. 11 cm, bearing 21 secondary veins, a petiole 1·7 cm long and ≥ 51 leaf teeth on the left-hand side of the leaf blade. Quite obviously it would be possible to view this unique specimen as indicating either a hybridisation event linking *S. aria* and *S. hibernica*, or as an aberrant member of either species: the available evidence does not easily allow a decision to be made on this question. In the

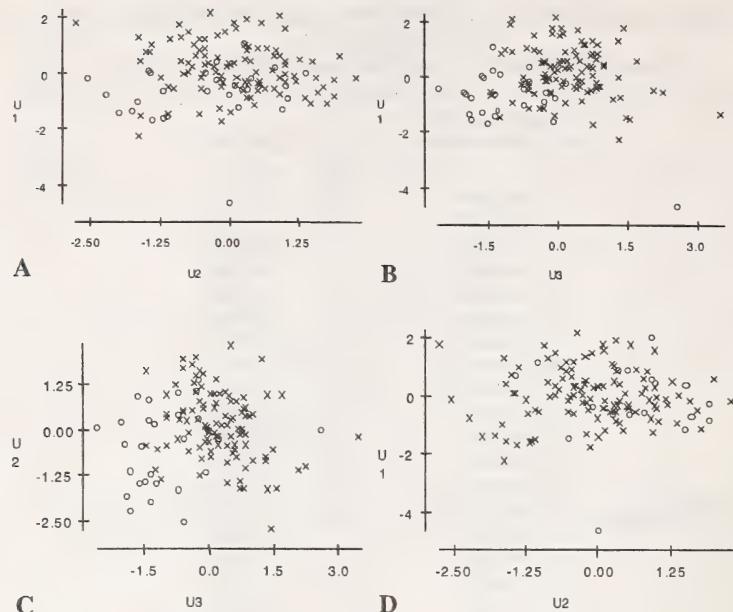


FIGURE 2. PCA plots showing the position of *S. aria* (o) and *S. hibernica* (x) for various combinations of PCA axes 1–3 (U1–U3). Axis 1 accounts for 29·9%, Axis 2 for 16·6% and Axis 3 for 12·8% of the variance respectively. In Fig. 2 D *S. hibernica* populations from v.cc. H15, 16 & 17, South-east, West and North-east Galway, are distinguished by (o), all other material is symbolised by (x).

TABLE 3. F-VALUES FOR A ONE-WAY ANOVA FOR PARTICULAR CHARACTERS MEASURED ON SPECIMENS OF *S. ARIA* AND *S. HIBERNICA*
Character numbers are as in Table 1 (d.f. = 1, 130). All F-values $\geq 3\cdot84$ are significant at $p \leq 0\cdot05$. F-values significant at $p \leq 0\cdot001$ are highlighted, by three stars.

Character number and its abbreviation	F-value
1. Angbotlf	0·01
2. Angbothr	2·08
3. Angof3ve	27·03***
4. Angof4ve	27·61***
5. Angtoplfl	0·36
6. Angtoprh	29·66***
7. Distbet34	2·62
8. Distbot3v	0·00
9. Distfrm3v	33·20***
10. Distteel	0·00
11. Distteer	0·01
12. Leaflen	25·24***
13. Leafwid	7·14
14. Leaflentwp	2·45
15. Noveins	58·67***
16. Noteeto	4·41
17. Notlhls	13·94***
18. Notthrhs	9·28
19. Petlen	35·95***
20. Petwid	0·67

TABLE 4. MEAN VALUES FOR CHARACTERS WHOSE UNIVARIATE F-RATIOS INDICATE A SIGNIFICANT DIFFERENCE AT $P < 0.001$ BETWEEN *S. aria* AND *S. hibernica* TOGETHER WITH THEIR 95% CONFIDENCE LIMITS, PRESENTED IN DECREASING ORDER OF F-VALUE

Character number and its abbreviation	F-value	Mean \pm 95% confidence limits for <i>S. aria</i>	Mean \pm 95% confidence limits for <i>S. hibernica</i>
15. Noveins	58.67	22.1 \pm 1.2	18.3 \pm 0.4
19. Petlen	35.95	1.8 \pm 0.1	1.4 \pm 0.07
9. Distfrm3v	33.20	8.3 \pm 0.5	6.7 \pm 0.3
6. Angtphrh	29.66	50.0 \pm 1.8	56.0 \pm 1.0
4. Angof4ve	27.61	48.6 \pm 2.5	43.4 \pm 0.8
3. Angof3ve	27.03	50.5 \pm 3.1	44.1 \pm 1.0
12. Leafflen	25.24	9.9 \pm 0.6	8.4 \pm 0.3
17. Notthlhs	13.94	50.5 \pm 3.8	43.5 \pm 1.7

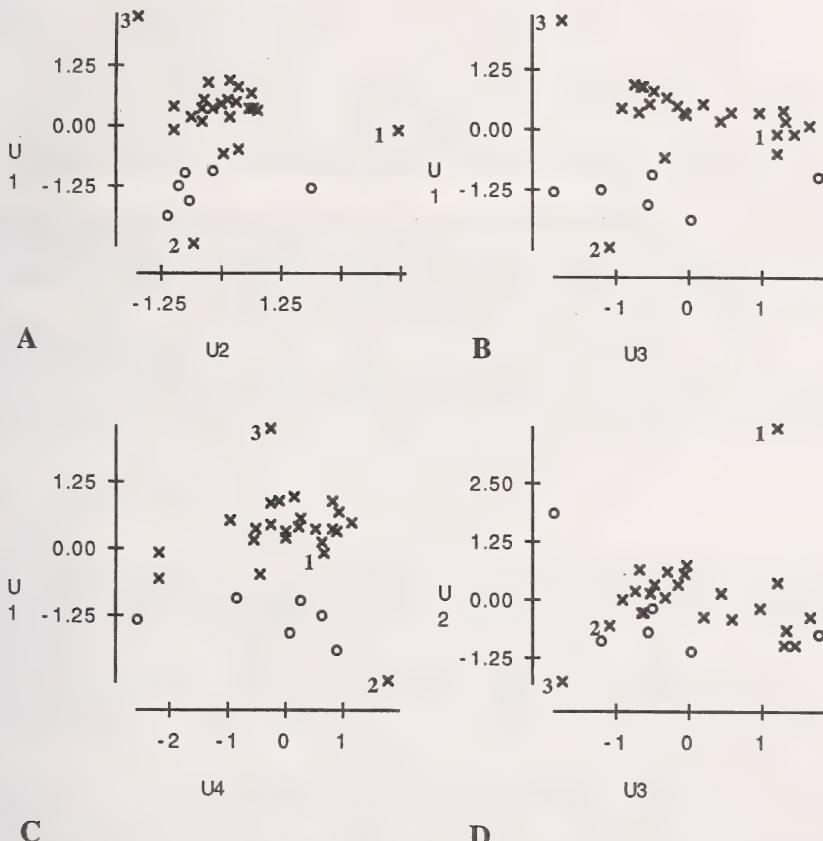


FIGURE 3. PCA plots of Axes 1–4 (U1–U4) for an analysis of individuals of *Sorbus* (*Sorbus aria* (o) and *Sorbus hibernica* (x)). Axis 1 accounts for 32.6%, Axis 2 for 17.2%, Axis 3 for 15.1% and Axis 4 for 10.1% of the total variance. Material from v.c. H2 North Kerry, from v.c. H22 Meath and from v.c. H26 East Mayo are indicated by the numbers 1–3 respectively placed to the immediate left of the appropriate symbol.

TABLE 5. MEAN VALUES FOR CHARACTERS WHOSE UNIVARIATE F-VALUES INDICATE SIGNIFICANT DIFFERENCES AT $P \leq 0.001$ BETWEEN VICE-COUNTY MEAN VALUES FOR *S. aria* AND *S. hibernica* TOGETHER WITH THEIR 95% CONFIDENCE LIMITS, PRESENTED IN DECREASING ORDER OF F-VALUE

Character number and its abbreviation	F-value	Mean \pm 95% confidence limits for <i>S. aria</i>	Mean \pm 95% confidence limits for <i>S. hibernica</i>
15. Noveins	51.75	22.8 \pm 1.2	18.3 \pm 0.6
17. Notthlhs	34.91	55.8 \pm 7.3	43.2 \pm 1.7
19. Petlen	32.01	1.9 \pm 0.2	1.4 \pm 0.1
9. Distfrm3v	28.02	8.3 \pm 0.5	6.6 \pm 0.3
12. Leaflen	23.06	10.0 \pm 0.6	8.3 \pm 0.3
13. Leafwid	17.97	6.5 \pm 0.4	5.6 \pm 0.2
18. Notthrhs	9.64	53.6 \pm 7.0	45.4 \pm 2.4

circumstances it may be most useful to accept that this specimen is not determinable at present and that therefore, from the perspective of describing the core characteristics of the species, it is best to lay it to one side. In fact by trial and error it was found that removal of this single point had very little effect on the scatter diagrams produced by PCA and those produced where the specimen had been removed are therefore not reproduced here. DSC analysis of the data, after removal of the aberrant Meath specimen, produced a similar result to that seen before, though naturally less importance should be attached to the values obtained through this analysis as they are based on vice-county means and exclude the, perhaps critical, Meath specimen (Table 5).

Though Table 5 indicates that this DSC gave results broadly similar to the previous analysis shown in Table 4, it is of interest that the new analysis indicates that leaf width is also a taxonomically useful feature enabling distinction to be made between *S. aria* and *S. hibernica* and that the angles that the secondary veins make with the midrib are less diagnostically important.

Further examination of Figs 2 D & 3 showed no evidence whatsoever for a closer morphometric linkage in the variation pattern of *S. hibernica* within a vice-county or for adjacent vice-counties than between geographically remote vice-counties (e.g. note Kerry, Mayo and Meath (nos 1–3 in Fig. 2) are obviously well separated from the rest of the *S. hibernica* records from their province and the wide spread of points in Fig. 2 D for material from Galway).

CONCLUSIONS

The above data analyses clearly show that it is possible to use a range of characters to distinguish *S. aria* from *S. hibernica* and that *S. devoniensis* is relatively easily distinguished from other *Sorbus* species in Ireland. The analyses have indicated a number of extra differential morphological characters, which are particularly useful for distinguishing sterile material. In particular it is clear that the number of teeth on the leaf, the angle of the secondary veins with the midrib and the length of the petiole are useful differential characteristics enabling *S. aria* to be distinguished from *S. hibernica*. It is clear that there are still difficulties associated with differentiation of material but these new characters allow most specimens to be determined without much error or difficulty.

The difficulty experienced in relation to assignment of specimens to either *S. aria* or *S. hibernica* is of relevance to the question of the level, if any, of outcrossing in the polyploid microspecies discussed by Proctor, Proctor & Groenhof (1989). It is clear that there are examples listed by Richards (1975) of apparent hybridisation between *S. aria* and various polyploid microspecies and it may well be that the difficulties faced in this work have arisen in part due to a rare hybridisation event(s).

One of the surprises of this work was the similarity in relative variability of the two species, or occasionally the greater degree of relative variability in *S. hibernica* as compared to *S. aria*. For

example the percentage coefficient of variation is 12% and 13% respectively for the number of veins in *S. aria* and *S. hibernica* and the corresponding figures are 18% and 24% respectively for petiole length. This seems to indicate that the assumption in the literature that *S. aria* is a relatively variable species is false, at least in Ireland. Experimental investigation by us of the breeding system of *S. hibernica* has so far proved inconclusive, but if outbreeding does occasionally occur in *S. hibernica* it may go some way towards explaining the relatively high degree of variability in that species.

Webb & Scannell (1983) speculate on the origin of some of the *S. aria* material in East Connaught (East of Galway), which is the main centre of distribution of this species in Ireland. They draw attention to the fact that some of this material may be derived from introductions or plantings. However, after considerable discussion they accept that the species is native. Scannell & Synnott (1987) draw attention to the fact that material in v.c. H21 (Co. Dublin) is probably introduced. However of the four localities cited (Doogue *et al.* (unpublished)), two are in hedgerows, are probably bird-sown and are not clearly non-native. Indeed none of the *S. aria* specimens in our survey appear to have been clearly planted or derived from planted material; however, the possibility remains that much Irish material has been derived from a relatively few introductions, which in turn could explain the relatively low variability of this species in Ireland.

Evidently further work is needed on *S. hibernica* to confirm its apomictic nature and also to look more closely at its relationship to other Irish and, eventually, British material. DNA sequencing, which we intend to commence soon, is likely to be able to resolve these difficulties but such work, interesting though it may well be, is not going to alter the difficulties experienced by field-workers: therefore more biometric work on this complex is required.

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J. E. Dandy & G. Taylor's unpublished study of *Potamogeton × sudermanicus* Hagstr. in Britain, with an account of the current distribution of the hybrid

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ABSTRACT

In 1942 J. E. Dandy & G. Taylor prepared an account of *Potamogeton × sudermanicus* (*P. acutifolius* Link × *P. berchtoldii* Fieber), a hybrid they reported as new to the British Isles on the basis of specimens collected near Wareham in Dorset (v.c. 9). The paper was intended for the *Journal of botany* but the journal ceased publication before it could appear. The text of the paper is published here for the first time. The hybrid was first collected in the Wareham area by J. H. Salter in 1920 or 1921. Recent surveys show that the hybrid is more frequent than *P. acutifolius* and grows in the absence of *P. berchtoldii*.

KEYWORDS: *Potamogeton acutifolius*, *P. berchtoldii*, Potamogetonaceae, vegetative reproduction.

INTRODUCTION

Our current understanding of the genus *Potamogeton* in the British Isles rests on foundations laid by J. E. Dandy and G. Taylor, colleagues at the Natural History Museum, London, who collaborated closely on taxonomic studies of the genus from the mid 1930s until Taylor left the Museum for Kew in 1956. One result of their work was a series of papers in the *Journal of botany* entitled "Studies of British Potamogetons", 18 of which were published between 1938 and 1942. In our view, these papers represent "one of the most critical and scholarly contributions made this century to the taxonomic study of the British flora" (Preston 1995a). This series of papers stopped abruptly when the *Journal of botany* ceased publication in 1942.

In 1985 C.D.P. visited Sir George Taylor, who generously lent him a copy of the manuscript monograph *The British species of Potamogeton L.*, which Dandy & Taylor had prepared but never published, together with other associated papers. Included amongst the latter was the completed typescript of a 19th paper in the "Studies of British Potamogetons" series. This paper covers *Potamogeton × sudermanicus* Hagstr., the hybrid between *P. acutifolius* Link and *P. berchtoldii* Fieber, and was virtually ready for publication when the *Journal of botany* folded. The hybrid had been detected by Dandy & Taylor from herbarium specimens collected near Wareham in Dorset (v.c. 9). It still survives in this locality, but has not been found elsewhere in Britain. The record of *P. × sudermanicus* was published by Good (1948) and included in Dandy's (1975) treatment of the British hybrids.

In this paper we publish the text of Dandy & Taylor's paper, which still merits publication for its treatment of the history and taxonomy of *P. × sudermanicus* in Britain (a striking illustration of the long shelf life of taxonomic publications). It is also of historical interest as a fine example of the work of Dandy & Taylor. Finally, the belated publication of this paper is an appropriate way to mark the 60th anniversary of the start of the "Studies of British Potamogetons" series in 1938.

We have ourselves been interested in the hybrid *P. × sudermanicus* for some years, making repeated

visits to the Wareham area to study its distribution in relation to that of its parents. We therefore follow Dandy & Taylor's paper with an updated account of the distribution of the hybrid in Dorset.

DANDY & TAYLOR'S UNPUBLISHED STUDY

THE TYPESCRIPT

The paper on *P. × sudermanicus* was initially numbered "Studies of British Potamogetons. – XVII", showing that it was written before the publication of Studies XVII and XVIII. In the event Studies XVII and XVIII were taken up with papers furthering the controversy between Dandy & Taylor and Professor J. W. Heslop Harrison, which appeared in the issue of the *Journal of botany* intended for publication in July 1942 (although not published until April 1944). Although the typescript is not explicitly dated, there is strong internal evidence that the copy in Taylor's possession was typed between June and October 1942. It discusses the collections of *P. × sudermanicus* made by F. C. Steward in June 1942, but details of his collections made in October 1942 are added in handwritten annotations. Further evidence comes from the fact that the typed phrase "This year..." has been altered twice by hand, initially to "Last summer..." and then to "In 1942...".

There is little doubt that the collapse of the *Journal of botany* was the main reason why Dandy & Taylor's 19th Study was never published. The *Journal of botany* had become closely associated with the Botany Department of the British Museum (Natural History) during the long period (1880–1924) when it was edited by James Britten, and it came to serve in place of an official periodical (Stearn 1981). John Ramsbottom, the Museum's Keeper of Botany, took over the editorship in 1938. The burden of running the Department of Botany in wartime must have been considerable, but in 1985 Taylor still blamed Ramsbottom's laziness for the collapse of the *Journal*. Ramsbottom had many gifts but his fellow mycologist G. C. Ainsworth (1986) noted that "to exasperate people by procrastination was an integral part of his character".

Letters from Taylor to Dandy now held in the manuscript collection of the Natural History Museum (DF440/63) show that Taylor pressed Dandy to publish the note on *P. × sudermanicus* after 1942, initially with papers on *P. × suecicus* published in the *Transactions of the Botanical Society of Edinburgh* (Bance 1946; Dandy & Taylor 1946). On 20 May 1945 Taylor wrote to Dandy and after discussing the *P. × suecicus* papers added "We might also put in the paper on *sudermanicus* if you can lay hands on it". On 3 July 1945 he reverted to this suggestion: "There should be no difficulty in getting the *suecicus* papers to [H.R.] Fletcher by the end of September. Do you think that we could plug in another paper of Pot records at the same time? He seems quite keen to have them and here is a grand opportunity for a grand slam. What about the *sudermanicus* effort as well? I do realize how much work will be required to prepare all these for publication but if you can let me know how I can help I shall gladly do so." Both *P. × suecicus* papers were read by title at a meeting of the Botanical Society of Edinburgh on 13 June 1946 and subsequently published. Another paper by Dandy & Taylor, "New and interesting British records of *Potamogeton*", was read by title on 15 May 1947, usually a formal prelude to publication, but it never appeared in print. On 13 June 1947 Taylor forwarded to Dandy some photographs of the leaves of *P. acutifolius* and *P. × sudermanicus* taken by Miss H. M. Bance, who had undertaken anatomical studies of *P. × suecicus* at Taylor's behest, but he clearly failed to prompt Dandy into the work needed to complete the paper on this hybrid.

The typescript of the unpublished study is marked up with corrections in Dandy's hand and some more tentative comments by Taylor. Our aim is to print it as Dandy & Taylor intended to publish it, incorporating the corrections made by Dandy. We have incorporated minor rewording without comment, but have drawn attention to some more significant changes or annotations as numbered notes. These changes show, for example, how the austere and authoritative style of the Studies was achieved by the ruthless excision of material of a more speculative nature. We have also added some other explanatory notes. We have retained the typographical conventions of the 1940s, e.g. the placement of the hybrid sign × before the generic name, to maintain conformity with the other papers in the series.

Sir George Taylor died in 1993 and his books and papers were bequeathed to the National Library of Scotland (accession no. 9533). The manuscript published here was presumably amongst them, but Taylor's manuscripts have not yet been catalogued and in any event all manuscripts held by the National Library are currently unavailable because of building work.

TEXT OF THE STUDY

The text of the study is as follows:

STUDIES OF BRITISH POTAMOGETONS. – XIX.

BY J. E. DANDY, M.A., AND G. TAYLOR, D.Sc.

XIX. \times *POTAMOGETON SUDERMANICUS* IN BRITAIN.

Hybrids between the "pusilloid" (linear-leaved) species of *Potamogeton* are remarkably rare when we consider the comparative frequency with which some of the broad-leaved species interbreed¹. It is true that Hagström in his 'Critical Researches' recognized eleven hybrid combination of "pusilloid" species in Europe, but some of the plants which he treated as hybrids are without doubt only states of species; and of the British plants identified in print as "pusilloid" hybrids by Hagström, A. Bennett, and others not one is of hybrid origin. Nevertheless genuine hybrids between "pusilloid" species do occasionally occur in Britain, as elsewhere, and one of them forms the subject of the present note².

In working through the pondweeds of the Druce Herbarium, Oxford, we came across an unidentified specimen from the Wareham district of Dorset which might at first sight have passed for a broad-leaved state of *P. Berchtoldii* but for the obvious strong compression of the stem and the presence of a fruiting-carpel of too large size. On examining the specimen more closely we found that the leaves have, besides the usual three vascular nerves, an irregular number of fine (often broken) sclerenchymatous nerves of the type which characterizes the leaves of *P. acutifolius* and *P. compressus*. The presence of these nerves, in association with a strongly compressed stem, at once suggested a hybrid of *P. Berchtoldii* with *P. acutifolius*, which occurs in the Wareham district whereas *P. compressus* does not. Further investigation of other characters showed the plant to be in all respects intermediate between *P. acutifolius* and *P. Berchtoldii*. For example, the fruiting-carpel (the only one developed, and possibly not fertile, is midway in size and form between the two species³. The stipular sheaths are open and convolute as in both *P. acutifolius* and *P. Berchtoldii*. Thus the morphological evidence convinces us that the plant is a hybrid between these species, a conclusion which is supported by the fact that both have been collected in the neighbourhood of Wareham.

The plant under discussion was collected by Mr. A. W. Graveson about 1927 in the ditches of the water-meadows near Redcliff Farm⁴, south-east of Wareham. In 1942, hearing that Dr. F. C. Steward intended to visit Dorset in June, we requested him to search for the plant: on being given details of the locality he succeeded in collecting a good series of specimens, though unfortunately these were not in flower⁵. In October he paid another visit to the place and obtained further specimens, again sterile but this time bearing winter-buds intermediate between those of the parent species⁶.

Highly interesting as it is, this hybrid between *P. acutifolius* and *P. Berchtoldii* is not new to science. It was described from Sweden by Hagström in his 'Critical Researches', p. 73, fig. 28 A–E, under the name \times *P. sudermanicus* and with the formula *P. acutifolius* \times *pusillus* (his "*P. pusillus*" being *P. Berchtoldii*). Hagström's description and figures agree well with the Dorset plant except that the peduncles of the Swedish plant are given as only 6–8 mm. long as against 24 mm. in Mr. Graveson's specimen, while the spikes are described as entirely barren whereas, as we have already mentioned, a single fruiting-carpel is present in the material from Dorset. This solitary fruiting-carpel may, however, be a chance development such as we have observed occasionally in such sterile hybrids as \times *P. fluitans*, \times *P. nitens*, and \times *P. sparganifolius*⁷. The longer peduncles of the Dorset plant is also without significance as its length comes well within the limits of variation to be expected from the character of the parent species.

\times *P. sudermanicus* was named after Sudermania, in Sweden, where the type was collected in 1831. The type-locality, as Hagström remarked in describing the hybrid, is at the most northern border of the distribution area of *P. acutifolius*. He added that the plant probably belongs to the greatest rarities of the vegetable kingdom, and this may well be true despite the discovery of the Dorset station⁸.

Mr. Graveson's specimen apparently ranks as the first authentic record of \times *P. sudermanicus* from the British Isles, an earlier record for East Sussex being an error⁹. The Sussex plant, which was collected near Camber Castle, Icklesham, by C. E. Salmon in 1900, is quite normal *P. pusillus*, and its

treatment as $\times P. sudermanicus$ by Bennett in Journ. Bot. Ix. 55 (1922) is inexplicable as its stipular sheaths are of course tubular, whereas those of $\times P. sudermanicus$ and both its parent species are open. This erroneous record of $\times P. sudermanicus$ has been repeated in other works including the 'London Catalogue', Ed. 11 (1925), p. 46; Druce's 'British Plant List', Ed. 2 (1928), p. 117; and Wolley-Dod's 'Flora of Sussex' (1937), p. 465. It was referred by us to $P. pusillus$ in our note on that species (Journ. Bot. Ixxviii. 5) in 1940.

Following is the brief synonymy and distribution of $\times P. sudermanicus$ as a British plant.

P. ACUTIFOLIUS \times BERCHTOLDII =

$\times P. SUDERMANICUS$ Hagstr. Crit. Res. 73, fig. 28 A-E (1916)¹⁰.

$P. acutifolius \times pusillus$ Hagstr. op. cit. 73 (1916).

We have seen specimens from only one vice-county:-

(9) DORSET. Ditches in water-meadows near Redcliff Farm, Arne, c.1927, A. W. Graveson, Ref. 5 (Herb. Druce); June and Oct. 1942, F. C. Steward (Herb. Brit. Mus.).

NOTES

1. The sentence "The reason may well be that the "pusilloid" species depend more on vegetative winter-buds than on seeds for their reproduction." and Taylor's addition "and many are shy flowerers" follow this sentence but have been enclosed in square brackets, apparently to denote that they should be deleted.

The following paragraph, in Taylor's handwriting, is attached to the copy of the $P. \times sudermanicus$ typescript and also deals with this issue; it is not clear where, if anywhere, Taylor intended it to be inserted.

"[It is not] easy to understand why there should be apparent antipathy between closely allied species which grow in close association and in such circumstances frequently produce an abundance of fruit. Whether these fruits are viable or not is a matter for experiment or observation in the field but, in addition to possible increase by germination, the pusilloid species always provide for perpetuation by vegetative means: Fernald, indeed, has suggested that winter buds "are the usual, if not the only, means of reproduction". As the plants mature, whether they have fruited or not, they invariably produce winter-buds. In many situations pusilloid species are shy in[?] flowering and depend on vegetative propagules for their survival."

The first words in the paragraph are illegible on my photocopy and the material in square brackets is my interpolation. Taylor's quotation is taken from Fernald (1932, p. 21).

2. The other British pusilloid hybrids are $P. acutifolius \times friesii$, described as $P. \times pseudofriesii$ by Dandy & Taylor (1957), and $P. pusillus \times trichoides$, described as $P. \times grovesii$ by Dandy & Taylor in Sell (1967).

3. Dandy had marked this sentence by a line in the margin and added a question mark.

4. The spelling Redcliff was the norm when Dandy & Taylor wrote, although Redcliffe appears on modern maps.

5. The phrase "In 1942" originally appeared as "This year" and then as "Last summer". The phrase "On being given details of the locality ..." replaces "He responded with enthusiasm, and having obtained details of the locality from Mr. Graveson ...".

6. This sentence is a manuscript addition in Dandy's hand.

7. The first half of this and the second half of the preceding sentence have been marked with a double line in the margin and Taylor has commented "? Simpson's specimen". This presumably refers to a specimen of $P. \times sudermanicus$ collected by N. D. Simpson on 27 June 1945 and now in BM which also bears an enlarged carpel. The occasional development of swollen carpels resembling immature fruits is a feature of the Wareham population of $P. \times sudermanicus$ (Preston 1995b).

8. For a summary of subsequent records of $P. \times sudermanicus$ in Europe, see Ploeg (1987). The hybrid has been recorded from England, the Netherlands and Sweden; a more tentative report from Germany requires confirmation.

9. In 1973 Dandy determined as $P. \times sudermanicus$ a specimen collected as $P. acutifolius$ from Stoborough Meads by J. H. Salter in 1920 or 1921 (NMW), which predates Graveson's specimen.

10. The reference is to Hagström (1916).

MORPHOLOGY OF *P. \times sudermanicus*

A description and illustration of *P. \times sudermanicus*, based on studies of living plants and herbarium material from the Wareham population, has already been published (Preston 1995b) and need not be repeated here. Two aspects can, however, be elaborated. In studies of the living plant it became clear that the compression of the stems of the hybrid forms a useful quantitative character to distinguish it from both *P. acutifolius* (which has strongly compressed to flattened stems) and *P. berchtoldii* (which has terete to slightly compressed stems). This conclusion was based on measurements of the longest and shortest axes of the stems of all three species in cross section. These data are summarised in Table 1 and illustrated in Fig. 1. The hybrid is also intermediate in floral characters between *P. acutifolius* (which usually has one carpel per flower) and *P. berchtoldii* (which usually has 4–5), as demonstrated by the data in Table 2. *P. compressus*, which is closely related to *P. acutifolius*, usually has two carpels.

TABLE 1. COMPRESSION OF STEMS OF *POTAMOGETON ACUTIFOLIUS*, *P. BERCHTOLDII* AND THEIR HYBRID *P. \times SUDERMANICUS*

Taxon	Number of stems examined	Stem compression	
		Mean	Range
<i>P. acutifolius</i>	25	3.8	2.8–4.7
<i>P. \times sudermanicus</i>	43	2.0	1.6–2.4
<i>P. berchtoldii</i>	32	1.4	1.0–1.6

Stem compression is the ratio of the longest to the shortest axis of the stem in cross-section, measured on fresh plants. Based on material of *P. acutifolius* from Dorset, Norfolk and Sussex, *P. berchtoldii* from a range of sites in the British Isles and *P. \times sudermanicus* from Dorset.

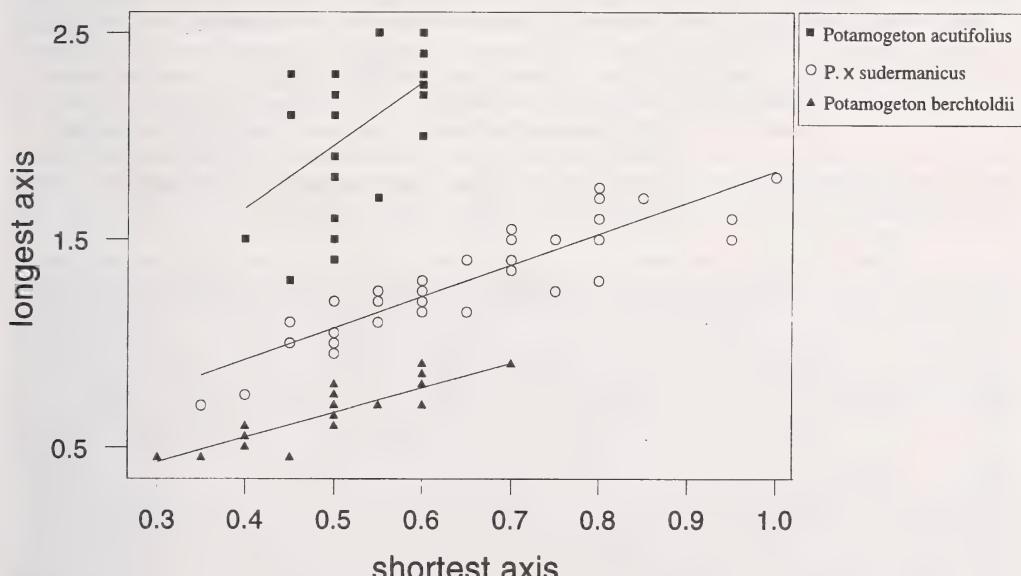


FIGURE 1. Stem compression of *P. acutifolius*, *P. berchtoldii* and their hybrid *P. \times sudermanicus*. The dimensions of the longest and shortest axes of the fresh stems (mm) were measured in cross sections of fresh material of *P. acutifolius* from Dorset, Norfolk and Sussex, *P. berchtoldii* from a range of sites in the British Isles and *P. \times sudermanicus* from Dorset. Regression lines are shown for *P. acutifolius* ($r^2 = 0.26$), *P. \times sudermanicus* ($r^2 = 0.78$) and *P. berchtoldii* ($r^2 = 0.77$).

TABLE 2. NUMBER OF CARPELS IN THE FLOWERS OF *POTAMOGETON ACUTIFOLIUS*, *P. BERCHTOLDII* AND THEIR HYBRID *P. × SUDERMANICUS*

Taxon	Number of flowers examined	Number of carpels per flower						
		1	2	3	4	5	6	7
<i>P. acutifolius</i>	19	19	0	0	0	0	0	0
<i>P. × sudermanicus</i>	59	12	36	10	1	0	0	0
<i>P. berchtoldii</i>	89	0	0	6	64	16	2	1

Based on material of *P. acutifolius* from Dorset and Norfolk, *P. berchtoldii* from a range of sites in the British Isles and *P. × sudermanicus* from Dorset. The data for *P. × sudermanicus* exclude one malformed flower with four carpels and eight stamens.

per flower, though a minority of flowers have one (Charlton & Posluszny 1991). The presence in *P. × sudermanicus* of a substantial minority of flowers with a single carpel perhaps provides morphological evidence for the fact that *P. acutifolius* rather than *P. compressus* is one parent, and thus supports a conclusion reached by Dandy & Taylor on geographical grounds alone.

DISTRIBUTION OF *P. × SUDERMANICUS* AND ITS PARENTS IN DORSET

All records of *P. × sudermanicus* in Britain are from ditches in grazing marshes by the River Frome south of Wareham. The earliest known specimen was collected from "Stoborough Meads, Wareham" by J. H. Salter (NMW). Salter's natural history diaries, now in the National Library of Wales at Aberystwyth (NLW MS 14444B), throw some light on the discovery of the hybrid. Salter visited Wareham on 6 September 1920, "with a special view to the old marsh ditches". On leaving Wareham, he "took the path alongside the river for Redcliff. Close to Redcliff Farm I turned into the Stoborough Meads and at once found the long-looked-for *Potamogeton acutifolius* in great plenty". On 9 August 1921 he returned "by first train to Wareham to have a good hunt for water plants in the old ditches". After visiting ditches north of the town he made for Ridge. "As I followed the path alongside the riverside to Redcliff I saw plenty more *Juncus obtusifolius* in the overgrown ditch on the right. I diverged into the meadows, but this time saw only a little *Potamogeton acutifolius* and that not in flower or fruit." Salter's specimen, labelled "*P. acutifolius*" but actually *P. × sudermanicus*, is dated 1921. It is, however, a flowering specimen which suggests that he may have collected it in 1920, the year he first saw the plant.

A. W. Gravesen collected specimens of *P. × sudermanicus* from "ditches of Stoborough water meadows near Redcliff" on 14 September 1928 (OXF, fide Dandy's card index at BM). The fact that both Salter and Gravesen unwittingly collected *P. × sudermanicus* near Redcliffe Farm in the 1920s suggests that it was already well established by then. F. C. Steward's specimens collected in June and October 1942 are labelled "drainage-ditch in water-meadows near Redcliff Farm, Arne". N. D. Simpson collected the hybrid from shallow ditches at "Stoborough Meadows" on 27 June and 31 October 1945, A. H. G. Alston gathered it "near Redcliff Farm" on 26 May 1946 and Taylor made a copious collection "near Redcliff Farm" on 17 August 1946; all these collections are in BM but duplicates of Alston's and Taylor's were distributed to numerous other herbaria. All these specimens may have been collected from the same area. A map on the reverse side of N. D. Simpson's collecting stub for collection 45050 (BM) shows that he gathered *P. × sudermanicus* on 27 June 1945 from the straight ditch running west from Redcliffe Farm; he had collected *P. acutifolius* on 5 June 1945 from another ditch in this area west of the Farm. Writing to J. E. Dandy on 2 August 1945, Mrs W. B. Watt also described a site for *P. × sudermanicus* which must lie west of the Farm and south of the River Frome. This area is also shown on a map tipped into the *P. × sudermanicus* pages of G. Taylor's typescript of the monograph of *Potamogeton* he drafted with Dandy. It seems likely that all the early collections of the hybrid were made in the area west of Redcliffe Farm, where it still grows with *P. acutifolius* (Fig. 2).

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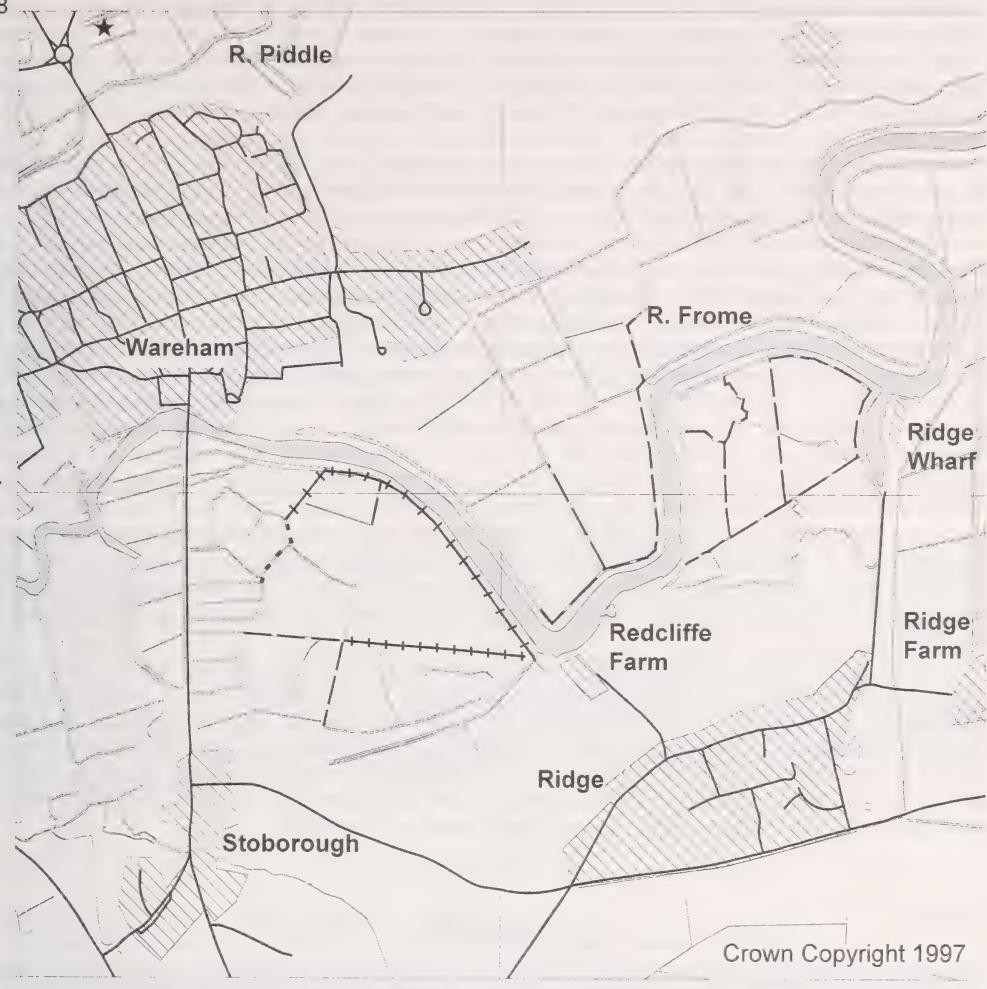


FIGURE 2. The distribution of *P. acutifolius*, *P. berchtoldii* and their hybrid *P. \times sudermanicus* in the area south-east of Wareham, as recorded between 1987 and 1997. Ditches in which *P. acutifolius* has been recorded in the absence of *P. \times sudermanicus* are shown by short dashes (- - - - -), those in which *P. acutifolius* and *P. \times sudermanicus* have been recorded are shown by a hatched line (- + + + +) and those in which *P. \times sudermanicus* has been recorded in the absence of *P. acutifolius* are shown by long dashes (— — —). The only locality for *P. berchtoldii* is denoted by a star (★). The grid lines are 1 km apart and the relevant eastings and northings are shown; the entire area lies within 10-km square SY/9.8.

Fieldwork between 1987 and 1997 has established that *P. \times sudermanicus* can usually be found both west and east of Redcliffe Farm south of the River Frome (Fig. 2). It grows in water 25–75 cm deep and of pH 7–8 in grazing marsh ditches. Like many aquatics, it may vary in quantity from year-to-year and it is sometimes abundant, especially in the meadows east of Redcliffe Farm. It may be the most numerous macrophyte in some lengths of ditch, either occurring as dense masses in well-vegetated areas or as scattered plants on the rather open substrate of ditches cleared out the previous year. Interestingly, specimens collected by N. D. Simpson on 31 October 1945 were "growing up out of the mud after partial clearing of the ditches". *P. \times sudermanicus* may grow in smaller quantity, sometimes as scattered plants amongst dense populations of *Elodea canadensis*, and it persists in shaded water

amongst dense stands of *Phragmites australis*. It often grows with *Callitricha* sp., *Eleogeton fluitans*, *Elodea canadensis*, *E. nuttallii*, *Lemna minor*, *L. trisulca*, *Potamogeton natans* and *Spirodela polyrhiza*; less frequent associates include *Alisma plantago-aquatica*, *Glyceria fluitans*, *Hydrocotyle vulgaris*, the aquatic variant of *Juncus bulbosus*, *Mentha aquatica*, *Persicaria amphibia*, *Potamogeton acutifolius*, *P. pectinatus*, *Ranunculus flammula*, *Sparganium emersum* and the moss *Fontinalis antipyretica*.

In 1996 Bryan Pickess reported a narrow-leaved pondweed from ditches north of the River Frome. Exploration of the site, an R.S.P.B. reserve, revealed that the plant was *P. × sudermanicus* and that it was widespread but not abundant in this area. This represents a new site for the hybrid, adjacent to the known sites but separated from them by the river. The ditches north of the Frome have a limited aquatic flora, and in many places they are almost choked by *Phragmites australis*. In 1997 *P. × sudermanicus* grew in the more open areas of the *Phragmites*-lined ditches, with only a few associates including *Elodea nuttallii*, *Lemna minor*, *L. minuta*, *L. trisulca* and *Persicaria amphibia*.

The putative parent *P. acutifolius* has a much more restricted distribution than *P. × sudermanicus* in the area (Fig. 2). We have consistently found it only in ditches west of Redcliffe Farm; repeated surveys of the ditches east of the Farm have failed to reveal it there. *P. acutifolius* formerly had a more widespread distribution in the Wareham area. Nineteenth century records indicate that it grew north of Wareham, between the railway station and the town, as well as in the area where it still occurs near Redcliffe Farm, south of the town. The meadows by the River Piddle north of Wareham still have a rich aquatic flora (despite the fact that they have been bisected by a major road) but *P. acutifolius* has not been seen here since 1921. Unfortunately, the historical records from the area near Redcliffe Farm are too imprecise to indicate the particular meadows in which the species grew, and we do not know whether it was formerly found east as well as west of Redcliffe Farm. The Wareham localities are the only ones recorded in Dorset for *Potamogeton acutifolius*, which is a rare species in Britain (Preston & Croft 1997).

P. berchtoldii is more common in Dorset and nationally than *P. acutifolius*. It has been recorded from the vicinity of the *P. × sudermanicus* sites in the past. It was collected from a "stream on the way to Ridge Farm, Wareham" in 1917 (BM) and from a "pool near Ridge" in 1934 (BM). D. A. Cadbury gathered specimens of *P. acutifolius* and *P. berchtoldii* in 1959 which are both labelled "ditch by R. Frome above Stoborough" but it is not clear whether they were growing in the same ditch. *P. berchtoldii* has not been collected subsequently in the immediate vicinity of *P. acutifolius* or *P. × sudermanicus*, but it still persists in several places north of Wareham.

DISCUSSION

The presence of *Potamogeton × sudermanicus* in the Wareham area since 1920 or 1921, when it was first collected by J. H. Salter, is a striking example of the local persistence of *Potamogeton* hybrids. It is particularly noteworthy that it has persisted in grazing marsh ditches. In this respect its history provides a contrast with *P. × lanceolatus* Sm., the hybrid between *P. coloratus* Hornem. and *P. berchtoldii*. This hybrid failed to persist in a ditch in Cambridgeshire where it was recorded once, in 1880, but has survived since the 19th century in three streams in western Ireland. Preston (1993) argued that as a sterile hybrid it might be more likely to persist in the open habitats provided along the beds of a stream or small river than in a ditch, where it could be eliminated by competition from emergent species during phases when the ditch becomes overgrown. Postcards of Wareham taken from Redcliffe which were published by the Dorset firm of Delpool in 1984 and 1987 (numbers WM-3 and WM-3(R)) show that the ditches in which *P. × sudermanicus* grows north of the river Frome and which are now narrow and colonised by abundant *Phragmites australis* have been broad and open in the past. The Dorset population of *P. × sudermanicus* is presumably dependent for its survival on the occasional clearing of the ditches in which it grows.

Another noteworthy feature of the distribution of the hybrid is that for much of its Dorset range it is present in the absence of both parents. It seems likely that the hybrid arose in a ditch where both parents grew at Wareham, rather than arriving by long-distance dispersal of pollen or seed. *P. berchtoldii* formerly grew in the Redcliffe Farm area although it has not been found there in recent years. It is possible that *P. × sudermanicus* first arose in the area where it still grows with *P. acutifolius* west of

Redcliffe Farm and attained its current distribution by spreading to the ditches east of the Farm and north of the River Frome. Another possibility is that *P. acutifolius* formerly grew in the ditches now occupied by the hybrid alone, but has contracted in distribution. In this case *P. × sudermanicus* might have arisen anywhere in this area, or indeed in more than one locality. Evidence from molecular studies, such as that obtained for the other rare Dorset *Potamogeton* hybrid, *P. × schreberi*, by Hollingsworth *et al.* (1995), might establish the relationship of *P. × sudermanicus* to the *P. acutifolius* plants currently present at Wareham and determine whether the hybrid is represented by one or more clones. Although it is clear that *P. × sudermanicus* normally reproduces vegetatively by turions, it would also be interesting to know whether the small fruits produced by occasional flowers of the hybrid are ever capable of germination.

Occasionally, *Potamogeton* hybrids may be found at sites where both parents are absent. *P. acutifolius* not only has a very restricted distribution in the Wareham area but is also much less frequent in those ditches where it does occur than it is at some sites in Sussex where it is present in abundance (Preston & Croft 1997). This suggests that we may be witnessing a late stage in the process by which a hybrid which has become established in the vicinity of its parents is then left alone following the disappearance of both parents from the locality.

ACKNOWLEDGMENTS

We are very grateful to Sir George Taylor for making his unpublished paper available to C.D.P. and for his permission to use this and other papers in our work on *Potamogeton*. A. O. Chater kindly extracted relevant passages from Salter's diaries, Mrs O. M. Geddes and H. J. Noltie gave us information about the current whereabouts of Sir George Taylor's papers, R. Vickery helped us with N. D. Simpson's papers at BM and Dr T. C. G. Rich provided details of herbarium material at NMW. Dr H. J. M. Bowen, J. Fant, Lady Rosemary FitzGerald, M. Gurney, Miss A. Horsfall, Dr A. E. Newton and Mrs A. V. Pearman joined us to search for *P. × sudermanicus* at Wareham, and J. Day and B. Pickess provided us with information on plants north of the River Frome and access to the R.S.P.B. reserve. We thank Dr & Mrs L. A. Boorman for translating passages from Ploeg (1987) and D. B. Roy and Miss A. Stewart for generating Figs 1 and 2 respectively.

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Genetic conservation of Black poplar (*Populus nigra* L.)

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ABSTRACT

Current interest in the conservation of *Populus nigra* L. (Black poplar) (Salicaceae) in Britain is set in a European context. A Black poplar network, set up under the European Forest Genetic Resources Programme, is described, and the reasons for choosing Black poplar as one of the first forest tree species to conserve are considered. The botanical status of Black poplar and its status in Britain are described, and against this background European and British strategies for genetic conservation of the species are discussed. Conclusions are drawn on the need to conserve the British native tree flora.

KEYWORDS: taxonomy, characteristics, status, Britain.

INTRODUCTION

The continued health of managed forests (i.e. virtually all European forests) depends on the availability of suitable genetic material. Genetic diversity allows organisms to adapt to changes in the environment, and to changing patterns of predation and pest attack, so the irretrievable loss of genetic diversity in forest trees reduces our ability to maintain healthy, vigorous forests in the future. Until recently, mankind has taken genetic diversity for granted, largely because the scale of our activities was not sufficient to pose a serious threat. This is no longer the case; natural populations of forest trees are under threat on a global scale. In Britain, only about 1% of our forests are classified as "ancient and semi-natural" (Peterken 1981) with native species occupying sites which have been under forest since at least 1600 A.D. This is the first place to look for natural genetic diversity, because plantation forests are likely to contain trees which have been selected for timber producing characteristics, and which may well have been imported from elsewhere in the world. So, in Britain, the genetic diversity of our native trees is undoubtedly threatened.

The European Forest Genetic Resources Programme (EUFORGEN) is a collaborative programme among European countries aimed at ensuring the effective conservation and sustainable utilization of forest genetic resources in Europe. It was established to implement Resolution 2 of the Strasbourg Ministerial Conference on the Protection of Forests in Europe in 1990. The programme of EUFORGEN operates through a small number of networks, and one of the first of these to be set up was the *Populus nigra* network (Frison *et al.* 1995). Fig. 1 illustrates a typical example of Black poplar. In setting about the genetic conservation of forest trees, it is perhaps surprising to find that Black poplar has been seen as a good place to start.

The reasons for choosing Black poplar are:

- a. Its natural habitat – the floodplain forest – has been widely cleared to provide productive agricultural land;
- b. Control of rivers is widespread, and this disallows the conditions necessary for natural regeneration;
- c. It is easy to propagate by cuttings;
- d. It is one parent of the commercially important hybrid *Populus × canadensis* (syn. *P. × euramericana* (Dode) Guinier) (*P. deltoides* × *P. nigra*);
- e. It is highly resistant to bacterial canker (*Xanthomonas populi*) and shows some resistance to other important diseases of poplar;
- f. On a European scale, poplar is highly significant economically. For example, in France, about 35% of all hardwood timber produced is poplar, although the species only occupies about 1% of the area of broadleaved woodland; and
- g. It is relatively easy to identify which trees to conserve.



FIGURE 1. Mature Black poplar (*Populus nigra*) growing at Crickhowell in South Wales (May 1994). This tree recently blew down and has been removed.

This last point requires some explanation. In the absence of clear information about the genetic make-up of a given population, and about the origins of these genes, it is difficult to be clear about whether the population is "native" or not. It is also difficult to define the boundaries of the block of genetic material which is to be conserved. The Common or Pedunculate oak (*Quercus robur*), for instance, presents a much more confused picture than Black poplar. Gardiner (1974), before DNA analysis was available, reviewed the evidence for and against the native status of the species, and of Sessile oak (*Q. petraea*). In his concluding remarks he indicated that Pedunculate oak has been planted in Scotland, and this has resulted in much introgression with the native Sessile oak, whilst in southern England it seems reasonable to suggest that both species are native. Using analysis of chloroplast DNA, Ferris *et al.* (1997) were able to distinguish an East Anglian population of Pedunculate oak from the many introduced specimens, and also found a marker which distinguished eastern and western European populations of both species of oak. This also showed that a number of very old oaks in Britain were in fact introductions from eastern Europe. The genetic diversity of our Common oak will therefore be difficult to conserve without first investigating its origins in detail using modern techniques of molecular genetics.

BOTANICAL STATUS

Populus nigra belongs to the family Salicaceae (poplars and willows). Within the genus *Populus*, it belongs to the section *Aigeiros* (Jobling 1990) along with *P. deltoides*, although study of the chemical composition of bud exudates has placed it in the section *Tacamahaca* (Greenway *et al.* 1990) along with *P. trichocarpa*. Varieties of *P. nigra* were listed by Zsuffa (1974), and the first two varieties distinguished (as recorded by that author) are:

Variety:

1. *P. nigra* var. *typica*
Schneid. (1904)

Synonyms:

P. nigra L. (1753), *P. nigra* Dode (1905), *P. europaea* Dode (1905), *P. nigra* var. *Dodeana* A. et G. (1908), *P. nigra* var. *europaea* A. et G. (1908)

2. *P. nigra* var. *betulifolia*
(Pursh) Torr. (1843)

P. hudsonica Michx. (1813), *P. betulifolia* Pursh. (1814),
P. pubescens Pursh (1814), *P. nigra* var. *viridis* (1838), *P. nigra*
var. *pubescens* Parl. (1867), *P. nigra* var. *hudsonica* Schneid.
(1904), *P. Henryana* Dode (1905), *P. vistulensis* Dode (1905),
P. vaillantiana Dode (1905), *P. Mulleriana* Dode (1905),
P. Lloydii Henry (1913).

"*P. nigra* var. *typica*" is no longer used, "*P. nigra* L." being used to describe the species as a whole. The accepted name for the second variety or subspecies listed above is now *Populus nigra* L. subsp. *betulifolia* (Pursh) Dippel. (Stace 1997), and this is the tree which is considered to be native in Britain. Throughout its world distribution (Fig. 2) *P. nigra* is typical of the alluvial forests of large European and Siberian rivers. According to Zsuffa (1974), subsp. *betulifolia* has been described in western Europe, especially in France and Great Britain, and "a pistillate form *P. Lloydii* Henry, is cultivated in England". Possession of the following characteristics distinguish Black poplar from its hybrids:

- a. Leaning trunk with large, swollen bosses;
- b. Deeply fissured dark bark;
- c. Absence of glands at leaf bases (of mature leaves);
- d. Presence of *Pemphigus* galls on the petioles;
- e. Complete resistance to mistletoe;
- f. Large, downward arching branches;
- g. Yellowish terete twigs, shining, becoming greyish; and
- h. Long reddish-brown buds curving outwards at the apex.

P. nigra subsp. *betulifolia* is distinguished by having hairs on the juvenile shoots, leaf petioles and midribs, and main flower stalk. The leaves are somewhat smaller (although leaf size varies on individual trees), and new growth is said to start earlier (Krüssman *et al.* 1986).

It remains to be seen if this subspecies can be clearly distinguished using DNA analysis. This will be important in the current context, as we will wish to know whether the British population (or the entire subspecies) should be conserved as something different and separate from *P. nigra* as a whole.

STATUS OF BLACK POPLAR IN BRITAIN

At about the time that the EUFORGEN Black Poplar Network was set up, concern for the future of *P. nigra* was growing in the UK (White 1993). It is no longer of importance in Britain as a timber tree



FIGURE 2. Natural world distribution of *Populus nigra* L. (after Zsuffa 1974).

in its own right, and it is so rare that it is no longer a generally recognised feature of our landscape. It certainly has been an important feature of certain landscapes – John Constable's famous painting “The Hay Wain” painted in 1821 shows mature Black poplars, and in all probability Black poplar was used in the manufacture of the hay wain itself. Serious recording of the distribution of Black poplar started with the Botanical Society of the British Isles (B.S.B.I.) survey in 1973 (Milne-Redhead 1990). Milne-Redhead records that the *Atlas of the British flora* (Perring & Walters 1962) recorded a confusion of Black poplar and poplar hybrids, and the survey set out to clarify the true distribution of Black poplar, with the assumption that the old Black poplars (>150 years old) were “native”. *The Flora of the British Isles* (Clapham, Tutin & Warburg 1987) records Black poplar as “Native. Along river valleys south of the Mersey and Humber, but only introduced in Cornwall and W. Wales...”. According to Milne-Redhead (1990), all the current population derives entirely from planted stock. This is because the establishment of Black poplar from seed requires the seed to fall on bare wet mud, soil or silt at the end of June, and the site has to remain bare and wet until leaf-fall in October. Such conditions have vanished with the taming of rivers and the conversion of floodplain forests to agriculture. However, the most obvious source of cuttings would have been pre-existing native trees, and because the planted trees are very generally of subsp. *betulifolia*, it seems reasonable to assume that they are descendants from native trees. The pollen record gives us little information on this since the pollen of Black poplar is indistinguishable from that of Aspen (*P. tremula* L.) and White poplar (*P. alba* L.) (Huntley & Birks 1983).

The database created by the B.S.B.I. catalogues over 2000 trees, and is still being maintained at the Biological Records Centre at the Institute of Terrestrial Ecology at Monks Wood. Records of Black poplar are verified and recorded by 6-figure Ordnance Survey grid reference and vice-county. Over 200 are positively identified as female, but the majority of trees are “unsexed”. Rogers (1995) is therefore pessimistic in asserting that “there are only about 150 female trees in Britain”.

The first hybrid between European *P. nigra* and the American *P. deltoides* introduced to Britain was probably ‘Serotina’, and this was introduced about 200 years ago (Jobling 1990). At the same time, *P. nigra* ‘Italica’, the familiar Lombardy poplar, was introduced from Northern Italy, although in both cases it would have taken some time for specimens to become widely distributed. Since both varieties are male, we cannot be certain that any seedlings dating from later than this are free from imported genes. Therefore, the database contains records of “mature” trees, which are difficult to date precisely, but which are probably more than 150 years old.

‘Manchester Poplar’ is a horticultural synonym for *P. nigra* var. *betulifolia* (Stace 1971; Bean 1976) but it has come to refer to urban trees planted in Manchester and the industrial north generally. These urban trees have been largely excluded, since Stace (1971) examined 100 specimens and found that they were all male, and therefore possibly representing a very narrow genetic base propagated vegetatively. However, since there is a great preponderance of males among the British population generally, this hardly seems to be adequate grounds for the exclusion of the urban trees, and they should be included in DNA studies of the British population.

GENETIC STUDIES

Modern molecular methods for analyzing genetic material now offer means for examining genetic diversity, and defining relationships between individual taxa. Legionnet (1997) used isozymes to examine genetic diversity and population biology in *P. nigra* growing in France, and found that there was more genetic diversity within rather than between stands. As a consequence, it would be more efficient to conserve more individuals from a small number of stands than vice versa. Cottrell *et al.* (1997) used RAPD markers to study 36 accessions of Black poplar broadly sampled within Great Britain, and found only 17 distinct genotypes. Genotypes were local in their distribution and genetic diversity was low. These authors also concluded that there had been so much interference by man that there are unlikely to be distinct Eastern and Western types. In a more concentrated study of Black poplar in the Upper Severn area, Winfield *et al.* (1998) used AFLP analysis to examine genetic diversity in 146 individuals and three individuals considered to be non-*betulifolia* poplars. Genetic diversity was low, confirming the results of Cottrell *et al.* (1997). There was a general correlation between geographic proximity and genetic similarity. They concluded that it was possible to identify a

small number of individuals exhibiting maximum diversity for inclusion in a replanting/conservation programme.

Of the 36 trees sampled by Cottrell *et al.* (1997), only six were female, and DNA analysis of these revealed that there were only two distinct genotypes, despite the fact that they were sampled from a wide geographical range.

METHODS OF GENETIC CONSERVATION

The Biodiversity Action Plan (Anon. 1994), was written following the UK signature to the *Convention on biodiversity* at the United Nations Conference on Environment and Development at Rio de Janeiro in 1992. It distinguishes between in situ and ex situ conservation measures, and states that "for successful conservation the establishment of ex situ populations should precede any crisis period and should be implemented when wild populations are still quite numerous." In the case of Black poplar, we can assume that the in situ population (in Britain) is entirely of planted origin. We might seek to conserve standing trees because they have not yet been identified and conserved, or because they have particular cultural associations, e.g. the Aston-on-Clun Flag Tree (Mabey 1996), but the principal work must be in identifying the genetic diversity of the taxon (species or subspecies) and its distribution, and seeking the most efficient way to conserve it in ex situ collections.

There is not much time available for this process, since there is significant loss of the oldest and most valuable trees, at a rate which has not yet been measured. It could be measured by revisiting a sample of trees taken from the B.S.B.I. database at regular intervals. Meanwhile, a clone bank has been built up by the Forestry Commission, but this contains less than 100 accessions and, on the basis of the molecular studies, might be expected to contain less than half this number of distinct genotypes. No collection has yet been made based on genetic information of the type obtained for the River Severn area (Winfield *et al.* in press).

The current collection is held by the Forestry Commission at three separate sites (for security) in Bedfordshire, Norfolk and Gwent. In all cases, the trees are planted at wide spacing, with the intention of allowing them to grow into mature trees. Another strategy is to hold reference collections in closely-spaced stool-beds, which are cut annually, so that it is relatively easy to provide cuttings, e.g. for DNA studies. Part of the National Poplar Collection at Alice Holt (Surrey) is already managed in this way, and it would be relatively easy to add a Black poplar collection. Such a collection would be more efficient if we could be certain that it contained no duplicate genotypes. This could be achieved following a broad survey of genetic variability (using DNA analysis) in putatively native standing trees.

EUROPEAN CONSERVATION STRATEGY

The *P. nigra* network of EUFORGEN has adopted a workplan (Turok *et al.* 1996) with the following activities:

1. Exchange of reference clones: a common set of vegetative material of well-known poplar clones has been distributed to interested countries for use as a base-line in genetic studies.
2. Core collection of *P. nigra*: vegetative material from identified clones in member countries has been collated at the Poplar Research Institute at Casale Monferrato in Italy. The aim is to set up a common basis for the characterization and evaluation of national clone collections.
3. "Passport data": an agreed list of attributes has been compiled to identify material in a database, and for inventories and exchange of material.
4. European database: an organised list of accessions available in each country has been compiled to avoid confusions about clonal identity.
5. Descriptor list for *P. nigra* clones: the aim is to produce common minimum standards for characterizing clone collections in each country.
6. Identification sheet: an illustrated sheet (Turok *et al.* 1996) is available as a simple guide to distinguish *P. nigra* from its hybrids (though it does not go down to subspecies level).
7. Synthesis of in situ gene conservation measures and activities: published in Turok *et al.* (1996).
8. Guidelines for ex situ field collections: published in Turok *et al.* (1996).

9. Guidelines for seed and pollen storage: published in Turok *et al.* (1997).
10. Review of literature: initial version in Frison *et al.* (1994). Updated versions to be made available through the Internet.
11. Public awareness: assembly of colour slides related to *P. nigra*.
12. Country reports: published in the various reports, and updated regularly.
13. Molecular methods available for the characterization of *P. nigra*: to review and develop modern methods for the characterization of existing collections. Not yet published.

This list indicates the breadth of activity that has been deemed necessary to conserve Black poplar. Similar progress is being made by other EUFORGEN networks on *Picea abies*, *Quercus suber* and the "Noble Hardwoods". This last category includes alder, ash, *Sorbus*, elm and fruit woods, but excludes oak and beech, which are classified as "Social Hardwoods" presumably because they tend to form large single-species stands.

U.K. NATIONAL STRATEGY FOR THE GENETIC CONSERVATION OF TREE SPECIES

Efforts to prevent the disappearance of our most endangered species of timber tree have highlighted the need to ensure that the genetic base of all our native trees is not eroded. Britain has a native tree flora of only 33 species (Mitchell 1981). The natural distributions of these species and their genetic diversity are still unknown or imperfectly understood. Indeed, in many cases, it is difficult to tell which trees are "native" and which have been imported by man. A strategy for conserving the genetic diversity of our native trees must first organise the existing information, and then seek to identify which individuals should be protected. A start on this has already been made in relation to Black poplar, and in collaboration with the EUFORGEN *P. nigra* network.

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Notes

TYPIFICATION OF SOME BARTON & RIDDELSDELL NAMES IN *RUBUS* L. (ROSACEAE)

In the two successive papers in which they described *Rubus bakerianus*, *R. furnarius*, *R. newbridgensis* and *R. pistoris* Barton & Riddelsdell (1935, 1936) indicated holotypes identified by numbers in Barton's herbarium. The gatherings to which those numbers referred were respectively:

Wimbledon Common, v.c. 17, 3 August 1934, *Barton & Riddelsdell* 4376

Sedbergh, v.c. 65, 1934, *Barton & Riddelsdell* 4378

Newbridge, v.c. 14, 2 August 1934, *Barton & Riddelsdell* 4519

Gormire, near Thirsk, v.c. 62, 1 August 1933, *Riddelsdell* 4351.

Unfortunately, the two were inadequately versed in the typification procedure prescribed in the new edition of the *International rules* (Briquet 1935) which had just then come into force. This explicitly stated that a holotype must consist of "a specimen" (Art. 18, Rec. IV). A specimen for the purposes of the microspecies of *Rubus fruticosus* agg. has long been accepted by specialists in this group as necessarily consisting of a flowering spray together with part of the primocane with at least one stem leaf attached to that. It is conventionally regarded as unsafe to venture a determination in the absence of either of those components. While Barton & Riddelsdell observed this convention impeccably, after Barton's herbarium (incorporating Riddelsdell's) passed to BM after his death it emerged that the designated holotypes in each of these four cases consisted not of a single specimen but of several. In the case of *R. bakerianus* as many as five sheets of specimens turned out to be sharing the particular number cited, three of those sheets bearing more than one flowering spray a piece. That in each case the specimens comprising the so-called holotype all came from the same bush is rendered likely by the fact that Barton labelled some of the sheets "co-type" (a term without official standing in the *International rules* either then or since); however, that word is not present on all, leaving open the possibility that more than the one bush may have been involved.

As more precise typification was clearly called for, at some unstated date one appropriate sheet was chosen in each case as the lectotype and labelled as such in an anonymous hand. Unfortunately, the fact that this had been done was not published, allowing Edees & Newton (1988), in their monograph of the group in the British Isles, to repeat from Barton & Riddelsdell's papers the details of what they supposed to be particular single specimens and similarly to cite these as holotypes.

The handwriting on the labels has now been identified as that of G. A. Matthews, a former member of the BM British Herbarium, and to him the lectotypifications are now here belatedly credited – except in the case of *R. pistoris*. Of that species the sheet in question bears three flowering spray pieces and five primocane pieces, making it necessary to restrict the lectotypification further to just one pair of those. The lower right-hand spray plus associated primocane piece (as indicated on the sheet) are accordingly here so designated.

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TRIFOLIUM OCCIDENTALE D. E. COOMBE (FABACEAE) IN ANGLESEY (V.C. 52)

The Western Clover, *Trifolium occidentale* D. E. Coombe, is an early-flowering and self-compatible coastal species, which is stoloniferous and superficially resembles *T. repens* L. Since it was first described by Coombe (1961), detailed information on the narrow maritime Atlantic range of *T. occidentale* has been reported at intervals, as discoveries of new localities have accumulated. In a recent summary review with accompanying map, Coombe (1994) outlined its specialised ecological distribution in exposed coastal-fringe grasslands in the Channel Isles, the Isles of Scilly and mainland W. Cornwall, with isolated records in N. Devon and on the Gower peninsula in Glamorgan; he was also able to report *T. occidentale* as frequent in south-west Ireland and north-west France, and rare on the west Iberian coast. It has since been recorded by R. S. Cropper at three localities in south-west Pembrokeshire (Evans 1997). A new record from Anglesey outlined in this note marks a further northward extension of its range on the west coast of Britain. The most northerly locality for *T. occidentale* in Europe is in Co. Dublin where it was reported by Preston (1980) and Akeroyd (1983).

In May 1995, Alan Lewis informed RHR (then vice-county recorder for v.c. 52) that he had recently found a few plants which resembled *T. occidentale* near Trearddur Bay, on Holy Island, in west Anglesey. A subsequent visit to the locality was delayed until April 1997, when we were able to examine plants and confirm them as undoubtedly *T. occidentale*. Very shortly afterwards, the site was visited by another party of botanists including C. D. Preston who also confirmed this determination.

The Anglesey population of *T. occidentale* is evidently quite small and highly restricted in extent. On 19 April 1997, about 20 separate patches were observed on a low bank above a small car-park at the landward end of a short rocky headland forming the south side of Porth Diana (SH/253.782). The soil of the bank has a high fraction of wind-blown sand; it is somewhat unstable and was probably disturbed during construction of the car-park. A single plant was also noted by a gateway on the opposite side of the minor road from the car-park. There is no evidence to indicate whether *T. occidentale* is a long-established native or if it has recently arrived in west Anglesey.

The population is close to the rocky shore-line and, as in other parts of its range, some of the associated species at Porth Diana are strongly maritime. Among the species growing in close proximity to *T. occidentale* are *Anthyllis vulneraria* L., *Bellis perennis* L., *Bromus hordeaceus* L., *Carex arenaria* L., *Catapodium marinum* (L.) C. E. Hubb., *Cerastium diffusum* Pers., *Cochlearia danica* L., *Erodium cicutarium* (L.) L'Hér., *Festuca rubra* agg., *Galium verum* L., *Hypochaeris radicata* L., *Lotus corniculatus* L., *Medicago lupulina* L., *Ononis repens* L., *Plantago coronopus* L., *P. lanceolata* L., *Poa pratensis* agg., *Ranunculus bulbosus* L., *Sanguisorba minor* L., *Scilla verna* Huds., *Senecio jacobaea* L. and *S. vulgaris* L.

TABLE 1. COMPARISON OF SEED SET AND SEED SIZE IN *TRIFOLIUM OCCIDENTALE* AND *T. REPENS* FROM ANGLESEY, v.c. 52

a. Seed set	No. of seeds per flower*				
	0	1	2	3	4
<i>T. occidentale</i> (29 June 1997)	33	31	30	6	—
<i>T. repens</i> (5 August 1997)	51	24	14	10	1
b. Seed size	Seed length (mm)**				n
	Mean (range)				
<i>T. occidentale</i>	1.2 (1.0–1.6)		111		
<i>T. repens</i>	1.1 (0.8–1.4)		88		

*Counts of seed set for samples of 100 flowers in each species, obtained from ten inflorescences, each from a separate individual.

**Seed length data obtained from samples of ten inflorescences per species, each from a separate individual.

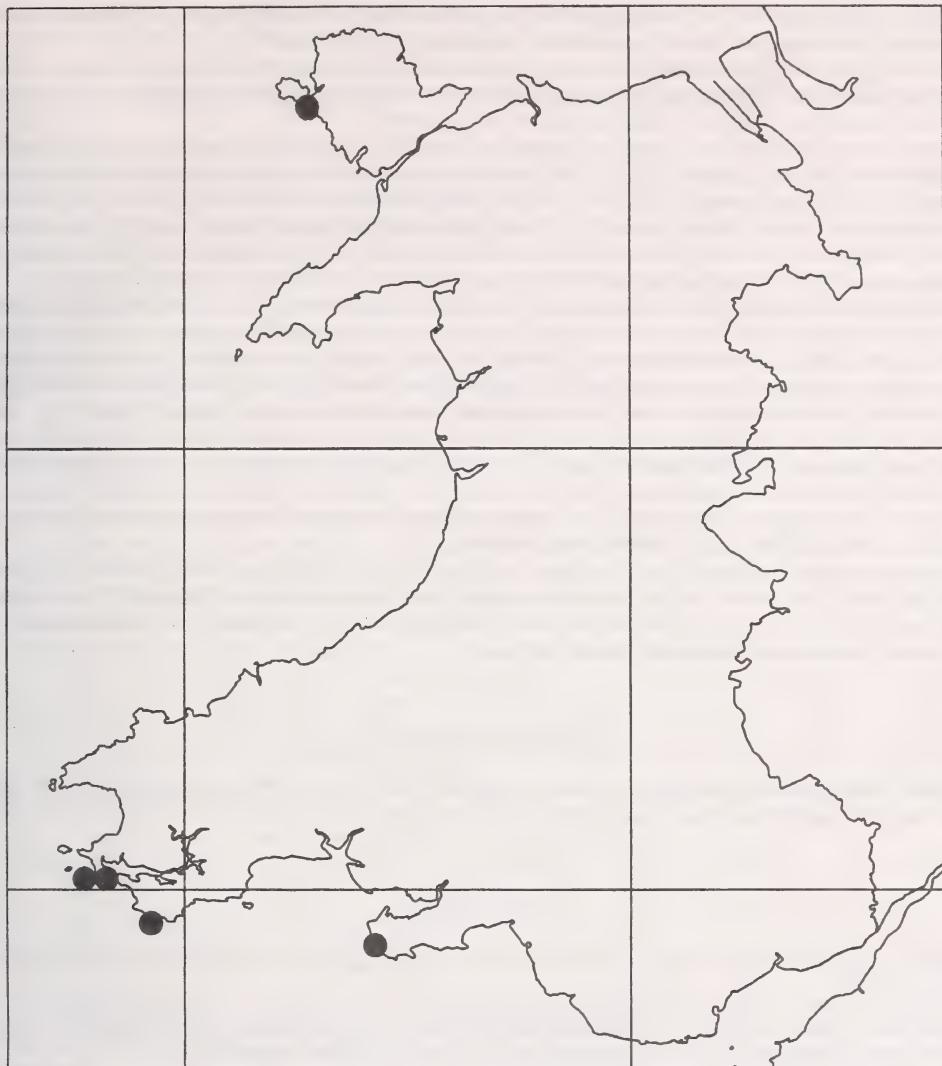


FIGURE 1. The distribution of Welsh records of *Trifolium occidentale*. ● Occurrence in 5×5 km squares of the national grid.

When it was observed on 19 April 1997, a few plants of *T. occidentale* had early inflorescences with flowers in bud. The locality was visited on several subsequent occasions during 1997 to make comparisons between *T. occidentale* and the much larger population of *T. repens* present in coastal turf on the headland. The main flowering period of *T. occidentale* lasted until mid-June, with a few stragglers appearing beyond this period. In contrast, *T. repens* started to come into flower in late May and early June, with its main flowering period persisting through to early August.

Material gathered from several plants of *T. occidentale* showed little variation. They agreed with descriptions given by Coombe (1961) and Coombe & Morisset (1967), having small (c. 10×10 mm), orbicular leaflets, of a darker green than in *T. repens* and without the leaf-markings common in that species; their upper leaflet surface is matt and minutely crystalline when viewed under low-power magnification, and the underside is strikingly glossy; the lateral veins are characteristically non-

translucent when a leaflet is viewed against strong diffuse light. In addition, the stipules are a deep vinous red, which was particularly apparent in the young creeping shoots.

This set of vegetative characteristics is diagnostic of *T. occidentale*. The presence of sparse, short, colourless hairs on the petioles and peduncles has often been cited as an additional distinctive character, but in our experience they also occur frequently in *T. repens*.

Floral characters in the Anglesey plants were also found to be equally uniform and in full agreement with those described by Coombe (1961). The flowers are creamy white with no tinge of pink, the standard is broadly elliptical and emarginate (a very shallow emargination also occasionally occurs in *T. repens*); the upper teeth of the calyx are parallel or convergent, broadly triangular or ovate-triangular and often minutely denticulate. As seed pods ripen, the flowers become a dark chocolate brown in *T. occidentale* with no trace of pink or red pigment which frequently suffuses the fruiting heads of *T. repens*.

Comparative estimates of seed set and seed size were made between *T. occidentale* and *T. repens*. Seed counts were recorded from samples of ten flowers taken from each of ten inflorescences per species from different plants; data were obtained in the main fruiting period in each species, and seeds damaged by insect attack or by pathogens were ignored. For both species seed length measurements were made on samples from ten inflorescences, each from a separate plant. The results are given in Table 1.

Seed germination was tested in two plants of *T. occidentale*, sown on 30 June 1997. Of 16 seeds sown from Plant A, 15 germinated between 13–24 July, while four seeds out of 13 sown from Plant B germinated between 5–10 August.

These findings suggest that seed size and productivity are similar in the two species, and also that at least a proportion of the *T. occidentale* seed is viable.

We have searched several other headlands and stretches of rocky coast in south-west Anglesey, extending from Holy Island to Llanddwyn Island, but have found no further colonies of *T. occidentale*. It also appears that it is very scarce on the Gower peninsula (Kay & Ab-Shukor 1988) and elsewhere in Wales; the only known records are shown in Fig 1.

ACKNOWLEDGMENTS

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LECTOTYPIFICATION OF *POTAMOGETON FLABELLATUS* BAB. (POTAMOGETONACEAE)

Since it was first described by Babington (1851), the name *Potamogeton flabellatus* has been applied to a variety of taxa. In Britain these have included broad-leaved plants which are now subsumed within

the variable *P. pectinatus* L. and superficially similar plants which are now known to be *P. × suecicus* K. Richt. (Dandy & Taylor 1946). Although the name is now usually reduced to synonymy, it survives as a convenient informal label for certain variants of *P. pectinatus* (Preston 1995). Lectotypification of the name is desirable both in itself and as part of the general need to typify names in the genus (Wiegleb 1988).

C. C. Babington was one of the first British botanists to take a critical interest in the genus *Potamogeton*. In his *Manual of British botany* (1843) he published a serviceable account of the genus as it was then known. He split the species into five groups, one of which corresponds with the current Subgenus *Coleogeton* Rchb. In this group he recognised *P. filiformis* (which had not previously been reported from the British Isles) and he divided the plants which we would now call *P. pectinatus* into two taxa, *P. pectinatus* and *P. zosteraceus* Fr. He described *P. zosteraceus* as having linear-acuminate, obscurely 3-veined leaves and fruits rounded on the back with a prominent keel, whereas *P. pectinatus* had narrower, linear-setaceous, 1-veined leaves and fruits with lateral ridges but no keel. He reported *P. zosteraceus* from only one site, the Serpentine in Hyde Park, London, where it had been collected by Dr J. A. Power. In the second edition of the *Manual* Babington (1847) retained *P. zosteraceus*, again on the basis of Power's plant from the Serpentine. Although there are minor changes in wording, his description of the plant is essentially the same as in the first edition. He had, however, begun to doubt whether the plant he described was the same as that described by Fries (1828). In an additional note at the end of this group of species he also drew attention to plants from Bath and Somerset which were "probably a new species but I am not sufficiently acquainted with it to describe it".

By the time that he prepared the third edition of the *Manual*, Babington (1851) had concluded that Fries' *P. zosteraceus* was not the plant that he had previously described under that name. He therefore introduced the name *P. flabellatus* for the British plant, with the synonym "*P. zosteraceus* Bab. (not Fr.)". He rewrote the description of the plant, characterising it as having broadly linear, abruptly apiculate or acuminate 5-nerved lower leaves which are normally decayed at the time of flowering, narrow, acute 3-nerved upper leaves borne on stems which are branched and spread like a fan, and keeled fruits. The flowering period is given as June–July, whereas previously *P. zosteraceus* had been described as flowering in July. This description is more detailed than that of the earlier descriptions of *P. zosteraceus* and it places more emphasis on vegetative characters. In particular, the description of the habit and broad lower leaves is new. *P. flabellatus* was said to occur in "ponds and ditches" in England, but Babington cited no specific localities. The plants from Bath and Sandwich mentioned as a possible new species in the second edition are not explicitly cited.

Although the concise entry for *P. flabellatus* in Babington's *Manual* provides no indication of the source of the material he described, Babington (1853) later provided a more detailed account of his species. In this he stated that he described *P. zosteraceus* in the first two editions of the *Manual* on the basis of a plant "which was very slightly known to me, it having been noticed in Hyde Park only". In 1849, however, he obtained "a series of most characteristic specimens" from Mr [Thomas] Kirk of Coventry, which convinced him that the plant was distinct from both *P. pectinatus* and from the true *P. zosteraceus*. "Accordingly, in the 'Manual' (ed. 3) the name of *zosteraceus* is changed into *flabellatus*, a term derived from the usually fan-shaped habit of the flowering plant." At the time he prepared the account of *P. flabellatus* for the *Manual* he thought that the plant from Bath was referable to *P. pectinatus*, but visits to Bath in 1853 had enabled him to re-examine the plant and convinced him that it was in fact *P. flabellatus*. Babington makes no mention in this paper of the plant from Sandwich.

It is clear from this historical resumé that the name *Potamogeton flabellatus* Bab. must be treated as a species described afresh in 1851, rather than simply as a replacement name for the plants from the Serpentine hitherto treated as *P. zosteraceus*. It is therefore appropriate to consider as syntypes all the material which Babington had available to him in 1851 and which he then considered referable to *P. flabellatus*. The following specimens from Babington's herbarium (now incorporated into CGE) were collected before 1851 and labelled as *P. flabellatus* by Babington and are available for selection as the lectotype. The names on the specimens are given in the order in which they were applied; names in inverted commas were given by the collector and the rest are in Babington's handwriting.

- A. *Potamogeton pectinatus/zosteraceus/zosteraceus* Bab. not Fries/*flabellatus*. Serpentine, Hyde Park, London. J. A. Power, 9 July 1838.
- B. "*Potamogeton zosteraceus* Bab."/i>*flabellatus*. Canal, Stoke Heath, Warwick. T. Kirk, June 1847.
- C. "*Potamogeton zosteraceus* Bab."/i>*flabellatus*. Canal, Stoke Heath, Warwick. T. Kirk, 26 May 1849.

- D. "Potamogeton zosteraceus Bab."/flabellatus. Canal, Stoke Heath, Warwick. T. Kirk, July 1849.
 E. Potamogeton zosteraceus/flabellatus. Coventry. T. Kirk, 29 May 1850.
 F. Potamogeton zosteraceus Bab.? River Lea below Ware, Herts. W. H. Coleman, 1848.

Specimen A is the plant described under the name *P. zosteraceus* in the first two editions of the *Manual*. Specimens B–E represent the series of specimens Babington received from Kirk which convinced him that the plant was a distinct but undescribed species. "Warwick" on Kirk's labels indicates the vice-county of Warwickshire; Stoke Heath is actually in Coventry and the canal which runs through it is the Coventry Canal. As specimen F was initially labelled "Potamogeton zosteraceus Bab.?", Babington must have received it before he coined the name *P. flabellatus*. In including it in the above list I have assumed that Babington decided that the specimen was *P. flabellatus* before he published this name, but I cannot prove it. Other than these six specimens, the only sheet in CGE collected before 1851 and labelled as *P. flabellatus* by Babington is a sheet from the "canal at Bath" collected by Babington himself in June 1830. This is the material which he referred to *P. pectinatus* at the time he described *P. flabellatus* (Babington 1853), and *P. pectinatus* is one of three names Babington wrote on the sheet and subsequently crossed out. It cannot, therefore, be regarded as a potential lectotype.

An ideal lectotype of *P. flabellatus* would show both the fruits and the lower leaves, the two characters which Babington (1851) emphasised when describing the species. Unfortunately none of the syntypes show both these features, presumably because the lower leaves have usually decayed by the time that the plants flower (as Babington noted). Specimens B and F are upper flowering stems with neither lower leaves nor fruits, and need not be considered further. The choice therefore lies between the single specimen from the Serpentine (A) and the Stoke Heath specimens (C–E). The plant from the Serpentine (A) is cited indirectly in the protologue via the reference to Babington's earlier description of *P. zosteraceus*. It was J. E. Dandy & G. Taylor's choice of lectotype: it is cited as such in their unpublished monograph "*The British species of Potamogeton L.*", and they labelled the specimen in CGE "Type specimen of Potamogeton flabellatus Bab., Man. Brit. Bot. ed. 3, 343 (1851)". This choice was never published, however, and does not constitute effective lectotypification (see *International code of botanical nomenclature* 1994, Article 7.10). Although the argument for selecting this specimen as lectotype is strong, I do not believe that it is conclusive. The protologue of *P. flabellatus* incorporates features which could not be derived from the Serpentine specimen, and it is clear that the Stoke Heath plants provided the main source for Babington's revised description. It is appropriate, therefore, to select specimen C, D or E as the lectotype. It is better to select a fruiting plant rather than a vegetative shoot and I have therefore selected specimen C; it is an upper fruiting stem and the specimen includes one fruit which Babington removed and sectioned. Specimen D, which consists of broad lower leaves, is mounted on the same sheet. Specimen E, which is labelled "Spring leaves" consists of very broad lower leaves. All the syntypes were determined as *P. pectinatus* L. by J. E. Dandy and G. Taylor in 1939, determinations with which I concur.

The nomenclature and typification of *P. flabellatus* can be summarised as:

Potamogeton flabellatus Bab., *Man. Brit. bot. ed. 3*, 343 (1851). Lectotype: Canal, Stoke Heath, Warwick. T. Kirk, 26 May 1849, CGE (designated here).

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AQUATIC PLANTS AT HIGH ALTITUDES IN THE BREADALBANE MOUNTAINS
(V.C. 88), SCOTLAND

The standard work on the altitudinal range of British plants is Wilson (1956), which was based on papers originally published in 1930 and 1931 and is now somewhat dated. Some groups treated by Wilson have subsequently been the subject of taxonomic revision, and the altitudinal ranges of the taxa now recognised need to be established. There is also a need to localise many of the records cited. We believe that altitudinal limits should be based on precisely localised records, but in many cases Wilson (1956) relied on earlier authors who occasionally cited upper altitudinal ranges from areas as large and vague as the Scottish Highlands. Finally, there is a need to collate records made since Wilson's compilation was published.

In compiling data on the maximum altitude of aquatic plants in Britain and Ireland for publication (Preston & Croft 1997), it became clear that several species reached their upper limit in the Breadalbane mountain range. Many of these altitudinal limits are derived from White (1898). White usually stated the upper limits of species in Perthshire without citing the exact localities where these limits were reached, although for less common species these localities can often be deduced from the list of records. Our enquiries suggested that there were surprisingly few recent localised records of aquatic plants from these much-visited mountains: presumably botanists visiting the area have been preoccupied by the rich terrestrial montane flora and have seen no need to record aquatic plants which can be seen much more easily elsewhere. We therefore visited some lochs and lochans at high altitudes in the Breadalbane area in July 1995. The significant altitudinal records we made are detailed in this note. All the sites we visited in this area are in v.c. 88. We also refer to records made on a visit to Loch Vrotachan, v.c. 92, in 1996.

In the records which follow, altitudes cited by earlier authors have been converted from feet to metres, and all altitudes are rounded to the nearest 5 m. The term lowland is used here for altitudes below 300 m; Wilson (1956) used it similarly, for altitudes below 1000 feet (305 m). The card index of *Potamogeton* specimens compiled by J. E. Dandy and held in BM is referred to as the "Dandy index". Unless stated the records quoted here from the index refer to specimens which Dandy cited from BM but which are not now incorporated into the herbarium, probably because they were lost or damaged in the Second World War (cf. Preston 1988). Nomenclature follows Stace (1991) for vascular plants and Moore (1986) for charophytes.

Carex lasiocarpa. With *C. rostrata* in swamp around lochan N. of Lochan Achlarich, E. of Beinn Heasgarnich, altitude 650 m, NN/432.381, 26 July 1995. Although *C. lasiocarpa* often fails to flower or flowers very sparingly, this was not the case at this site in the summer of 1995, where flowers were frequent. Wilson (1956) follows White (1898) in giving the upper limit of this species as 425 m in the Atholl region of Perthshire.

Carex limosa. Bog pools in flat-bottomed valley N.E. of Lochan Achlarich, E. of Beinn Heasgarnich, altitude 650 m, NN/436.385, 26 July 1995. Although this just exceeds White's (1898) and Wilson's (1956) upper limit, 640 m in Breadalbane, the species has been recorded by R. W. David at 830 m on Meall nan Tarmachan, NN/589.390, where it grew with *C. saxatilis* in a mire on a level shelf. This altitude, originally recorded as 2725 feet, is erroneously cited as 817 m by Jermy, Chater & David (1982); details of the original record are held at the Biological Records Centre.

Carex nigra. Edge of lochan fed by two melting snowpatches, 200 m S.E. of the summit of Beinn Heasgarnich, altitude 1005 m, NN/415.382, 26 July 1995. Also present at lochans at 995 m (NN/417.384) and 970 m (NN/418.385) elsewhere in this area. The upper limit for this species cited by Wilson (1956) is based on Macvicar's (1894) report of plants at 990 m within a radius of 10 miles [16 km] from Killin, v.c. 88.

Carex rostrata. Swamp on flat ground between Meall Garbh and Beinn nan Eachan, altitude 930 m, NN/572.386, 25 July 1995. This exceeds Wilson's (1956) upper limit for this species, 915 m, based on White's (1898) unlocalised record from the Breadalbane area. However, D. A. Ratcliffe recorded this species at 1040 m E. of the main plateau of Creag Meagaidd, NN/432.875, on 2 August 1957 (cf. McVean & Ratcliffe 1962, pp. 116–117).

Equisetum arvense. In *Sphagnum* at the edge of lochan fed by two melting snowpatches, 200 m S.E. of the summit of Beinn Heasgarnich, altitude 1005 m, NN/415.382, 26 July 1995, CGE (Preston 95/55). Also present by lochans at 995 m (NN/417.384) and 970 m (NN/418.385) elsewhere in this

area. The upper limit for this species given by Wilson (1956) is 945 m, based on Macvicar's (1894) record from a radius of 10 miles [16 km] from Killin. Macvicar reported his plant as var. *alpestris*, a variant with short prostrate stems and suberect branches. The plants we collected would be covered by Babington's (1881) description of this variant.

Equisetum palustre. By large lochan S.W. of the summit of Meall nan Tarmachan, altitude 945 m, NN/581.387, 25 July 1995. This exceeds the unlocalised upper record of this species, 915 m in the Breadalbane area (White 1898; Wilson 1956); the species is also reported by McVean & Ratcliffe (1962, p. 351) from 915 m at NN/635.409 on Ben Lawers.

Menyanthes trifoliata. Tiny plants at edge of lochan fed by two melting snowpatches, 200 m S.E. of the summit of Beinn Heasgarnich, altitude 1005 m, NN/415.382, 26 July 1995, CGE (Preston 95/54). Also present by a lochan 500 m N. of the summit, NN/418.385, at an altitude of 970 m. Swamp on flat ground between Meall Garbh and Beinn nan Eachan, altitude 930 m, NN/572.386, 25 July 1995. Wilson (1956), citing White (1898), gives 925 m in Breadalbane as the upper limit for this species.

Myriophyllum alterniflorum. In water 20–30 cm deep at edge of Lochan an Tairbh-uisge, Meall nan Tarmachan, altitude 780 m, NN/591.396, 25 July 1995, CGE (Preston 95/52). Frequent in water c. 1 m deep over sand, E. end of Loch Vrotachan, v.c. 92, altitude 750 m, NO/124.784, 27 July 1996, CGE (Preston 96/96). Lochan Coire Dhubhclair, altitude 735 m, NN/497.329, 27 July 1995. These records exceed the upper altitudinal limit given by Wilson (1956), 715 m in Breadalbane and in Wales.

Potamogeton alpinus. Water 16–50 cm deep over an otherwise bare schistose substrate, large lochan S.W. of the summit of Meall nan Tarmachan, altitude 945 m, NN/581.387, 25 July 1995, CGE (Preston 95/53). A large population of *P. alpinus* was present in this windswept lochan. The plants were small and reproducing vegetatively by stolons: small plants were growing at the tips of the stolons and rooting from stolons which were still attached to the parent plant. Some plants were also in bud. Similar dwarf plants with short stolons have been collected at high altitudes on Meall nan Tarmachan for many years, most recently by R. Mackechnie & E. C. Wallace on 8 July 1937 (BM). Meall nan Tarmachan is cited as the highest locality for this species by Dandy & Taylor (unpublished) on the basis of these collections. Wilson's (1956) upper limit of 3350 feet [1020 m] is based on Bennett (1907), who actually cited an unlocalised record from 3300 feet [1005 m] as the upper limit for this species in Britain. This higher value is best disregarded in the absence of further information. The altitudinal limits in Bennett (1907) are based on specimens he himself had seen, and he perhaps derived this figure from an imprecisely labelled sheet from "near the summit" of Meall nan Tarmachan (1043 m).

Potamogeton filiformis. Although this species has a northern distribution in Britain, it is primarily a lowland plant which ascends to 350 m in Drumore Loch, Angus, v.c. 90 (Stewart, Pearman & Preston 1994). The only exception is a specimen collected from "alt. near 2500 ft. [760 m]" at "lochan above Coire Dhubh Ghalaig, Breadalbane" by D. A. Haggart on 1 August 1889 (PTH). The identification of this specimen was initially confirmed by Dandy & Taylor in 1939 and subsequently by C.D.P. in 1997. The site, Lochan Coire Dhubhclair, lies at an altitude of 735 m. We revisited it on 27 July 1995: it is a stony lochan with no emergents, although green algae cover the rocks. Small plants of *Juncus bulbosus* grew around the edge of the loch but we could find no *Potamogeton filiformis*. There is no reason to suppose that the specimen at PTH is mislabelled (M. Simmons, in litt., 1997), but it is possible that the species was only a transient colonist at this apparently unsuitable site which is 50 km from any other known population.

Potamogeton perfoliatus. With *P. praelongus* in water 20–30 cm deep at the shallow edge of Lochan an Tairbh-uisge, Meall nan Tarmachan, altitude 780 m, NN/591.396, 25 July 1995, CGE (Preston 95/51). Although *P. praelongus* has been collected at this site before (see below), *P. perfoliatus* appears to have been overlooked (or perhaps regarded by earlier botanists as too common to collect). This site exceeds the upper altitudinal limits given by Wilson (1956) and Dandy & Taylor (unpublished), both of which are based on E. S. Marshall's collection from 750 m at Loch Vrotachan, v.c. 92 (Marshall 1893; voucher in CGE), a site where the species was still present in 1996.

Potamogeton polygonifolius. Outflow of Lochan an Tairbh-uisge, altitude 780 m, NN/591.396, 25 July 1995. This exceeds the published upper limit of this species, 700 m in Breadalbane (White 1898; Wilson 1956). According to Dandy & Taylor (unpublished), the species occurs "up to about 3000

ft. [915 m] on Meall nan Tarmachan"; there are no specimens with precise altitudinal data in the Dandy index, although it details one collection by A. B. Hall from "pools near the summit of Meall nan Tarmachan" (July 1892). We failed to find this species at higher altitudes on Meall nan Tarmachan, although it might occur there.

Potamogeton paelongus. Flowering plants in water 50–60 cm deep, and a few scattered plants with *P. perfoliatus* in water as shallow as 20–30 cm, Lochan an Tairbh-uisge, Meall nan Tarmachan, altitude 780 m, NN/591.396, 25 July 1995, CGE (Preston 95/49, 50). This has hitherto been regarded as the highest locality for this species in Britain: it has been collected here since 1881, most recently by A. O. Chater in 1953 (LANC). However, a higher locality was discovered in 1995 by the Scottish Natural Heritage Loch Survey team, who collected *P. paelongus* at 800 m at Loch Coire Cheap, NN/480.754, in v.c. 97 (voucher specimen confirmed by C.D.P.). References to the occurrence of *P. paelongus* at higher altitudes on Meall nan Tarmachan are based on a specimen collected by H. N. Dixon & A. H. Vallance in 1893 (Dandy index) on which the altitude of this site is given, rather imprecisely, as 2500–3000 feet [760–915 m]. Both Bennett (1903) and Wilson (1956) chose the upper of these two values as the upper limit for the species.

Potamogeton × zizii (*P. gramineus* × *P. lucens*). Clear water 1 m deep, with *Littorella uniflora*, *Lobelia dortmanna*, the aquatic variant of *Juncus bulbosus* and *Myriophyllum alterniflorum*, Loch na Craige, altitude 395 m, NN/88.45, 29 July 1995, CGE (Preston 95/64). Wilson (1956) described this as a lowland plant, although there are earlier collections from this site, made by G. Taylor in 1932 and 1933 and by J. W. Clark in 1973. These collections were initially determined as *P. lucens* by W. H. Pearshall and J. E. Lousley respectively (Dandy index).

Sparganium angustifolium. A few plants in a lochan fed by two melting snowpatches, 200 m S.E. of the summit of Beinn Heasgarnich, altitude 1005 m, NN/415.382, and larger populations in a stony lochan 500 m N.E. of the summit, altitude 970 m, NN/418.385, CGE (Preston 95/56), 26 July 1995. Wilson (1956) includes both this species and *S. natans* in his entry for *S. angustifolium*, although suggesting (doubtless correctly) that the higher altitude records probably refer to *S. angustifolium*. None of his entries, however, is for an altitude as high as 1005 m. Druce (1932) cites a record made by P. Ewing at 990 m from Ben Lawers; this puzzling record may refer to the Lawers area as there does not appear to be any suitable habitat at this altitude on Ben Lawers itself.

Sparganium natans. Growing with *Potamogeton natans* in water 30–40 cm deep over peat (with submerged inflorescences), and as tiny plants in liquid mud (with emergent inflorescences), Lochan Achlarich, E. of Beinn Heasgarnich, altitude 650 m, NN/434.380, 26 July 1995, CGE (Preston 95/57). As explained under *S. angustifolium*, Wilson (1956) does not specify an altitudinal limit for this species. This record is higher than any others we have traced.

Triglochin palustris. By lochan 500 m N.E. of the summit of Beinn Heasgarnich, altitude 970 m, NN/418.385, 26 July 1995. Macvicar (1894) and White (1898) give the upper limit for this species as 855 m in Breadalbane, the value cited by Wilson (1956), although Druce (1932) cites an upper limit of 975 m on Lochnagar. The presence of this species at high altitudes in Britain is not unexpected, as it reaches high latitudes in the Arctic (Hultén & Fries 1986).

Utricularia intermedia sensu lato. Shallow water over peat, Lochan Achlarich, E. of Beinn Heasgarnich, altitude 650 m, NN/434.380, 26 July 1995, CGE (Preston 95/59). Also present at the same altitude in a small lochan N. of this site, NN/432.381. This exceeds the upper limit given by White (1898) and Wilson (1956), 550 m in the Breadalbane and 565 m in the Rannoch areas of Perthshire. However, Druce (1932) cites a record made by P. Ewing at 990 m on Ben Lawers, a record so much higher than the others that confirmation is desirable.

Nitella flexilis. In lochan fed by two melting snowpatches, 200 m S.E. of the summit of Beinn Heasgarnich, altitude 1005 m, NN/415.382, 26 July 1995, CGE. Forming low sward in water 20–30 cm deep over soft silt, in absence of vascular plants, smaller lochan S.W. of the summit of Meall nan Tarmachan, altitude 950 m, NN/581.386, 25 July 1995, CGE. Deep water in lochan on peat (but just below rock outcrops), N. end of Coire Heasgarnich, altitude 930 m, NN/420.389, 26 July 1995, CGE. Lochan Coire Dhuhclair, altitude 735 m, NN/497.329, 27 July 1995, CGE. N. F. Stewart now splits this species into the segregates *N. flexilis* and *N. opaca*. The specimens from 1005 m on Beinn Heasgarnich can only be identified as *N. flexilis* sensu lato but N.F.S. has identified the other three plants as *N. opaca*. Wilson's (1956) upper limit for the genus, *N. flexilis* at 545 m, is clearly much too low.

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COLONISATION BY *COCHLEARIA OFFICINALIS* L. (BRASSICACEAE) AND OTHER HALOPHYTES ON THE ABERDEEN-MONTROSE MAIN ROAD IN NORTH-EAST SCOTLAND

Clumps of *Cochlearia officinalis* L. (Common Scurvygrass) have been visible on the verges of the A92 road south of Stonehaven since the 1980s, and possibly earlier. Because halophytes have been increasing elsewhere in Britain along trunk roads in the last 20 years (Scott & Davison 1982; Scott 1985; Leach 1994), a similar spread could be occurring in N.E. Scotland. We therefore made a car-borne survey of the coastal main road in Kincardineshire (v.c. 91) in late April and early May 1997, driving slowly along its whole length in the vice-county looking for flowers of halophyte species. On finding plants we assessed their distribution pattern across the road verges.

For the survey we searched between the North Esk bridge just north of Montrose and the Dee bridges in Aberdeen, with extra traverses on key sections. We also checked the branches of the coast road leading into Stonehaven (designated A92 until the mid 1980s when Stonehaven was by-passed) and the A956, which gives a second entry to Aberdeen further east than the main road (Fig. 1). From Aberdeen to the south end of the Stonehaven by-pass, the road is now a dual carriageway and numbered A90;

- + Population <10 clumps
- Population 10–100 clumps extending 5–200 m
- Population >100 clumps extending c. 1 km

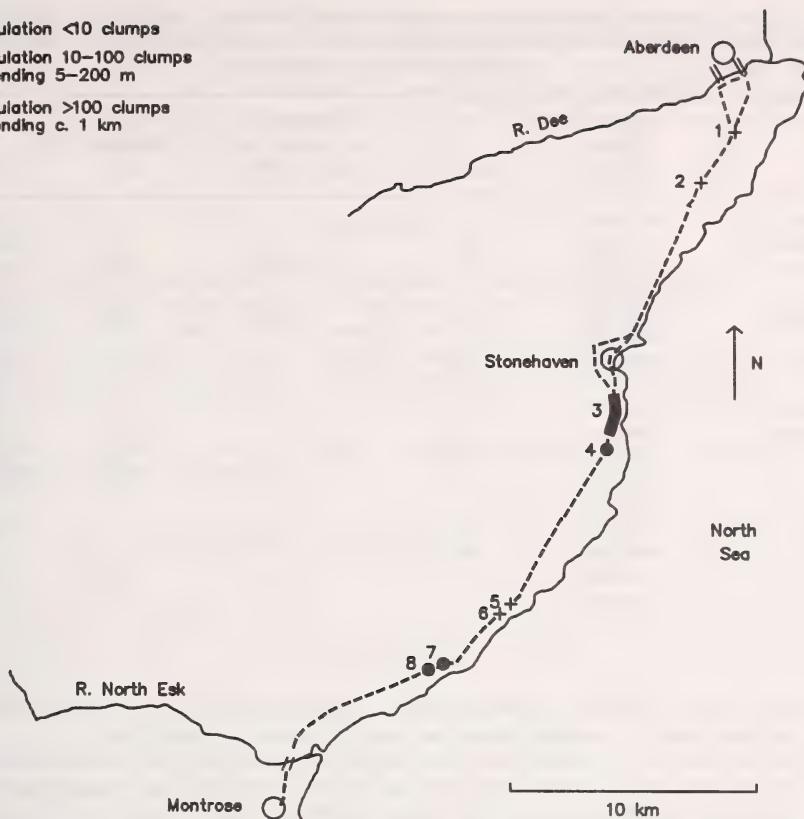


FIGURE 1. Distribution of *Cochlearia officinalis* on the Aberdeen – Montrose main road in spring 1997.

from the Stonehaven by-pass to Montrose the road is a single carriageway apart from a short section near Gourdon (location 5, Fig. 1).

Clumps of *Cochlearia officinalis* were recorded in eight locations, and *Armeria maritima* (Miller) Willd. (Thrift) in three locations (Table 1). Although we would have missed any non-flowering plants of *A. maritima* and *C. officinalis*, and perhaps also some small flowering clumps if obscured by tall grasses, we are confident that major colonisation has occurred on only two sections of road near Dunnottar (locations 3 and 4, Table 1) and Johnshaven (locations 7 and 8). At three other locations only single clumps of *C. officinalis* were seen. The *A. maritima* colonies were all small, although the size of the clumps indicates that they have been established for several years. *Plantago maritima* L. (Sea Plantain) and *Spergularia marina* (L.) Griseb. (Lesser Sea-spurrey) were also found, each at one location (locations 5 and 3 respectively), when we were examining the verges on foot. They probably grow in more places along the A90/A92, but would not have been noticed as they flower later than *A. maritima* and *C. officinalis*. No plants of *Cochlearia danica* L. (Danish Scurvygrass) were seen in this survey, but in a check on the inland stretch of the A90 in Kincardineshire (v.c. 91) on 20 May 1997, four small clumps were found near Laurencekirk (NO/701.699–726.720). This road is a dual carriageway running W.S.W. from the Stonehaven by-pass (NO/861.843) to the vice-county boundary at North Water Bridge (NO/651.661); it was searched less thoroughly than the coastal main road and at greater speed, and no other halophytes were observed.

The distribution of *C. officinalis* within the colonies on the coast road was somewhat patchy, and at Lauriston the clumps appeared to be confined to one side of the road (Table 1). Across the verges there was a clear pattern of greater frequency of clumps at the road edge. However, this was much less marked than for *C. danica* on the M6 and M74 in northern England and southern Scotland (personal

TABLE 1. DETAILS OF OCCURRENCES OF *ARMERIA MARITIMA* (Am) AND *COCHLEARIA OFFICINALIS* (Co) ON THE ABERDEEN-MONTROSE MAIN ROAD IN SPRING 1997. ALL LOCALITIES ARE IN KINCARDINESHIRE (V.C. 91)

Locality	Grid reference (all NO)	Species	Population size (no. clumps)	Spread (m)	Position
1. Loirston	931.001	Co	1	< 1	East verge
2. Bourtreebush	910.955	Co	1	< 1	Central reservation
3. Dunnottar	872.837– 873.810	Co	c. 2000	2700	Both verges
4. Catterline	866.798– 867.799	Co	c. 20	100	Both verges
5. Gourdon	824.711	Am	1	< 1	East verge
		Co	10	3	East verge
6. Benholm	810.691	Co	1	< 1	S.E. verge
7. Johnshaven	795.672	Am	1	< 1	S.E. verge
	792.671	Am	1	< 1	S.E. verge
	788.670– 789.670	Co	c. 100	100	Both verges
8. Lauriston	787.699	Am	c. 10	50	Both verges
	784.698	Am	1	< 1	S.E. verge
	780.668– 782.669	Co	c. 50	200	N.W. verge

observations); some clumps of *C. officinalis* occur at a distance from the carriageway. Plants were also observed on both sides of boundary fences and next to boundary stone dykes.

Grass verges exist along 63 km of the 70 km of the coast road, nearly all outside built-up areas. The length of verged road lying within 1 km of the sea totals 17 km, and over approximately 18% of this length *C. officinalis* is now established (Fig. 1). On the 39 km of verged road lying 1–2 km from the sea there are presently just two clumps of *C. officinalis* (locations 1 and 2, Table 1). Despite the closeness of the road to the coast, direct links to maritime semi-natural plant communities are few; mostly there is a strip of arable farmland between the road and the shore, with housing at settlements such as Inverbervie (NO/83.72).

Nearness to the sea, and the consequential deposition of salt by wind, seem to be the primary factors controlling halophyte colonisation on the Aberdeen-Montrose road. But once plants have got established they appear to be being spread by gusts of wind from passing traffic (Scott 1990), hence the patchy longitudinal distribution of *C. officinalis* along the verges. The two isolated clumps of *C. officinalis* at locations 1 and 2 (Table 1), nearly 2 km inland and 12 km from other roadside locations, have probably been dispersed by vehicles. Salting to prevent ice and snow accumulation is moderately intensive on the coast road, and may be creating bare ground and niches for colonisation immediately next to the carriageway (as suggested by Scott & Davison 1982), hence the greater frequency of *C. officinalis* in the 50-cm band closest to the road where about half the area is bare soil. In some sections of the A90 near Aberdeen, tracks with bare earth have been created by people walking along the verge, but no colonisations were observed there.

C. officinalis has spread along inland roadsides much less rapidly than *C. danica* (Scott & Davison 1982; Leach & Rich 1989; Leach 1994), although sizeable populations of the former are now established in S.W. England. Colonisation of roadsides in an area of S.W. Wales (Chater 1975) was judged by Scott & Davison (1982) to be a spread from adjacent long-established colonies in semi-natural vegetation rather than a consequence of road salting, but the distribution map given by Leach & Rich (1989) shows a clear relationship to trunk roads in Devon and Somerset. *Armeria maritima* has few inland records along roads (Scott 1985), and one reported occurrence in N.E. Scotland is associated with serpentine soils, there being adjacent populations on serpentine outcrops (Welch & Welch 1988).

We therefore conclude that the present populations of *C. officinalis* and *Armeria maritima* along the Aberdeen-Montrose coast road are largely colonisations of suitable non-ploughed habitat within the

coastal zone affected by natural salt deposition. But with a considerable population of *C. officinalis* now established and many seeds being dispersed, more rapid advance along trunk roads could occur in N.E. Scotland in the next few years, as has happened in S.W. England. However, as *Cochlearia danica* is now well established on the A74/M74 in southern Scotland as far north as Hamilton, and has begun to colonise inland trunk roads in northern Scotland, at Laurencekirk and probably elsewhere, there could well soon be a fascinating meeting here of the two species.

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Book Reviews

The wild plants of Sherkin, Cape Clear and adjacent islands of West Cork. Edited by J. Akeroyd. Pp. 180. Sherkin Island Marine Station, Sherkin Island, Co. Cork. 1996. Price IR£20.00. ISBN 1-870492-86-2.

This well-produced book covers the flora of two islands off the south-west tip of Ireland, Sherkin and Cape Clear, as well as over a dozen smaller islands and groups of islets in Roaringwater and Long Island Bays (v.c. H3). Building on Oleg Polunin's work when he visited and botanised on Sherkin and adjacent islands in the late 1940s, the work for this Flora was carried out mainly in 1981 and 1982 and from 1990 to 1995 by young botanists based at the Sherkin Island Marine Station, which also financed the project.

The thorough and readable introductory sections cover the climate, geology and soils, human history and land use, vegetation history, plant communities in a wide range of habitats, botanical exploration and a brief description of the islands, with two maps. Nearly 600 taxa of higher plants, including subspecies and hybrids, were recorded as well as two charophytes. It should be noted that planted taxa are included, for example, the conifers and some willows, so that the Flora is not just an inventory of wild plants as stated in the Introduction. Because of the generally acid nature of the island soils, relatively few calcicole plants occur. However, the richness of the flora is emphasised, and this West Cork "hotspot" is compared with other good botanical areas in Ireland such as the Burren. The concentration of rare plants is noted, and a particular feature is the arable weed flora, considered to be of national significance.

Entries in the Systematic List are clearly laid out. Scientific names follow *Flora Europaea* in the main. For each taxon, English and Irish names, habitats and distribution are given, and there are often additional interesting comments. Where there are historical records, some dating back to the 19th century, they are included. Over 80 references are listed (with a few inaccuracies, e.g. Praeger's major work is *Irish topographical botany* and *The way that I went* was first published in 1937) and two appendices contain a previously unpublished manuscript and agricultural notes by Polunin. Interspersed throughout the Systematic List there are 18 pages of useful line drawings, several to a page, by Elspeth Beckett. There are also 16 pages of colour plates which mostly show habitats and close-ups of plants and eight pages of black and white plates which show views on the different islands, especially interesting to those who are not familiar with the area. However, the line drawings, plates and maps are not listed in the table of contents.

The Flora is a welcome addition to earlier publications on the floras of other Irish islands, for example, Lambay Island, Clare Island, the Aran Islands, Inishbofin, the Magharees and Foynes Island. The editor and contributors are to be congratulated on this user-friendly and comprehensive work. It provides a baseline against which future changes can be compared, and it will undoubtedly stimulate botanists and others to visit the islands of Roaringwater Bay and Long Island Bay in West Cork.

S. C. P. REYNOLDS

Flora of North America north of Mexico. Volume 3: Magnoliophyta: Magnoliidae and Hamamelidae. Edited by the Flora of North America Editorial Committee. Pp. xxiii + 590. Oxford University Press, New York and Oxford. 1997. Price £65.00. ISBN 0-19-511246-6 [v.3].

Inevitably, a British botanist will compare *Flora of North America* with *Flora Europaea*; the floras are not much different in number of species, and the volumes of each work are virtually identical in shape and size, but the parallels end almost there. Whereas *Flora Europaea* is complete in five volumes, the American Flora is projected to extend to 25 volumes on the vascular plants, plus an introductory volume, three covering the bryophytes, and a final one with a cumulative index and bibliography. The sequence of the vascular plants is that of Cronquist, now familiar to British botanists. The keys are indented.

The volumes have so far been produced in sequence; Volume 3 (with 56 authors) is the first one on flowering plants, covering Magnoliaceae to Casuarinaceae (equivalent to Lauraceae to Betulaceae in our flora). Volumes 1 (Introduction) and 2 (Pteridophytes and Gymnosperms) were published in 1993 (for review of the latter see *Watsonia* 21: 141 (1996)). To illustrate the more expansive treatment in the American than in the European work with *Ranunculus*, 77 species occupy 47 pages in the former *Flora* while 133 species occupy 17 pages in the latter. On a page containing only species accounts usually three species appear in the former, about ten in the latter work.

The more detailed coverage of *Flora of North America* includes a full infrageneric classification, citation of basionyms with places of publication, authorities' names in full, flowering times, vernacular names, various supplementary observations on nomenclature, taxonomy and ethnobotany, etc., thumbnail distribution maps and very helpful line-drawings of a selection of species (e.g. 26 in *Ranunculus*), as well as a more extensive bibliography and rather fuller descriptions of taxa at all levels than in *Flora Europaea*. One item conspicuously missing is a key to families of angiosperms; the Introduction states that it "will be published separately". Most of the information provided here but not in *Flora Europaea* is extremely welcome, although in my opinion the text is often unnecessarily wordy.

The great majority of American species, even in genera familiar to us, are non-European. The number of European species (21) I counted in *Ranunculus* is probably unusually high; nine are introductions from Europe, ten are native boreal species, and two are native aquatics. The treatments of European taxa are occasionally unfamiliar to us: *Ranunculus reptans* is considered a variety of *R. flammula*; *Mahonia* ("seldom recognized by botanists") is included in *Berberis*; and *Papaver pseudoorientale* (wrongly given a hyphen), but not *P. bracteatum*, is included in *P. orientale*. On the other hand *Dicentra formosa* and *D. eximia*, and *Myrica cerifera* and *M. pensylvanica*, are kept as separate species.

This is an excellent Flora and, when complete, it will rank alongside *Flora of Turkey* and the like as one of the great Floras of the world. Unfortunately no indication of the time-scale for completion is given. Rather than repeat the map with geographical regions on both sets of end-papers, a conspectus of families on one of them, with volume numbers and the date of publication where relevant, would be much more helpful.

C. A. STACE

A Flora of Cumbria. G. Halliday. Pp. 611. Centre for North-West Regional Studies, University of Lancaster. 1997. Hardback £42.00, ISBN 1-86220-020-3. Paperback £32.00, ISBN 1-86220-051-3.

It has long seemed to me amazing that Cumberland (v.c. 70), a county of manifest botanical interest and countless visitors, should have no Flora more recent than 1898. That omission has now been handsomely rectified by Geoffrey Halliday's new Flora which also embraces the whole of Westmorland (v.c. 69) and Furness (v.c. 69b) as well as part of v.c. 65 (Sedbergh area) and one parish from v.c. 60. It replaces W. Hodgson's *Flora of Cumberland* and A. Wilson's *Flora of Westmorland* (1938).

First impressions of the Flora are good. It has an eye-catching cover, the page layout and typeface are clear and the text is liberally interspersed with colour plates and figures. More detailed examination does nothing to dispel the initial reaction and amongst the preliminary essays I particularly liked the summary tour of the main botanical regions and the chapter on conservation, a more balanced account than is fashionable. Rather surprisingly the number of species recorded in Cumberland is similar to that noted by Hodgson 100 years ago, but these totals obscure losses of many casuals and over 50 native species which have largely been compensated for by new garden escapes and a small number of other natives.

The species accounts are the core of any Flora. For all but the scarcer species they are accompanied here by tetrad distribution maps which are greatly improved by being printed on a base map showing relief in colours. Where no map is given localities are listed, with 10-km grid reference only. For some species there are references to the distribution elsewhere in Britain which put the present findings in context. Historical records are in general only quoted where plants have not been refound. All accounts give statistics of tetrad frequency and presence/absence in each of the five vice-counties from which Cumbria is assembled, as well as the highest altitude at which the plant was found during the survey.

This latter feature applies also to the critical genera for which such data have not readily been available. There are frequent comparisons with records and comments from the previous Floras.

A notable feature of the work is the detailed treatment given to the critical genera *Rubus*, *Hieracium* and *Taraxacum* (the *Hieracium* and *Rubus* species are even mapped at the tetrad level). The accounts reflect not only a great deal of effort by the author and others in the field but also considerable contributions by the relevant specialists. For *Rubus*, *Hieracium* and a few other difficult genera the provision of keys will be a real help to the ordinary botanist and could well be found useful beyond Cumbria.

All in all, this is a work of considerable scholarship. A massive amount of information has been presented in a clear and digestible form. The colour plates are almost uniformly of high quality as well as being nicely varied. I particularly liked the choice of aerial photographs for sites like High Cup Nick and Humphrey Head which show their unique character in a way that no view from ground level could. The quotations scattered about the text came as a pleasant surprise, particularly the extracts from Norman Nicholson's poems, and when such pleasures seemed to be at an end, the wonderful Kafkaesque piece from the 1980 Wastwater/Ennerdale Public Inquiry provided entertainment of a different and wholly unexpected order.

The size (A4) and weight (c. 2.2 kg) of the volume are somewhat daunting but given the amount of information presented it could hardly be otherwise. Errors in the text are commendably few.

I can unreservedly recommend this Flora and expect it to be consulted with profit not just by those resident in or visiting Cumbria.

D. J. McCOSH

The Plant-Book: a portable dictionary of the vascular plants. D. J. Mabberley. Pp. xvi + 858. Cambridge University Press, Cambridge. 1997. Price £32.50. ISBN 0-521-41421-0.

This second edition of *The Plant-Book* is 150 pages longer than the first, has nearly 2500 new entries and almost all the longer entries have been amplified. Owners of the original are strongly recommended to upgrade. Botanists who do not have a copy should know that this wonderful book is an alphabetical list of family, generic and English names of vascular plants. Descriptions and synopses are given of the families. For each genus the family, numbers of species and distribution are always given, as well as in many cases much other information. The citing of revisions is one of the most valuable features.

To give a flavour of the book (with items new to the second edition italicised), under rose-bay willow-herb (which Mabberley includes in *Epilobium*; he tends to be conservative in his taxonomy, especially in generic splitting) we learn that it has been included in *Chamaenerion* and *Chamerion*, that it is also called fireweed and wickup, is cultivated for ornament, is indigenous in the North temperate region, its distribution has greatly increased in Great Britain (where the highland populations are possibly indigenous, and the lowland ones come from America or Europe) in the 20th century possibly through the increase in habitats (bomb sites, etc.), autogamy is almost impossible for it (it is highly protandrous, and dichogamy was first described by Sprengel from this plant), the roots live for 20 years, the leaves are eaten as greens by the North American Indians and are used by them and in Russia for tea, the pollen concentrates gold, and the honey is excellent.

The range of information throughout is fascinating, other new items including facts such as that the balls used to draw the fixtures in the F.A. Cup are made from box, that the leaf juice of *Carpobrotus* is smeared over newborn Hottentots, that McDonald's uses the potato cultivar 'Russet Burbank' for its chips, and that male seedlings of the *Salix myrsinifolia* - *S. phylicifolia* complex in N. Sweden are consumed by voles three times as much as females (there are more males on vole-less islands). *The Plant-Book* can also be very helpful in everyday life. Being over-stimulated by caffeine, I recently bought a guarana instant drink as the label said it was an uplifting alternative to tea or coffee and especially because it said "contains no coffee beans". The second edition (but not the first) tells me that guarana (*Paullinia cupana*, Sapindaceae) when dried as a tea contains "4·3% caffeine, i.e. 3-5 times that in coffee".

Errors and misleading statements (e.g. *Luronium* rootless, *Epilobium brunnescens* naturalised in N.W. England) are inevitable though disconcerting, but seem to be few. A plaintive bibliographic note on p. xvi, which the publishers unfortunately seem not to have read, observes that in the first edition the

first printing was on thick paper and without the rounded page corners to match those of the soft cover. The proper thin paper with rounded corners came only with the second printing two years later. The first printing of the second edition reverses these faults with a vengeance and is one of the nastiest pieces of book production I have seen. On good thin paper, of genuinely pocketable size, it is encased in thick boards, with sharp corners accentuated by the rounded corners within; it would destroy any pocket within minutes, and could be used to kill. Potential purchasers who need a pocketable book might await a reprint in the hope that it will then have the soft, rounded covers of the first edition.

A. O. CHATER

Plant breeding systems, 2nd ed. A. J. Richards. Pp xii + 529. Chapman and Hall, London. Hardback £75.00. ISBN 0-412-57440-3. Paperback £29.99, ISBN 0-412-57450-0.

The importance of the role of the breeding system in the evolution of plant species is widely recognised. Breeding system transitions, be they driven by subtle changes or major developmental shifts, can have profound effects on microevolutionary processes and the partitioning and maintenance of genetic variability within and among populations. This striking effect of the breeding system on genetic architecture is plainly evident to taxonomists. Deviations from random outbreeding that lead to either preferential mating within lineages, or clonal propagation, are responsible for much of the taxonomic confusion associated with many of the "difficult" groups in the British flora such as *Epipactis*, *Euphrasia*, *Hieracium*, *Rubus*, *Taraxacum* and *Ulmus*.

The publication of the first edition of *Plant breeding systems* in 1986 was an attempt to provide a synthetic volume covering a diverse array of aspects of plant reproductive biology. That the book remained in print for ten years is a testament to John Richards' success in bringing together a wealth of information in one volume and also the importance of the subject to the botanical and broader scientific community. A total of 281 citations of the first edition in the journals covered by the Bath Information Database (BIDS) is an impressive number for a book in the field of plant natural history.

The second edition of *Plant breeding systems* reflects the massive advances in the field over the last ten years, and much of the text has been rewritten. Some 500 new references are included, and the bibliography alone makes this a useful publication. The new edition supersedes the last, and in particular I found the section on self-fertilization and inbreeding informative. My only disappointment was the omission of the chapter on vegetative reproduction, as much work has been done in this area since 1986, and a summary of the work on the extent and distribution of clonal diversity and interactions would be timely. I accept, however, John Richards' point (made in the preface to the second edition) that this chapter was somewhat tangential to the rest of the book.

The second edition of *Plant breeding systems*, like its predecessor, represents a significant contribution to the field and is to be strongly recommended to all those interested in plant taxonomy, reproductive biology, population biology, ecology and evolutionary biology. Its chapters on sexual theory, sexual reproduction, floral diversity and pollination, pollination biology and gene flow, self-incompatibility, heteromorphy, dicliny, self-fertilization and inbreeding and finally agamospermy, represent a valuable and accessible summary of the subject.

P. M. HOLLINGSWORTH

Rothschild's reserves: time and fragile nature. M. Rothschild & P. Marren. Pp. xv + 242. Balaban Publishers in association with Harley Books, Rehovot, Israel. 1997. Price £15.00. ISBN 0-86689-048-3.

The history of nature conservation in Britain has been well studied by John Sheail and others, but little attention has been given as to what might have been the position today if one of the founding fathers of nature conservation, Nathaniel Charles Rothschild, had not died prematurely in 1923. Rothschild's vision was to protect and preserve the varied habitats of rare and dwindling species by setting up a nationwide network of nature reserves through the co-operative efforts of government, local naturalists' societies and private landowners, assisted by scientists within and without the United Kingdom. Such a network would encompass the geographical range of habitats and would pay particular attention to formations, such as shingle beaches, western heathlands and bogs, which were rare or unknown on the

Continent. This was being said in 1912, some 40 years before the first national nature reserves were, in fact, established. It is also worth recording that Rothschild formed the Society for the Promotion of Nature Reserves (S.P.N.C.), which later became the parent body of the county wildlife trusts and played an important role in the establishment of an official nature conservation agency in Britain.

In this beautifully written book, Miriam Rothschild (Charles Rothschild's daughter) and Peter Marren use previously unpublished documents, as well as other public archives, to explore what went on behind the scenes as Rothschild attempted to persuade and cajole other bodies and individuals to support his efforts to save Britain's wild places. One of the first things he did was to compile a list or dossier of places most "worthy of permanent preservation". Information on these sites came from a variety of sources: amateur naturalists, eminent botanists such as G. C. Druce, university-based ecologists such as A. G. Tansley and W. H. Pearsall, entomological friends and Rothschild proposed 27 sites himself. By 1915, a list of 284 proposed nature reserves in the U.K. had been compiled, of which 182 lay in England and are the main focus of study in this book.

The reasons why some sites were included and others not chosen make fascinating reading. There was a detectable bias towards coastal sites and localities for rare lepidoptera, or certain rare flowers like the pasqueflower (*Pulsatilla vulgaris*) and orchids. Mesotrophic grasslands, including sites famous for attractive species such as *Fritillaria meleagris*, were ignored on the grounds that they were associated with human occupation and intensively managed as hay-meadows. Oolitic grassland in Northamptonshire (near Rothschild's home) was well-represented whereas large tracts of similar grassland in the Cotswolds were ignored. Woods and uplands were under-represented, possibly because the threat from conifer plantation was not perceived at the time. Some large areas, such as the New Forest, Ashdown Forest, The Mendips and the Norfolk Broads, were included but the main interest lay in protecting areas of special interest within them.

The aim was to distribute "reserves as evenly as possible over the whole country" but there was a strong degree of bias in the England list towards southern counties which reflected surveyors' interests and knowledge (the same potential bias was one of the things we tried to avoid in the Nature Conservation Review of 1977!).

With all their limitations and oddities, the "Rothschild lists" were a milestone in the history of nature conservation in Britain. Some measure of their worth may be judged by the fact that most of the sites are now scheduled as Sites of Special Scientific Interest. A large proportion are now nature reserves and many formed the core from which the initial tranche of National Nature Reserves were selected when the Nature Conservancy was set up in 1949.

About two-thirds of this book is devoted to what became of the 182 "Rothschild Reserves" listed for England. The same formula is used for each site. Its original character and the reason for its selection is given, together in many instances with the names of the people most associated with the site. This is then followed by a brief account of what has happened to the site over the past 70 years or more and ends with a succinct assessment of the main effects.

Assessments range from "no overall loss" (Barton Hills, Bedfordshire), through "severe loss from habitat destruction (ploughing, reseeding and fertiliser)" (Aston Upthorpe Downs, Berkshire) to "complete destruction of botanical interest within the proposed reserve" (Babbacombe Cliffs, near Torquay).

The thumb-nail sketches of each of the 182 reserves are gems in themselves and as they are arranged alphabetically, readers can easily find out about sites which they know and love. What makes this book so readable and enjoyable are the snippets of information which illustrate the foibles of human nature and how these have affected the survival of a particular reserve or site. Regarding the fate of Braunton Burrows N.N.R., "the military's proposals to lay down an 18-hole golf course there were fortunately averted after Miriam Rothschild invited the C.O. to lunch and convinced him of its disadvantages, with the help of a bottle of Chateau Lafite". O for modern administrators with such foresight and good taste! A second example concerns the shingle beach at Dungeness, Kent, whose preservation Rothschild regarded as "of the utmost priority". This site contained ancient holly groves which are unique in Europe but the main interest has always been ground nesting birds, including the rare Kentish plover, and the R.S.P.B. had for long taken the lead in opposing any threats. Unfortunately, they did not oppose shingle extraction and today half the shingle is gone and only 28% remains intact. The last blow was the nuclear power station, built after a bitterly contested public inquiry in 1957. The last two sentences succinctly summarise what has happened to Dungeness "half of Rothschild's Dungeness lies beneath Britain's motorways. Its story is a national scandal".

The text of the book is interspersed with black-and-white photographs of some of the more important personalities involved in the story of Rothschild's Reserves. These, and other photographs of the original maps on which the reserves were marked, and old photographs of sites such as Cheddar Gorge and Box Hill, provide added interest to a text which is a joy to read. The book also has a fair smattering of colour photographs of sites and key species which further enhance the text.

I unreservedly recommend this book to all who have an interest in nature conservation and particularly to those who would like to know more about how nature reserves were selected and what became of them.

T. C. E. WELLS

Cultivating women, cultivating science: Flora's daughters and botany in England, 1760–1860. A. B. Shterir. Pp. xi + 301. Johns Hopkins University Press, Baltimore, Maryland, U.S.A. & London. 1996. Price £20.50. ISBN 0-8018-5141-6.

Do not be put off by the main title: as the subsidiary one indicates, this book introduces us to a remarkable range of women botanists in England over a century that saw enormous social change, not least in the place of women in the society in general. Most of us, I feel, would be hard put to it to mention a single woman author of a botanical book in the period covered. In my own case, Anne Pratt, whose children's book *Wild flowers* (1852–3) was reprinted many times in the Victorian period, was the only one I would have known before reading Ann Shterir's fascinating book. Perhaps my single author was an appropriate choice for a B.S.B.I. member, for here is how Anne Pratt begins her book:

"Every child who has wandered in the woods in the sweet months of April and May knows the Bluebell or Wild Hyacinth."

Younger members of the Society will, of course, be familiar with the English Bluebell as the Society's logo (though they may not know that it was only recently adopted, to replace the earlier, grossly inappropriate, though patriotic, *Victoria* water-lily). And it is good to think that our Society's predecessor, the Botanical Society of London, founded in 1836, did not hesitate to admit women as full members, so that Anne Pratt could well have been an early member – though there is no evidence that she joined.

Ann Shterir's book, like much modern American "women's writing", is parti pris. Her general thesis is that able and devoted English women throughout the century from 1760 (a random starting point) could study botany, as opposed to most other sciences, by operating "within the dominant gender ideology of the time". She makes a convincing case for seeing the period as consisting of an earlier "Enlightenment" phase where, for both men and women, rational science was an acceptable pursuit for the aristocracy and the members of the increasingly numerous professional class, and a later, more complex and difficult late Georgian and early Victorian culture, in which both the rise of professional science and the spread of an evangelical, often relatively illiberal theology within the established Church made the society more overtly opposed to most movements for equality in educational opportunity between women and men.

So much of Shterir's material is new to me that I hardly know where to pick to illustrate how rich and varied is this feast of learning. I was especially pleased to learn that one Elizabeth Warren, helped greatly by the elder Hooker, published the first botanical wall-chart as early as 1839. Entitled *Botanical chart for schools*, it set out the Linnaean classes and orders, and lists typical genera, but unfortunately did not sell well.

One weakness of the book reveals itself fairly quickly: there are occasional botanical errors which might have been avoided. On p. 155, for example, there is a short passage which purports to explain how and why the natural system of plant classification associated with de Jussieu and de Candolle gradually gained acceptance over the sexual system of Linnaeus. This passage fails to clarify the essential differences between the two systems, partly by apparently using the term "physiological" in a now wholly outmoded way; and we are told that "it was Candolle who grouped plants in monocotyledons and dicotyledons" – with no acknowledgment that John Ray had in fact done just that over a century earlier!

One delicate subject crops up throughout the book: the anthropomorphised sexual parts of the Linnaean flower. Is this *really* a suitable subject for ladies? Generalising, one might say that censorship

of phrases like "two husbands in one bed" for *Diandria Monogynia* was more obvious in the popular books of the early Victorian period than it was in the late eighteenth century. But Shteir's numerous examples show a surprisingly wide range of reaction, and no simple generalisation is possible.

The volume is handsomely printed and bound, with an excellent bibliography and index. It should be in every institutional botanical library, and deserves a place in the private libraries of all botanists, amateur and professional, with any interest in the history of their science.

S. M. WALTERS

Notes on the British and Irish orchids. D. M. Turner Ettlinger. Pp. 161. Published privately by the author (Royden Cottage, Cliftonville, Dorking, Surrey). 1997. Price £17.95 + £0.85 p. & p. ISBN 0-9530380-0-9.

This book is a genuine novelty – an illustration-free iconograph! Derek Turner Ettlinger has devoted much of his life to photographically documenting all of the variation shown by European native orchids. Surprisingly, despite the general popularity of illustrated books on orchids, potential publishers fought shy of the concept of a comprehensive iconograph of the British and Irish taxa – we are left with only the superb cover illustration of a hyperchromic *Dactylorhiza fuchsii* to hint at what might have been. Instead, the author was eventually obliged to scale down the project as first conceived to these expanded notes, originally intended to supplement the photographs. The result is a slender softback, published by the author and therefore inevitably rather expensive, but for me at least sufficiently stimulating to warrant the cost.

Ettlinger believes that detailed studies of morphological variation capture the essence of evolution. More controversially, he also believes that recent "popular" taxonomic treatments such as Delforge's *Orchids of Britain and Europe* (1995) strongly emphasise species over infraspecific taxa and hence are unjustifiably "flat", in contrast to more hierarchical treatments such as Sundermann's *Europäische und Mediterrane Orchideen* (3rd ed., 1980). Yet more controversially, he believes that every minor variant merits formal taxonomic distinction (but adds that he lacks "the facilities" to perform the necessary taxonomic changes). His thoughtful and clearly expressed taxonomic philosophy is captured primarily in six all-too-brief introductory pages and 21 pages of enumerated "Notes", irritably aggregated near the back of the book. Between are sandwiched 95 pages of taxonomic descriptions, short and sharp, informal and informed. The author readily admits that these need to be read in conjunction with a comprehensive iconograph such as that of Delforge and, as befits a study of variation, he eschews oversimplistic dichotomous keys. A sometimes idiosyncratic glossary and critiqued bibliography complete the ensemble.

Ettlinger determinedly tackles several sacred cows. Most are in my view successfully sacrificed. Most of the uncritical assertions of interspecific hybridisation still so popular in orchidological circles are given short shrift (see also Pridgeon *et al.*, *Lindleyana* 12: 89–109, 1997). Well-intentioned but misdirected conservation measures are epitomised by the potentially lethal effect of slug pellets on the essential mycorrhizal fungi of the saprophytic Ghost Orchid, *Epipogium aphyllum*. Chastising the wilful reluctance of many orchid systematists to take satisfactory account of morphological overlap between supposed "morphospecies" inevitably raises the perennial spectre of the dactylorhids. He further debunks popular errors regarding certain diagnostic characters, geographic distribution and phenological constraints, including incorrect assertions of monocarpism. Other cows scotched in passing, notably the "God Objectivity and his disciple Statistics", might have been better left unmolested (but then I too am biased on this topic!).

Unusually explicit statements of the taxonomic rationale used throughout the book are laudable. Presumed isolation mechanisms are prioritised over degrees of morphological differentiation for both species and subspecies, with non-isolated morphs being assigned to a large number of varieties. This is logical, though I would treat some of these entities as formae and leave the rest wholly outside the realms of formal taxonomy. Ettlinger's bravery extends to the imperfect art of prediction, notably regarding taxa that have thus far passed unrecorded but should be British natives, the arguably natural origins of several recent "adventive" occurrences, and the likely beneficial impact of the battery of modern molecular techniques on delimiting native orchid taxa and determining their relationships. This revolution has in fact already begun (e.g. Hedren, *Plant systematics and evolution* 201: 31–55, 1996;

Bateman *et al.*, *Lindleyana* **12**: 112–141, 1997) and, somewhat ironically, may well undermine some of the more controversial taxa recognised in this book: examples include *Epipactis youngiana*, *E. helleborine* subsp. *neerlandica*, *Dactylorhiza majalis* subsp*p. cambris*, *ebudensis* and *lapponica*, *D. majalis* subsp. *traunsteineri* var. *bowmannii* and *Orchis mascula* subsp. *ebudium*.

Overall, the ever-growing legion of orchid enthusiasts will find much of interest in this individualistic, rational and educated update on current knowledge of our native orchids. It is without doubt sufficiently provocative to gather the extensive emarginations explicitly encouraged by the author.

R. M. BATEMAN

The new Oxford book of food plants. J. G. Vaughan & C. A. Geissler. Illustrations by B. E. Nicholson, E. Dowle & E. Rice. Pp. 239. Oxford University Press, Oxford. 1997. Price £25.00. ISBN 0-19-854825-7.

A new edition of that most valuable reference and teaching aid, *The Oxford book of food plants* (1969), has long been overdue. Now we have it, and this welcome reissue comes too in a much updated, expanded and reworked version. The revised work has certainly absorbed an upbeat contemporary feel, yet retains its classic, slightly old-fashioned air of authority and respectability. The text is full of useful information and avoids the contemporary trend to dumb down popular science. The plates are elegant and informative.

The book is laid out, in both editions, with the simplicity of W. Keble Martin's *Concise British Flora*: colour plates (95 in all) on the right, explanatory text (unlike the *Flora* usually filling the page) on the left. Crops, with some wild plants, are arranged by family or by structure: leaf, petiole, root, etc. Here is a celebration of edible plants, their central role in our lives and the efforts of generations of farmers and gardeners who carefully selected and nurtured the crops that we eat today.

This is truly a new book, in both textual and species content. The last three decades have seen plant foods in Britain derived from more cosmopolitan sources than ever before. Our affluent, seemingly food-obsessed society has taken to its heart large numbers of novel (at least to us in the West) fruits, vegetables and grains, especially from the Mediterranean and Orient. Mass communications and expanded trade and travel make the world a smaller place than in the 1960s, and immigrants from all over the globe have brought us their own cuisine and allotment crops (and the odd weed). This copiously illustrated book provides a handy means of identifying foodstuffs, seeing what they look like in a native state and how they are related to each other taxonomically and in plant structure. Students especially have here a ready source of information about the cultivation, geography, history and nutritional content of food plants.

The plates are slightly clearer and more luminous in the new edition. They are also set off nicely by a wider page border. Plates added to this edition include prickly pear and kiwifruit, icon of the upwardly mobile fruit-salad; several types of squash, a frequently undervalued vegetable (in the U.K. at least) now popularized by Hallowe'en and Prize Pumpkin shows; and the severer pseudo-cereals like buckwheat and, from the high Andes, quinoa. These last two are increasingly appearing in the British countryside as food for game birds.

Other helpful additions are a revised, longer Introduction, a list of books for "Recommended reading" and separate subject and species indices. The final section on nutrition has evolved into a substantial 26 pages, including tables of food value. These, and a new title "Nutrition and Health", will probably capture a wider readership among students of cookery, food and health. The unkinder reader might well detect a nasty whiff of Matron, or even of the prigs and bullies at the Department of Health.

Expanding the range of plants covered not only updates an indispensable work and makes it even more useful, but also emphasises the diversity of plant foods and how all plants need protection. Nobody knows, least of all the powerful plant breeding lobby and its acolytes in academia and government, just which cultivated and wild plants, intraspecific taxa and gene combinations we shall need in the long-term. Conservation of wild and cultivated food crops, even the obscurer leaves and tubers, is vital for us all and for future generations. *The new Oxford book of food plants* is an educational tool towards this end.

J. R. AKEROYD

Obituaries

NICHOLAS POLUNIN C.B.E., M.S., M.A., D.Phil., D.Sc., F.L.S., F.R.G.S. (1909–1997)

Professor Nicholas Polunin died in Geneva 8 December 1997. Polunin was so far sighted in environmental ethics of the earth and the future of the biosphere that the impact of his contribution will be greatly felt for many generations to come. He had been a member of B.S.B.I. since 1944, and one of his brothers, Oleg, was also well-known to B.S.B.I. members.

They were the sons of a Russian father and an English mother, Elisabeth Violet Hart, both artists at heart, although Vladimir, his father, was originally a forester. Nicholas' first marriage to Helen Lovat Fraser gave him a son and his second marriage to Helen Eugenie Campbell gave him two sons and a daughter. Helen Eugenie Campbell was of great assistance till the end of his life since she shared his vision, aspirations and knowledge of this fragile and endangered world.

Polunin had a brilliant career after obtaining a First Class Honours degree in Botany and Ecology from Christ Church, Oxford in 1932. He then left Oxford for two years to study at Yale for his M.Sc. which he received in 1934. He then resumed his research at Oxford and obtained his D.Phil. in 1935 and D.Sc. in 1942. Besides his academic prowess he was a great explorer with a particular penchant for Arctic regions and their botany, phytogeography, ecology, aerobiology and conservation. He was appointed the conservation editor of *International industry* from 1943 to 1946. This journal demonstrated the flair he had for global issues long before they became popular with other scientists.

Polunin's early interest was biased towards plant geography with emphasis on the flora of Spitzbergen, Lapland, Greenland, Iceland and Labrador, as well as various islands of the Canadian eastern Arctic. This involved a great amount of travel in times when communications were quite primitive and hazardous and while aviation was still in its infancy. In the great North he relied on the most environmentally friendly mode of travel, dog-sledge transport.

While an undergraduate at Oxford he joined a number of expeditions from which he collated much information for his books. The first, *Russian waters* was published in 1931. In 1932, he studied the plant life on Akpatok Island in the Hudson Strait which is described in the *Isle of auks*. During further botanical explorations in the 1930s in Arctic Canada, Greenland, Iceland and Lapland he recorded widely. He discovered many plant species new to science and continued his geographical interest by documenting botanical evidence for Viking movements between the North American continent and Greenland. He held a chair at McGill University, Montreal from 1947 to 1952. This post gave him geographical proximity to his study sites. He was in the party that discovered Prince Charles Island in the Foxe Basin, which was the last major island to be marked on the world's map, as well as Foley Island. Accounts of these discoveries appear in *Arctic unfolding* (1949). Between 1940 and 1948 he published in three volumes the *Botany of the Canadian Eastern Arctic: Pteridophytes and spermatophytes; Thallophytes and bryophytes* and *Vegetation and ecology*, followed by *The circumpolar Arctic flora* in 1959. He also published a standard field guide in 1960 called *Introduction to plant geography and some related sciences*. The number of scientific articles he managed to publish is also awesome, but all his invaluable contributions have been much needed considering the gloomy future for his planet – although Polunin remained hopeful all along as he outlined in *Rays of hope for planet earth and even its biosphere* in 1991.

Polunin also played a major role as research project director with the U.S. Air Force floating ice island project in the Arctic Ocean which continued when he took up the post of scientific adviser to the U.S. Army Corps of Engineers. Universities in Iraq (1956–58) and Nigeria (1962–66) also benefited immensely from his appointment in their Faculty of Sciences; however, political unrest forced him to return to Europe.

In 1967 he founded *Biological conservation* and edited it until 1974. That same year he founded the quarterly journal *Environmental conservation* aimed at influencing government policies. He was its editor until 1995 by which time he was 86 years of age! His reputation for boundless energy was well founded.

From the 1970s, without losing interest in botanical matters, he began to concentrate on global issues

vital to the survival of the planet. He sponsored and organised a multitude of international conferences on environmental and social issues with the aim of bringing together the world's academic scientists, industrialists, agriculturalists and governments. Some of these included: *The environmental future* (1972), *Growth without ecodisasters* (1980), *Surviving with the biosphere* (1990), *1st recycling congress* (1993). Public and governments' awareness were his utmost concern. He created a World Council for the Biosphere in 1983 in Geneva to promote public awareness of the growing threat to the environment. He contributed greatly to East-West relations as early as 1966 and in 1988 had a big impact with the International Vernadsky Foundation in Russia and its associated Centre for World Biosphere Studies in Pushchino. The 1986 Chernobyl nuclear tragedy demonstrated concretely the urgency for international cooperation on environmental matters and the need for nuclear disarmament. Acid rain travels over thousands of kilometres, chemical waste is dumped in poorer countries, large scale deforestation goes on daily for instant profit, the list is now endless. Polunin helped nations to communicate on a worldwide basis in organising and participating in many world symposia on an immense range of issues and topics irrespective of the countries' political persuasion. He sensed that highly populated countries such as India and China deserved as much attention as the industrialised polluting countries.

Polunin received many accolades such as the prestigious U.N. Sasakawa prize in 1987, the order of the Golden Ark in the Netherlands, the addition of his name to the Global 500 Roll of Honour, etc. These honours symbolised the world's appreciation and gratitude for his immense and far-sighted contribution to our environment and ecological ethos.

His early global approach to conservation was expressed in the 1971 International Conference in Finland. Twenty years later, in 1991, his belief in people power had not dwindled: he instigated the annual World Biosphere Day to be celebrated on 21 September each year to increase public awareness and celebrate the autumnal equinox. It is to be hoped that in future World Biosphere Day will be better publicised through his creation of Biosphere clubs and the resulting dissemination of his global concern for our planet.

Polunin also saw the importance of encouraging excellence among academics, he created the "Best paper" prizes given by the Confidential Award Committee of *Environmental conservation*.

Polunin's last major work in 1997 was the editing of a comprehensive text from the Foundation for Environmental Conservation compiled by Lynn M. Curme who has worked for the *Environmental conservation* journal for the last eleven years.

As a tribute to his quintessential work on our planet I would like to quote his own words from 1980: "One retains the abiding impression that Man now has the knowledge and means to save his world but still shows inadequate signs of acting in time and unselfish urge to do so" and from 1994 "... human existence on Earth is, after all, sustainable, we nevertheless must remember the fear of many that it is not, and the prophecy of some that all life on Earth is doomed. There being no other known source of life in the Universe than Planet Earth, the extreme threat, however remote, places on our species, as evidently the only existing organism with the intelligence of conscious foresight, the tremendous responsibility of safeguarding life – which, for healthy biospheric existence, means conserving all forms and manifestations of life that can be saved for posterity".

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A. BATAILLE

CAPTAIN R. G. B. ROE O.B.E., R.N.
(1911–1997)

Captain Robert Roe served a distinguished career in the Royal Navy and came to live in Somerset in 1951, to take up an appointment with the Admiralty in Bath. Both he and his wife became very interested in the rich local flora and this gradually led to more detailed botanical studies. He joined the Somerset Archaeological and Natural History Society and became plant recorder for the society. He also became a member of the Botanical Society of the British Isles in 1956 and the B.S.B.I. vice-county recorder for North Somerset 1965–1993 and South Somerset 1978–1993.

During this time he realised there was an urgent need for an up-to-date Flora of Somerset and in 1966 he organised a meeting at Crewkerne to launch this project. Over the next 15 years he encouraged and organised a group of many local botanists to record Somerset plants on a tetrad basis. His records were kept meticulously and with instant access so that one could always be sure of a rapid and considered response to queries.

The Flora was published in 1981, adding Somerset to the counties at that time provided with a modern Flora. He also produced maps of Somerset plants, preparing the way for a future more detailed Flora. The production of the Flora was a remarkable achievement, considering it was all maintained on record cards as was the custom before the use of computers. He added several new species to the Somerset list. Especially notable was the discovery in 1959 of several clumps of *Leersia oryzoides* along the Bridgwater and Taunton Canal.

Chris Boon tells me the following story about Captain Roe's enthusiasm for plants. "This tale was recounted to me by my late father. It may be apocryphal, but it has all the hallmarks of a dedicated amateur botanist: Captain Roe was in command of a ship in waters off the coast of Eire and, being the good botanist that he was, he knew of the presence of *Pinguicula grandiflora* in the southwest of Ireland. He had not seen this plant in the wild before and, being so close to its native habitat, he thought that the opportunity was too good to miss. The obvious course to take was to have himself rowed ashore and search the coastal hills. The adventure was successful but whether any evidence was taken in the form of a specimen I do not know."

He was also a keen conservationist and a member of the Somerset Wildlife Trust. His wide knowledge of Somerset plants helped a great deal with site recording and the assessment of new sites for possible reserves. Captain Roe will be remembered as a kindly man with a quiet sense of humour, and we extend our sympathy to Isabell, his widow and constant recording companion.

J. G. KEYLOCK

DAVID ALLARDICE WEBB (1912–1994):
BIBLIOGRAPHY OF PUBLISHED WRITINGS – ADDITIONS

A bibliography of the published writings of David A. Webb compiled by one of us (M.B.W.J.) was recently published in this journal (**21**: 7–13). It comprises 206 entries covering a wide variety of topics, written over a period of more than 60 years. It was there stated that further publications by David Webb would undoubtedly surface – as indeed they have. The present list of 28 includes overlooked botanical works, non-botanical articles published, for the most part, in Trinity College Dublin periodicals, a letter to *The Times*, and two works which had not been published when the bibliography was compiled.

Since publication of his bibliography a more accurate count of the number of families edited and species accounts written or co-written by David Webb for *Flora Europaea* has been made. Revised figures presented here replace those given in his bibliography: Volume **1**, 1st ed. (1964) – editor of 14 families and author of 303 species accounts; volume **2** (1968) – editor of 14 families and author of 192 species accounts; volume **3** (1972) – editor of six families and author of 351 species accounts; volume **4** (1976) – author of 30 species accounts; volume **5** (1980) – editor of nine families and author of 146 species accounts.

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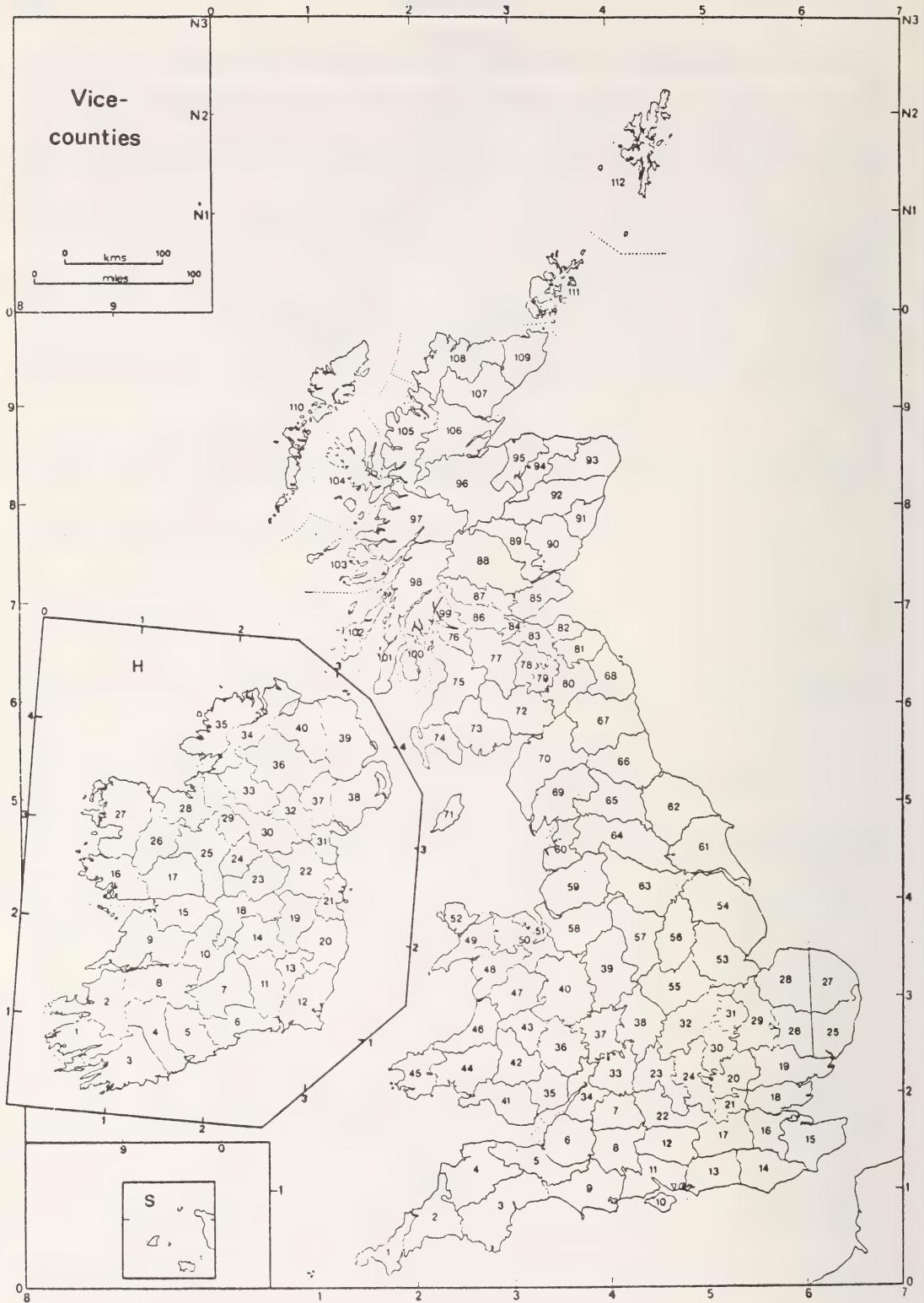
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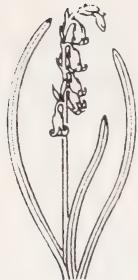
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August 1998 Volume twenty two Part two

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of registration of new non-fungal plant names.

The cover illustration of *Primula scotica* Hook. (Scottish Primrose) was drawn by
Rosemary Wise.

Identification, distribution and a new nothosubspecies of *Trichophorum cespitosum* (L.) Hartman (Cyperaceae) in the British Isles and N. W. Europe

G. A. SWAN

81 Wansdyke, Morpeth, Northumberland, NE61 3QY

ABSTRACT

The common form of *Trichophorum cespitosum* (L.) Hartman (Cyperaceae) in Britain and Ireland, growing in acidic peat, is subsp. *germanicum*, while subsp. *cespitosum* is rare in South Northumberland (v.c. 67) in marginal areas of *Sphagnum* mires, with base-enrichment, although specimens exist from elsewhere in Britain and Ireland. The characteristic *Trichophorum* of raised mires in v.c. 67 is a sterile hybrid between subsp. *cespitosum* and subsp. *germanicum*, corresponding to a plant found by E. Foerster in 1970 in the Harz Mountains and elsewhere in N. W. Germany, and for which the name *Trichophorum cespitosum* (L.) Hartman nothosubsp. *foersteri* G. A. Swan, nothosubsp. nov. is now proposed. The identification and distributions of these taxa are discussed. Possibly, in earlier times, subsp. *cespitosum* was the plant of raised mires in Britain, as in Norway today, but was displaced by the hybrid except in base-enriched, marginal areas. In Britain, proliferous forms of the hybrid and subsp. *germanicum* also occur.

KEYWORDS: Deergrass, raised mires, Harz Mountains, nothosubsp. *foersteri*, floral proliferation.

INTRODUCTION

NOMENCLATURE

The existence of two forms of *Trichophorum cespitosum* (*Scirpus cespitosus* L.), Deergrass (Cyperaceae) in Europe was noticed by Palla (1897), who described these as separate species, *T. austriacum* (= *T. cespitosum*) and *T. germanicum*. These species were separated on the basis of sheath character, stem anatomy and geographical distribution, the former being common in Austria and the latter in Germany. In recent years, only in Hess *et al.* (1967) have they been maintained as separate species. In De Filipps (1980) these are given as *Scirpus cespitosus* L. subsp. *cespitosus* and subsp. *germanicus* (Palla) Brodreson, respectively; and in Clapham *et al.* (1987) as *T. cespitosum* (L.) Hartman subsp. *cespitosum* and subsp. *germanicum* (Palla) Hegi, respectively. The use of the generic name *Trichophorum* rather than *Scirpus* is upheld by Salmenkallio & Kukkonen (1989).

Subsp. *cespitosum* has an arctic-alpine distribution and subsp. *germanicum* a Subatlantic distribution according to Oberdorfer (1969). In Hegi (1966) it is stated that they occur in circumpolar and Atlantic-Subatlantic Europe respectively (for distribution maps see Hultén (1962) and Meusel *et al.* (1965)). In Norway, subsp. *germanicum* has a coastal distribution, rising to 850 m, and avoids areas of long snow-cover, according to Fremstad & Skogen (1978), while subsp. *cespitosum* occurs in the mountains. Some overlap of range occurs there, as also in Britain and Germany.

In the northern part of North America the common (circumpolar) plant, growing in acidic peat, is known as *Scirpus cespitosus* L. var. *callosus* Bigelow, which corresponds to the European *T. cespitosum* subsp. *cespitosum* (Bigelow 1824). *S. cespitosus* L. var. *delicatulus* Fernald grows in calcareous habitats, but as it appears to be unrecorded in Europe, it will not be mentioned again in this paper.

The Atlantic-Subatlantic subsp. *germanicum* is not recorded for North America, but Fernald (1921) knew of its existence in Britain, the lower regions of Sweden, Denmark, France and Germany, and stated that in Europe this plant was known as *Scirpus cespitosus*. Possibly this was not surprising as many botanists in Britain (and probably also in the neighbouring countries of low

TABLE 1. CHARACTERS SEPARATING THE TWO SUBSPECIES AND THE HYBRID
(ALL NON-PROLIFEROUS) OF *TRICHOPHORUM CESPITOSUM*

Character	Subsp. <i>germanicum</i>	Hybrid	Subsp. <i>cespitosum</i>
Length of spikelet (mm)	3–6		3–4(–5)
Number of flowers per spikelet	8–20		3–7
Length of sheath-opening (mm)	2–3(–5)	1–1.5(–2)	(<1–)1(–1.2)
Length of blade (mm)	3–6	3–7	4–6
Ratio of length of sheath-opening/ length of blade	>0.4	(0.15–)0.2–0.35(–0.4))	<0.25
Margin of upper sheath-opening in herbarium specimens	red-dotted	red-dotted	yellowish or yellowish brown
Aerenchyma in stem	+		
Depth of substomatal cavities (μm)	6–7	8–18	20–26
Stomatal length (μm)	42–51	39–46	36.5–40.5
Perianth bristles	papillose		smooth
Excretory cells in old herbarium specimens	+	+	
Fruiting	+	-	+

+ : present, - : absent

altitude and latitude) failed to realise that their common plant is not *T. cespitosum* subsp. *cespitosum*, but is subsp. *germanicum*. Clearly, however, Fernald (1921) regarded *Scirpus cespitosus* L. as being identical with Palla's *Trichophorum germanicum*, but considered the latter name unnecessary in view of Roth's *S. cespitosus* β *nemorosus* (Roth 1789). However, I do not think that Roth's description identifies the Atlantic-Subatlantic plant.

The crux of the matter concerns whether *Scirpus cespitosus* L. refers to the circumpolar or the Atlantic-Subatlantic plant. The European nomenclature is based on the former, while Fernald suggested that Linnaeus had intended it to be the Atlantic-Subatlantic plant.

There is a specimen (Sheet 71.8) in LINN, but it is believed that this could not have been in Linnaeus' possession until after 1753 and so cannot be considered as an original element for this name, even though it bears the Linnean annotation "cespitosus" (N. J. Turland, pers. comm., 1994). However, the specimen, Herb. Linn. No. 20 (LAPP), is almost certainly the circumpolar plant and can therefore be designated as the lectotype. This will fix the application of the name *Scirpus cespitosus* L. to the circumpolar taxon, i.e. *T. cespitosum* L. subsp. *cespitosum* as it is currently understood in Britain and the rest of Europe. In the present paper I shall continue to follow tradition by using the epithet *germanicum* for the Atlantic-Subatlantic plant.

Fernald's nomenclature has been followed by authors of North American Floras, e.g. Beetle (1947) and Scoggan (1978), as well as in Japan (Koyama 1958). However, Hultén (1962) and Hegi (1966) have reaffirmed acceptance of the European nomenclature.

DISTRIBUTION

In Clapham *et al.* (1952, 1962) subsp. *cespitosum* is stated to be known only from Ingleborough and Ben Lawers, but Clapham *et al.* (1987) say "rare and its distribution is imperfectly known". However, in Clapham *et al.* (1981) subsp. *germanicum* is given, quite erroneously, as "rare" and subsp. *cespitosum* as "common".

In Stace (1991) and Kent (1992) subsp. *cespitosum* is omitted, evidently because no clear evidence of its occurrence in the British Isles could be found. Sell & Murrell (1996) state "All our plants seem to be subsp. *germanicum*, for although there are records of subsp. *cespitosum* they have not been substantiated, but plants intermediate between the subspecies have been recorded in widely scattered localities." Nevertheless, in Stace (1997) subsp. *cespitosum* has been reinstated.

In Northumberland subsp. *germanicum* is the common plant, growing in acidic peat in moorland and it appears to tolerate a variety of habitats of varying degree of wetness. However, as I first recognised in May 1988, there is also another plant in Northumberland, which is characteristic of the Border Mires (raised mires), but which also occurs on other *Sphagnum* mires. The distribution

of this is given in Swan (1993), where it was named *T. cespitosum* subsp. *cespitosum*, although queried as being possibly a hybrid. The sheath character of this plant is closer to that of subsp. *cespitosum* than to subsp. *germanicum*.

This plant from Northumberland, which has never been found to produce mature fruits, is now believed to be a sterile hybrid between subsp. *cespitosum* and subsp. *germanicum*, as demonstrated by morphological and anatomical work described in this paper, and confirmed by work using isozyme electrophoresis carried out by P. M. Hollingsworth (Hollingsworth & Swan 1999). A proliferous form also occurs.

Since 1988 I have extensively investigated *T. cespitosum* in Northumberland, but have found subsp. *cespitosum* at only four sites (all in v.c. 67), all less strongly acidic, or base-rich, or less stagnant than those where subsp. *germanicum* or the hybrid occur.

AIMS OF THE WORK

1. To assess critically the values of the various characters which have been used in attempting to identify the three taxa, and where appropriate relating such characters to geographical range.
2. To establish the plant of the Border Mires as being a hybrid.
3. To determine the distributions and habitats of subsp. *cespitosum* and the hybrid in Britain and Ireland and (so far as possible) elsewhere in N. W. Europe, and in particular to resolve the apparent anomaly that in Norway subsp. *cespitosum* is the usual plant of raised mires, whereas in Britain and Germany it is the hybrid.
4. To investigate the distributions and habitats of the proliferous plants.

IDENTIFICATION

GENERAL

Nomenclature of vascular plants follows Kent (1992).

Subsp. *germanicum* is the common plant, forming large, dense tufts, growing in acidic peat, often with *Calluna vulgaris*, *Erica tetralix*, *Juncus squarrosum* and *Molinia caerulea*. The broad lower glume sometimes overtops the comparatively large spikelet, but these characters are not reliable for identification.

The hybrid is less often so densely cespitose as the above and grows in active *Sphagnum* bogs (blanket, raised or valley mires), often with *Andromeda polifolia*, *Calluna vulgaris*, *Drosera rotundifolia*, *Erica tetralix*, *Eriophorum angustifolium*, *E. vaginatum*, *Narthecium ossifragum*, *Vaccinium oxycoccus* and, occasionally, also *Drosera longifolia* and *Rhynchospora alba*.

Subsp. *cespitosum* has very small spikelets. In Northumberland it has not been seen in large, dense tufts; it sometimes occurs in base-rich habitats and never under such strongly acidic or stagnant conditions as the hybrid.

Characters which have been used to separate the three (non-proliferous) taxa are discussed below (followed by a description of proliferous forms) and are summarised in Table 1. Measurements relate to material from Northumberland.

UPPER SHEATH

In subsp. *germanicum* the uppermost sheath has an oblique opening 2–3(–5) mm long and 1 mm broad, the blade being up to 2 × as long as the opening (see key in Foerster 1963).

In subsp. *cespitosum* the opening of the sheath is suborbicular, c. 1 mm in diameter, with the blade 5–10 × as long as the opening. Note that Fremstad & Skogen (1978) give sheath-opening up to 1.5 mm, which overlaps with measurements on the hybrid.

It should be mentioned that in Hegi (1909) the drawings of the sheaths of the two subspecies (Fig. 186, p. 24) have been reversed, although the descriptions (on p. 25) are correct. Even in the third edition of this excellent work (Hegi (1966), Fig. 24, p. 37) this error still remains, which perhaps shows how neglected is *T. cespitosum* [Cinderella of the Cyperaceae!]. However, this character is correctly depicted in Clapham *et al.* (1987) and in Hess *et al.* (1967). Unfortunately in Stace (1997) the sheath characters of the two subspecies have also been reversed.

In the hybrid, the sheath-opening is 1–1.5(–2) mm long, with the blade 3–7 × as long as the opening.

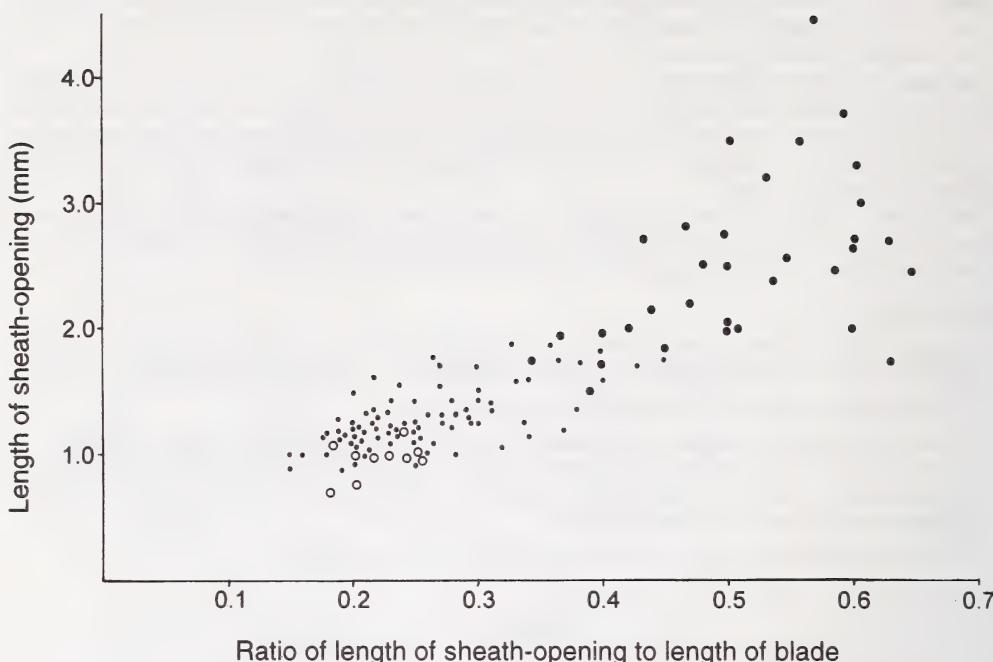


FIGURE 1. Scatter diagram of length of sheath-opening (mm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, non-proliferous, herbarium material). ○ subsp. *cespitosum*, ● subsp. *germanicum*, • hybrid.

Fremstad & Skogen (1978) showed diagrammatically the relationship between the length of the sheath-opening and the ratio of sheath-opening to blade length for subsp. *cespitosum* and *germanicum*. Figs 1 & 2 show this relationship in material from Northumberland, including the hybrid, for non-proliferous and proliferous material, respectively. Each point on the diagrams represents the average of three measurements on the same specimen. To see and measure the sheath-opening, it is convenient to first pull out the stem from the sheath.

Palla (1897) and various other authors have contrasted the sheath-opening of subsp. *germanicum* with that of subsp. *cespitosum* as being loose-fitting, with the scarious margin dotted with red or rusty brown, as opposed to close-fitting with the margin yellowish or yellowish brown. However, the first character is relevant only to herbarium material and is likely to be confusing on fresh material (Foerster 1963). Possibly, the presence of aerenchyma in subsp. *germanicum* results in shrinkage of the stem on drying, and hence the appearance of a loose-fitting sheath. The rusty colour is usually very obvious in herbarium specimens of subsp. *germanicum* and often also in those of the hybrid, so its absence can help to confirm subsp. *cespitosum*.

STEM ANATOMY

Cross-sections of fresh stems or dried stem material (the latter soaked in hot water), were cut with a razor blade and examined at $\times 30$. In subsp. *germanicum* aerenchyma is clearly seen (Fig. 3d), whereas in subsp. *cespitosum* it is completely absent (Fig. 3a, 3b). In many specimens of the hybrid, aerenchyma is also absent, although in some there are insular spaces, but not continuous channels (Fig. 3c).

The clearest distinction between the three taxa is seen in the substomatal cavities, best seen at higher magnification ($\times 400$). The stomata run in rows, lengthwise along the stem, and beneath each row of stomata lie the substomatal cavities, which in the case of subsp. *cespitosum* are lined by thick-walled, cutinised cells without chlorophyll. These rows are distributed around the circumference of the stem. In cross-sections of the stem, the substomatal cavities are seen around

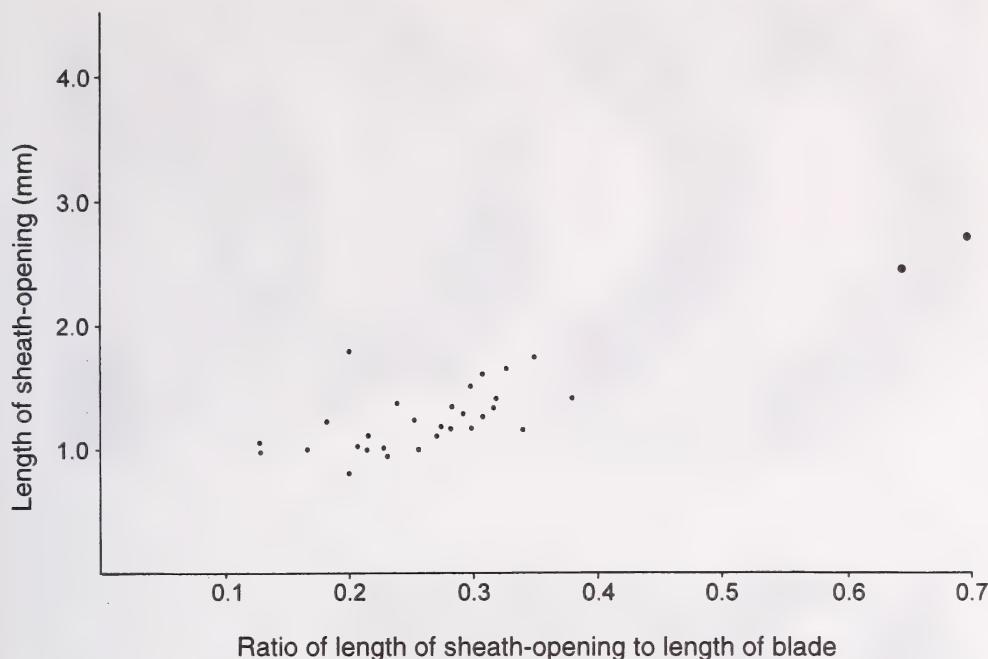


FIGURE 2. Scatter diagram of length of sheath-opening (mm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, proliferous, herbarium material).
 ○ subsp. *cespitosum*, ● subsp. *germanicum*, • hybrid

the periphery, and each with a guard-cell at the outside. The number of cavities through which a particular section cuts varies, but under favourable circumstances it may be up to 12 (some of them double) in subsp. *cespitosum*. The stem cross-sections of the two subspecies are illustrated in Broddesøn (1912), and the arrangement of the substomatal cavities in a length of stem as well as the construction of the cavities and guard-cells (in *T. alpinum*) is illustrated in Westermaier (1881). Illustrations of the cavities in subsp. *cespitosum* are given in Montfort (1918) and Metsävainio (1931). There is a good drawing (with scale) of a cross-section showing a substomatal cavity in Firbas (1931), p. 485.

Montfort (1918) showed that, unlike other species of raised mires, *Eriophorum vaginatum* and *T. cespitosum* both have substomatal cavities as described above, the physiological action of which may be to lower rates of transpiration. These cavities increase stomatal resistance and form physiological barriers to transpiration (diffusion pathway lengthened). As a consequence of this structure the plants are anatomically xeromorphic. Both species flower very early, often under semi-frozen conditions, so that the plants may suffer "physiological drought". *Eriophorum latifolium* flowers three to four weeks later than *E. vaginatum*, after the peat has thawed completely and lacks this xeromorphic character. In *T. cespitosum* subsp. *cespitosum* the xeromorphic anatomy is extremely strongly developed, not only in plants from raised mires, but also in other mire systems. The suggestion by Ellenberg (1988) and Lusby & Wright (1996), that the supposed xeromorphic character of bog plants is not true xeromorphism, but is peinomorphism, should perhaps refer only to evergreen ericaceous species. Montfort (1918) suggested that the xeromorphic character of *Eriophorum vaginatum* and *T. cespitosum* subsp. *cespitosum* dates back to the glacial period.

In subsp. *germanicum* (Atlantic-Subatlantic) the substomatal cavities are very small, their radial diameter (6–7 µm) being only half that of the guard-cells, while in subsp. *cespitosum* (circumpolar) they are large, with radial diameter (20–26 µm) up to twice that of the guard-cells. In a good section

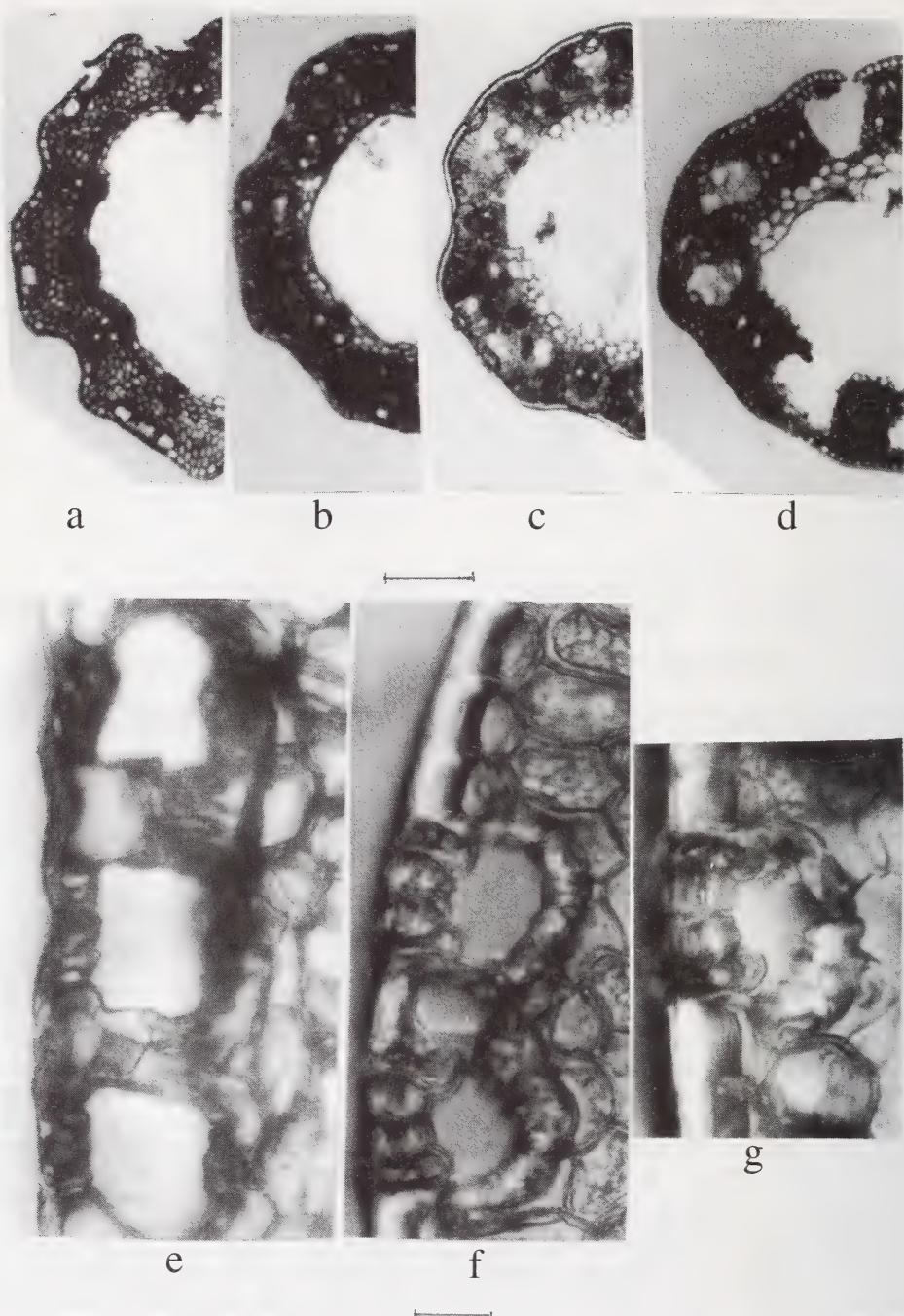


FIGURE 3. Cross-sections of stem of *Trichophorum cespitosum* subsp. *cespitosum* from below Schwarzsee, near Zermatt, Switzerland (a and e), of *T. cespitosum* subsp. *cespitosum* from Blackheugh End, S. Northumberland (v.c. 67) (b and f), of *T. cespitosum* nothosubsp. *foersteri* from Great Wanney Crag Moss, S. Northumberland (v.c. 67) (c and g) and of *T. cespitosum* subsp. *germanicum* from S. Northumberland (v.c. 67) (d). The scale bars represent 0.2 mm (a-d) and 20 µm (e-g).

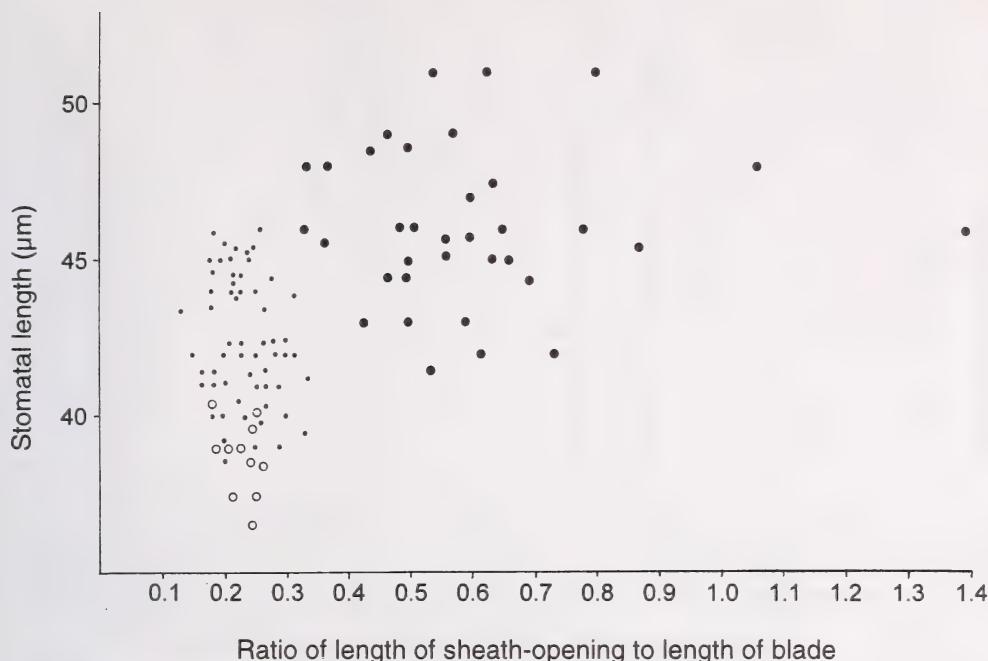


FIGURE 4. Scatter diagram of stomatal length (μm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, non-proliferous, herbarium material). ○ subsp. *cespitosum*, ● subsp. *germanicum*, • hybrid.

of subsp. *cespitosum*, under the microscope these substomatal cavities stand out as a ring of circular (or sometimes slightly squarish) "windows" (some double) around the section. In specimens collected below Schwarzsee, near Zermatt, in Switzerland, at c. 2500 m, the cavities were very large and numerous (Fig. 3a, 3e); in material from Northumberland they were somewhat smaller and less numerous (Fig. 3b, 3f), although the plants were taller than those from the Alps.

In the hybrid the substomatal cavities may be seen as circular (of smaller diameter than in subsp. *cespitosum*) (Fig. 3c, 3g), but more often as oval openings, their depth (towards the centre of the section) (usually 14–17 μm) being less than their width (along the wall of the section) (up to c. 28 μm). The number of cavities seen in a section of the hybrid is usually less than in subsp. *cespitosum*.

The aerenchyma of subsp. *germanicum* is presumably relevant to growth under wet Atlantic-Subatlantic conditions. Examination of a stem-section is an excellent means of separating the three taxa.

STOMATAL LENGTH

Fremstad & Skogen (1978) reported the stomatal lengths as being 48.62 ± 2.39 and 42.29 ± 2.63 μm in subsp. *germanicum* and *cespitosum*, respectively. They showed diagrammatically the relationship between stomatal length and the ratio of the lengths of sheath-opening and blade.

In the present work herbarium specimens of *T. cespitosum* from Northumberland were soaked in hot water before the epidermis was stripped. The lengths of 20 stomata from each specimen (from approximately the middle of a stem) were then measured (at $\times 400$) and the average stomatal length was plotted against the ratio of lengths of sheath-opening to blade, as shown in Figs 4 & 5 for non-proliferous and proliferous material respectively. In agreement with the Norwegian authors, the shortest stomata were found in subsp. *cespitosum* and the longest in subsp. *germanicum*; the hybrid occupied an intermediate position. In a small number of specimens it was found that the average stomatal length varied considerably in different parts of the stem.

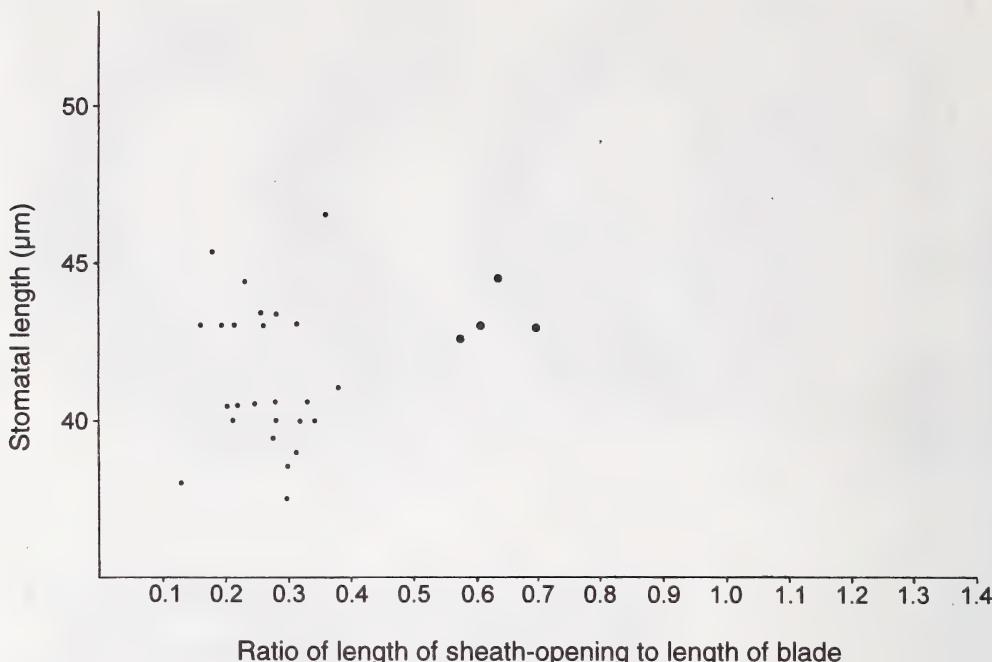


FIGURE 5. Scatter diagram of stomatal length (μm) against ratio of length of sheath-opening to length of blade for *Trichophorum cespitosum* (Northumbrian, proliferous, herbarium material) ● subsp. *germanicum*, • hybrid.

FURROWED STEM

Fremstad & Skogen (1978) stated that whereas the stems of subsp. *germanicum* were furrowed, those of subsp. *cespitosum* were smooth. I noticed that the stems of subsp. *cespitosum* were indeed often only shallowly grooved, while those of the hybrid were usually deeply grooved. However, this character is subject to seasonal variation and is of little value.

PERIANTH BRISTLES

In subsp. *germanicum* the perianth bristles are papillose. In subsp. *cespitosum* they are smooth, except sometimes near the apex.

In agreement with Palla (1897) who recorded this character, I did not find this to be a rigorous means of separation. There are excellent SEM photographs of bristles of the two subspecies in Fremstad & Skogen (1978).

BASAL SHEATHS

Clapham *et al.* (1987) and De Filippis (1980) describe subsp. *germanicum* as having basal sheaths scarcely shining, whilst subsp. *cespitosum* has basal sheaths shining. Sell & Murrell (1996) likewise give "dull" and "shining", respectively.

It is true that when one pulls the plant (e.g. the hybrid) out from a cushion of *Sphagnum*, the basal sheaths are usually shining, but I cannot regard this as a satisfactory character for identification. According to Ostenfeld & Gröntved (1934), the old leaf sheaths in subsp. *germanicum* are "pale-brown, often dark from decaying matter, hardly shining", while in subsp. *cespitosum* they are "bright-brown and shining". This agrees in the main with what is observed in Northumberland, but the difference may merely reflect the different sheath environments (i.e. peat as opposed to living *Sphagnum*) rather than being a character of the subspecies.

EXCRETORY CELLS

Palla (1897) and Fremstad & Skogen (1978) mentioned the presence and absence of excretory cells (red-brown) in the assimilatory tissue of subsp. *germanicum* and *cespitosum*, respectively. In

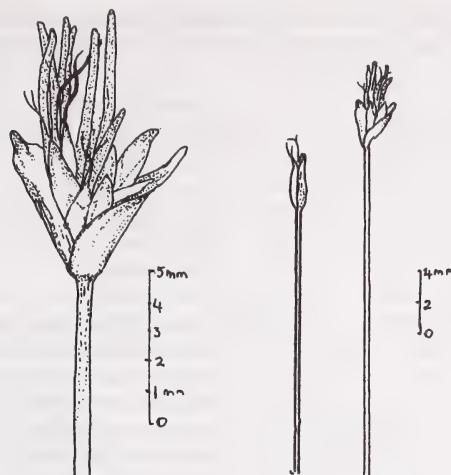


FIGURE 6. Spikelet of proliferous *Trichophorum cespitosum* nothosubsp. *foersteri*.

material from Northumberland these coloured cells were observed only in herbarium specimens which had been kept for at least seven years. Old specimens of either subsp. *germanicum* or the hybrid usually show these red cells, whereas they are absent in subsp. *cespitosum*, so this can be a useful confirmation in the case of herbarium specimens.

FRUITING

Flowering begins in May and, in the case of subsp. *germanicum*, well developed fruits (to c. 2 mm) are formed; spikelets with fruits (containing hard nutlets) and perhaps a few glumes can still be found in August. Subsp. *cespitosum* also produces smaller, short, broad heads of dark fruits. However, in the case of the hybrid, many of the tufts fail to produce fruit at all, and by early July the tops of their stems are more or less bare; in other tufts, development from the flowering to the fruiting stage proceeds and by the beginning of July some small, green, apparently sterile "fruits" (maximum length 1 mm) are present, but soon the glumes are shed. Hard nutlets have never been found.

The flowers of *T. cespitosum* are generally stated to be hermaphrodite, e.g. Clapham *et al.* (1987), Sell & Murrell (1996). However, the last sentence in the account of the species in Hegi (1909) states that some tufts have only protogynous, hermaphrodite flowers, while others have female and male flowers. The occurrence of some tufts with purely male flowers could account for the stems of some Northumberland material becoming bare at the top by early July.

Fruits of subsp. *cespitosum* from the Arctic have been described by Polunin (1959) and in North American plants by Beetle (1947), yet there seems to be a dearth of information on the occurrence or failure of fruiting of subsp. *cespitosum* in Germany and Scandinavia. However, Foerster (1963), on an excursion to the Hohes Venn (near the border between Germany and Belgium) described finding subsp. *cespitosum* on the southern slope of the Pannensterz, where it was growing sparingly among much subsp. *germanicum* and *Molinia caerulea*. He stated that on 27 July 1962 the fruits of the subsp. *cespitosum* there had already fallen and that the subsp. *cespitosum* there was not more delicate than the subsp. *germanicum*, which he suggested might be the result of the stems continuing to lengthen after the ripening of its fruit. In Northumberland the stems of the hybrid continue to lengthen during July and August, even though their tops are bare; and Foerster's observations seem entirely consistent with his plant in the Hohes Venn being the hybrid, rather than subsp. *cespitosum* and having failed to fruit, rather than having dropped its fruits, as stated.

PROLIFEROUS *T. CESPITOSUM*

In raised mires in Northumberland, in addition to the hybrid of *T. cespitosum* subsp. *germanicum* with subsp. *cespitosum*, a proliferous ("viviparous") form of this hybrid also occurs. From the middle of June onwards this can easily be distinguished at sight from the common form, the spikelets being broader and variegated with off-white and green (Fig. 6). This is reminiscent of

TABLE 2. SPECIES GROWING WITH *TRICHOPHORUM CESPITOSUM* SUBSP. *CESPITOSUM* AT BLACKHEUGH END AND GOWANY KNOWE (V.C. 67)

Blackheugh End	Gowany Knowe
<i>Cardamine pratensis</i>	<i>Carex dioica</i>
<i>Carex flacca</i>	<i>Carex hostiana</i>
<i>Carex hostiana</i>	<i>Carex lasiocarpa</i>
<i>Carex panicea</i>	<i>Carex limosa</i>
<i>Carex pulicaris</i>	<i>Carex panicea</i>
<i>Carex rostrata</i>	<i>Carex pulicaris</i>
<i>Carex viridula</i> subsp. <i>brachyrrhyncha</i>	<i>Carex rostrata</i>
<i>Drosera rotundifolia</i>	<i>Carex viridula</i> subsp. <i>brachyrrhyncha</i>
<i>Eleocharis quinqueflora</i>	<i>Dactylorhiza incarnata</i>
<i>Equisetum palustre</i>	<i>Dactylorhiza maculata</i> subsp. <i>ericetorum</i>
<i>Erica tetralix</i>	<i>Drosera rotundifolia</i>
<i>Eriophorum angustifolium</i>	<i>Menyanthes trifoliata</i>
<i>Eriophorum latifolium</i>	<i>Pedicularis palustris</i>
<i>Eriophorum vaginatum</i>	<i>Phragmites australis</i>
<i>Menyanthes trifoliata</i>	<i>Potentilla palustris</i>
<i>Pinguicula vulgaris</i>	<i>Ranunculus flammula</i>
<i>Polygala serpyllifolia</i>	
<i>Potentilla erecta</i>	
<i>Salix repens</i>	
<i>Selaginella selaginoides</i>	
<i>Taraxacum faeroense</i>	
<i>Triglochin palustre</i>	
<i>Vaccinium oxycoccus</i>	
<i>Viola palustris</i>	

Festuca vivipara. The lower flowers in the spikelets develop to form small, sterile "fruits", whereas the upper flowers proliferate to give green plantlets. Also, in all the flowers, the bristles are replaced by a membranous (petaloid) perianth. A particular tuft is either proliferous or non-proliferous, and the proliferous plants usually form smaller tufts than the non-proliferous ones and retain their glumes much longer, so that they can be found up to early September. Even so their "fruits" do not develop much beyond that of the non-proliferous hybrids, and it is unlikely that they ever produce viable seed. Spikelets of the proliferous hybrid, cut off and then planted in peat in late summer, failed to root satisfactorily, but this does not imply that the propagules fail to do so naturally, when they would fall into the *Sphagnum* bog. Although plants of the non-proliferous hybrid grew well in peat in pots, plants of the proliferous hybrid grew less well, rarely producing proliferous spikelets, and sometimes even dying during the winter.

In some mires, only a few tufts of the proliferous form have been found, whereas in others perhaps up to 20% of the tufts are proliferous. The proliferous tufts tend to be clustered together in the same area of the mire.

There is also a proliferous form of subsp. *germanicum*, but this seems to be rare in Northumberland. It was found on 15 August 1995 near Hareshaw Head at NY/856.884, 335 m (v.c. 67), the site probably being a remnant of a raised mire which had been partly drained.

HABITAT OF NON-PROLIFEROUS *T. CESPITOSUM*

The hybrid grows among living *Sphagnum*, while subsp. *germanicum* has less strict habitat requirements and grows in other types of peat bog, some of which were formerly *Sphagnum*-dominated and identical with many surviving *Sphagnum* mires. In Northumberland the hybrid sometimes grows in a rather bare area of bog, accompanied only by *Sphagnum tenellum*. Subsp. *cespitosum* in Northumberland has been found only at the margins of raised or valley mires, where there is some water-movement and base enrichment, never actually within the mire.

LOCALITIES OF SUBSP. CESPITOSUM IN NORTHUMBERLAND

Subsp. *cespitosum*, with mature fruits, has been found by G.A.S. at four sites in South Northumberland (v.c. 67). See Table 2.

1. Near Blackheugh End, NY/826.915 (330 m) on 17 July 1995. Here there is a more-or-less flat area of *Sphagnum* mire, with *Drosera rotundifolia*, *Erica tetralix*, *Narthecium ossifragum* and hybrid *T. cespitosum*. Running through this, in an approximately SW/NE direction, is a channel in which grow the species given in Table 2, many of which favour base-rich habitats. It is in this channel that *T. cespitosum* subsp. *cespitosum* grows and where it was first recognised in Northumberland. This site is by the Pennine Way and many walkers pass it, especially during the summer.
2. Gowany Knowe, NY/727.787 (280 m) on 20 July 1996. Gowany Knowe Moss is one of the Border Mires, a raised mire with *Carex magellanica*, *Drosera rotundifolia*, *Narthecium ossifragum*, *Vaccinium oxycoccus* and hybrid *T. cespitosum* (including proliferous material). However, *T. cespitosum* subsp. *cespitosum* does not grow in the raised mire, but by the side of a tiny streamlet at the margin of the mire, only a very short length of which still remains outside the afforested area. This small habitat also has the species listed in Table 2; it is probably rarely visited, although the Moss is a reserve of the Northumberland Wildlife Trust.
3. Head of Bucklake Sike, NY/69.94 (420 m). A specimen was collected by G.A.S. on 28 June 1990 and this appeared to be subsp. *cespitosum*, which was confirmed by the collection of a fruiting specimen on 31 August 1996. Here there is a raised mire containing *Betula nana*, *Calluna vulgaris*, *Carex rostrata*, *Molinia caerulea*, *Polygala serpyllifolia*, *Potentilla erecta*, *Salix repens* and *Vaccinium oxycoccus*. The lower end of this mire is drained by a tiny streamlet containing *Menyanthes trifoliata*, *Carex panicea* and *C. pulicaris* and this is where *T. cespitosum* subsp. *cespitosum* grows. Further downstream *Carex limosa* appears and also *Hammarbya paludosa*, although the latter has not been seen since 1973. Still further downstream is *Potamogeton polygonifolius*. This is a remote site on land owned by the Duke of Northumberland. The proliferous hybrid is also present.
4. Muckle Moss, 4 September 1996. This is a valley mire, which contains the hybrid. Subsp. *cespitosum* was not found in the mire itself, but in the margin ("lagg") at NY/796.670 (230 m), with *Calluna vulgaris* and *Salix repens*. This is a National Nature Reserve and the lagg has been reported to contain *Sphagnum balticum*, *S. majus* and *S. riparium*. Strangely, it is stated in Ratcliffe (1977) that *T. cespitosum* is conspicuously absent in Muckle Moss.

In addition, I investigated many base-rich flushes on peat in Northumberland, each containing several of the species listed in Table 2, but found no *Trichophorum* in any of these.

HABITS IN SCANDINAVIA

According to Fremstad & Skogen (1978), subsp. *cespitosum* is first and foremost a bog species which occurs throughout Scandinavia (Sjörs 1950). Osvald (1923) has described the occurrence in Sweden of raised mire communities, which appear to be very like those in Northumberland, referred to later in the present paper as *Erica-Sphagnum* mire (National Vegetation Classification M18, Rodwell 1991).

According to Fremstad & Skogen (1978), when subsp. *germanicum* appears in a mire it is usually the result of human influence in the form of peat-digging, burning, grazing or trampling. It also occurs where peat growth has stopped and where it is periodically drier than the normal bog. So, in Scandinavia, subsp. *germanicum* grows commonly with a range of species which are not normally associated with raised mires, such as *Carex binervis*, *Cornus suecica*, *Deschampsia flexuosa*, *Festuca vivipara*, *Luzula multiflora* and *Polygala serpyllifolia* in addition to the normal bog species. Subsp. *germanicum* also occurs on thin peat and at the edge of bogs. The moss cover is poorly developed, the commonest species being *Sphagnum compactum*, *S. molle*, *S. strictum* and *S. tenellum* and other species which thrive where peat growth stagnates. Subsp. *germanicum* also grows on thin peat on paths and trampled places, where peat erosion occurs. According to Fremstad & Skogen (1978), subsp. *germanicum* has never been found in west- or mid-Norway on intact peat bog.

COMPARISON OF HABITATS IN NORTHUMBERLAND AND SCANDINAVIA

From the above, it is seen that subsp. *cespitosum* is the plant which grows in intact peat bogs in Scandinavia, while in Northumberland the hybrid is the characteristic plant in raised mires. There may be two possible explanations for this apparent anomaly.

1. Perhaps subsp. *cespitosum* was once the plant of mires in both Scandinavia and Britain; but with the post-glacial amelioration of the climate, in the British mires it became too warm for subsp. *cespitosum*, so that it could not compete successfully with the hybrid, which gradually replaced it. In Scandinavia, the high altitude and/or latitude of the mires allowed subsp. *cespitosum* to thrive. According to Clapham *et al.* (1987), *T. cespitosum* is absent from base-rich soils in the British Isles, and this does indeed seem to be generally true for subsp. *germanicum*. However, Hegi (1966) and Hess *et al.* (1967) mention calcareous or base-rich habitats for subsp. *cespitosum* in particular. *T. cespitosum* is presumably wind-pollinated and in Northumberland the flowering seasons of the two subspecies probably overlap. Perhaps subsp. *cespitosum* has only escaped extinction through hybridisation by surviving in marginal areas of raised mires, where conditions are sufficiently base-rich to inhibit the growth of subsp. *germanicum*.
2. Possibly the hybrid does in fact occur in at least some mires in Scandinavia, but this has not yet been recognised. In the diagram of sheath-opening against the ratio of sheath-opening to blade length, given (as Fig. 1 on p. 136) in Fremstad & Skogen (1978), the group of records around 1·3/0·3 could represent the hybrid rather than subsp. *cespitosum* (cf. this paper, Fig. 1) and the same could be said of the diagram of stomatal length/ratio of sheath-opening to blade length, given (as Fig. 4 on p. 139), where the group of records around 44/0·2 could represent the hybrid (cf. this paper, Fig. 4). Also in their diagram (Fig. 3 on p. 138), the distribution of stomatal lengths for subsp. *cespitosum* looks as though it might more probably represent a superposition of two taxa (i.e. subsp. *cespitosum* and the hybrid).

Moreover, specimens in **BM** from Norway, Jämtland, marshy ground, 750 m, 2 August 1958, *H. Smith* and in **K**, Norway, Tromsö Island, in a peat bog, July 1921, *V. Summerhayes*, are evidently the hybrid. The northernmost locality yet recorded for subsp. *germanicum* is in Norway, Lofoten (Sortland 1992), somewhat south of Tromsö. There are specimens of what appear to be subsp. *germanicum* from Greenland (**K**); and from Iceland, 17 July 1876, *C. Ostenfeld* (**WU**). Another specimen from Iceland, collected by *N. Polunin* (**BM**) seems to be the hybrid.

In the intact raised mires of the Northumbrian Border Mires, the hybrid is the characteristic and perhaps the only *Trichophorum* present; the community in which it grows is evidently *Erica-Sphagnum* mire [*Erica tetralix-Sphagnum papillosum* raised and blanket mire, *Sphagnum magellanicum-Andromeda polifolia* sub-community (M18)].

According to Fremstad & Skogen (1978), when subsp. *cespitosum* grows in coastal areas of Norway it flowers much earlier than subsp. *germanicum*, thus preventing hybridisation. However in areas of higher altitude and latitude the growing season is short, so that the flowering seasons of the two subspecies overlap, making hybridisation possible. In these areas morphologically intermediate forms have in fact been observed.

Although most of the plants from Northumberland fall fairly clearly into one of the three groups (i.e. subsp. *cespitosum*, subsp. *germanicum* and hybrid) a few have been found with mixed characters. These few have been omitted from Figs 1 & 4; they may correspond to Fremstad & Skogen's (1978) intermediate forms. The hybrid sometimes has good pollen and it is possible that this could cause introgression into subsp. *germanicum*.

DISTRIBUTION

DISTRIBUTION IN NORTHUMBERLAND

In Northumberland subsp. *germanicum* mostly occurs from sea-level to 700 m. The large area of The Cheviot (815 m) above 700 m is virtually free from *Trichophorum*, although on 21 June 1995 I found two small tufts of subsp. *germanicum* on the summit plateau at 800 m. This absence may be a result of the long snow-cover there. In Northumberland the hybrid has been found at altitudes between 215 and 660 m and subsp. *cespitosum* from 230 to 420 m; the upward limits may perhaps

TABLE 3. MIRES IN SOUTH NORTHUMBERLAND (V.C. 67) WITH *TRICHOPHORUM CESPITOSUM* NOTHOSUBSP. *FOERSTERI*

No.	Name of mire	V. c.	Grid reference	Altitude (m)
1	Gowany Knowe Moss	67	NY/730.788	280
2	Felecia Moss	67	NY/721.775	310
3	Harelaw Moss	67	NY/757.771	275
4	Haining Head Moss	67	NY/714.748	260
5	Wedges Rigg Moss	67	NY/712.742	260
6	Humnell Knowe Moss	67	NY/705.714	250
7	Bell Crag Flow	67	NY/763.721	310
8	Coom Rigg Moss	67	NY/689.795	320
9	Muckle Samuel's Crags Moss	67	NY/678.789	300
10	Grain Heads Moss	67	NY/744.735	280
11	Butterburn Flow	70	NY/662.761	280
12	The Flothers	67	NY/699.763	290
13	Limy Sike Moss	67	NY/696.770	280
14	Ottercops Moss	67	NY/948.895	310
15	Drowning Flow	67	NY/760.975	405
16	Horse Hill Moss	67	NY/765.790	250]
17	Hobb's Flow	67	NY/569.902	380
18	Great Wanney Crag Moss	67	NY/938.834	275
19	Pundershaw Moss	67	NY/775.792	245
20	Sweethope Moss	67	NY/944.817	250
21	Peterstone Flow	67	NY/980.918	320
22	Towey Moss	67	NY/734.555	470
23	Falstone Moss	67	NY/708.860	250
24	Muckle Moss	67	NY/796.670	230
25	The Lakes	67	NY/740.773	285
26	Blackaburn Lough Moss	67	NY/765.795	265
27	Crane Moss	67	NT/911.034	250
28	Beldon Cleugh Moss	67	NY/917.504	365

* Site 16 was searched for *Trichophorum* sp. but none was found.

be due to the absence of *Sphagnum* mires at higher altitude. The hybrid occurs in most intact raised mires in Northumberland, notably the Border Mires (see Lunn & Lunn 1976), but can also be found in other places of higher altitude where *Sphagnum* cover is less continuous, e.g. near the summit of Windy Gyle (NT/855.152) at 600 m, where there is also some *Narthecium ossifragum*, or Scotsman's Knowe (NT/904.191) at 660 m. I also found the hybrid in 1995, just over the border (in Cumberland, v.c. 70) on the N.W. slope of Cold Fell (NY/60.56) at 520 m, growing not in *Sphagnum*, but in *Dicranum scoparium*.

The proliferous form of the hybrid was first noticed on Haining Head Moss (Table 3, Mire 4) on 13 June 1992, although an indeterminate specimen of a proliferous plant, collected on Harbottle Moor (v.c. 67) on 12 August 1934 by G. W. Temperley was later found in HAMU. During the summers of 1993 and 1994 I sought the proliferous hybrid in the 28 mires, thought to be relatively undisturbed, listed in Tables 3 & 4, as well as elsewhere in Northumberland. All these mires were found to contain *Drosera rotundifolia*, *Narthecium ossifragum* and *Vaccinium oxycoccos*. Mires 1–23 are essentially of the blanket or raised mire type, while 24–28 are more of the valley mire type. Mires 1–16 also contain *Andromeda polifolia*, hybrid *Trichophorum* and proliferous hybrid *Trichophorum*, with the exception of Mire 16, which lacks any *Trichophorum* at all and although it was in the same area and was otherwise similar to many others, it had been ploughed up by the Forestry Commission around 1949, but never planted with trees.

Mire 23 is very dry and lacks *Andromeda polifolia* and the proliferous *Trichophorum*.

The proliferous *Trichophorum* hybrid was not found in any of the valley mires, i.e. Mires 24–28, all of which contain the non-proliferous hybrid. Rose (1953) in comparing lowland British valley

TABLE 4. SPECIES ACCOMPANYING *TRICHOPHORUM CESPITOSUM* NOTHOSUBSP. *FOERSTERI* IN THE MIRE IN TABLE 3

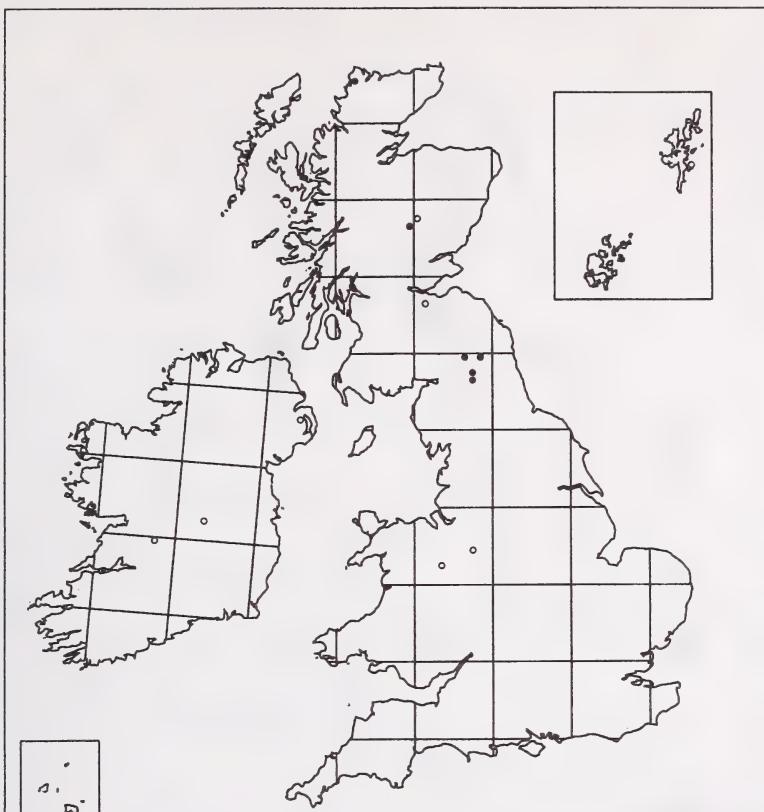


FIGURE 7. The distribution of *T. cespitosum* subsp. *cespitosum* in the British Isles, based on records in 1995–1997 (●) and herbarium records (○).

bogs with raised bogs, stated that the latter are of much greater age than the former; could the proliferous hybrid be a glacial relict? On the other hand, proliferation may be merely environmentally induced. For example, Lawrence (1945) showed that plants of *Deschampsia cespitosa* from Scandinavia, when transplanted to California, became proliferous.

In Coom Rigg Moss (Mire 8), apart from the usual proliferous form with a petaloid perianth, in one area were found many plants of a proliferous form with ordinary bristles.

One tuft of the proliferous plant was found on 16 July 1994 at a site quite different from any of the above. This was on a peaty, grassy slope on Carter Fell (v.c. 67) at an altitude of 550 m, at NT/687.062. This had short stomata like subsp. *cespitosum*, although its substomatal cavities were slightly less deep than those of the latter. This plant requires further investigation as it could be proliferous subsp. *cespitosum*, rather than the proliferous hybrid.

DISTRIBUTION IN THE BRITISH ISLES

Collections of *T. cespitosum* at **BEL**, **BM**, **DBN**, **E**, **HAMU**, **K**, **LIV**, **NMW**, **PTH** and **SUN** were searched and British specimens which, from visual inspection (without interfering with the specimen) appeared to be either subsp. *cespitosum* (Fig. 7) or the hybrid (Fig. 8) and for which it was possible to give an approximate grid reference, were mapped, along with my records (mainly from Northumberland). Among the herbarium specimens were a few of the proliferous hybrid and proliferous subsp. *germanicum* and these were mapped, along with the corresponding G.A.S. records (Fig. 9). Herbarium specimens of non-proliferous subsp. *germanicum* were also mapped for comparison (Fig. 10). Identifications of the hybrid and subsp. *cespitosum* were checked by cutting stem-sections, when permission to do so was granted.

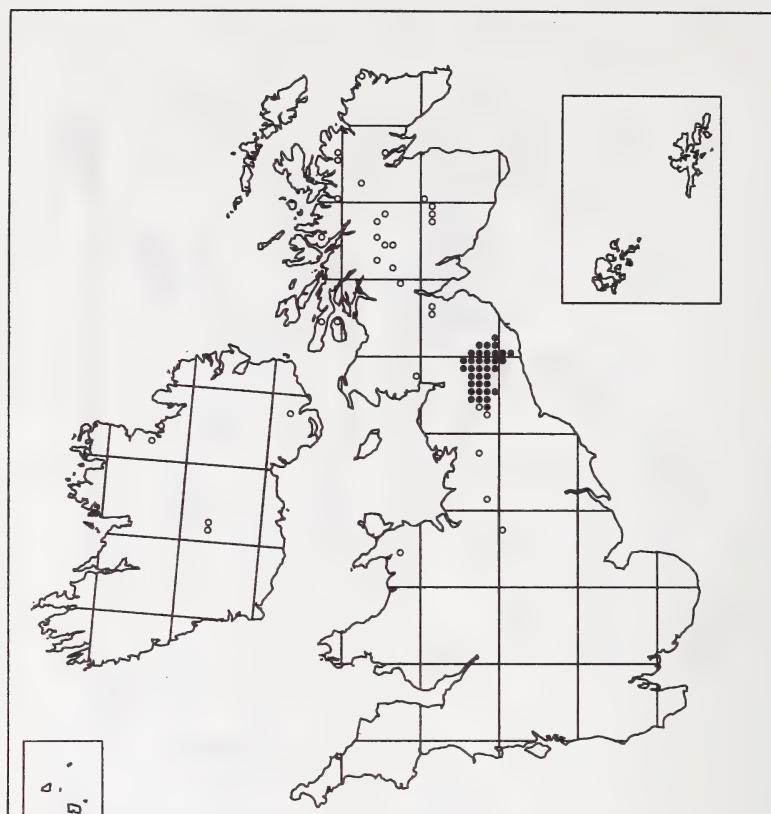


FIGURE 8. The distribution of non-proliferous *Trichophorum cespitosum* nothosubsp. *foersteri* in the British Isles, based on records by G.A.S. in 1988–1996 (●) and herbarium records (○).

HERBARIUM SPECIMENS OF SUBSP. *CESPITOSUM*

Very few specimens which were clearly subsp. *cespitosum* were found, and these are detailed below. Many of them are at low altitude and not in areas of the highest rainfall.

v.c. 40, Salop, Twyford Vownog, near West Felton (SJ/3.2), 26 June 1840, W. A. Leighton (BM).

A good, fruiting specimen. Also in E*.

v.c. 58, Cheshire, Wybunbury Moss (SJ/7.4), 27 August 1892, J. E. Nowers (SUN).

v.c. 83, Midlothian, Balerno Common (NT/1.6), May 1878, M. W. Evans (E)*, also June 1931, W. R. McNab (DBN).

v.c. 89, East Perth, Ben Vuroch, (c. NO/0.7), 24 July 1884, J. Brebner (PTH).

v.c. 112, Shetland, Bressay (HU/5.4) (NMW), with insular aerenchyma.

v.c. H15, S. E. Galway, bog on shore of Lough Derg, near Woodford (R/74.99), 22 June 1898 (DBN).

v.c. H18, Offaly, bog near Tullamore (N/34.25), 25 May 1895, R. L. Praeger (DBN).

v.c. H38, Co. Down, Ballygowan (J/43.64), bogs, June 1903, C. H. Waddell (BEL).

*These specimens in E had already been recognised and annotated as subsp. *cespitosum* by Dr H. A. P. Ingram in 1963.

HERBARIUM SPECIMENS OF THE NON-PROLIFEROUS HYBRID

v.c. 48, Merioneth, Llyn Morwynion, Ffestiniog (SH/7.4), 21 May 1938, N. Woodhead (NMW).

v.c. 57, Derbyshire, Goyt's Moss, Buxton (SK/0.7), May 1883, C. T. Green (LIV).

v.c. 59, S. Lancs., Ashworth Moor (SD/8.1), July 1853, Miss Graham (LIV).

v.c. 64, Mid-W. Yorks., moorland on Ingleborough (SD/7.7), 31 May 1953, V. Gordon (LIV).

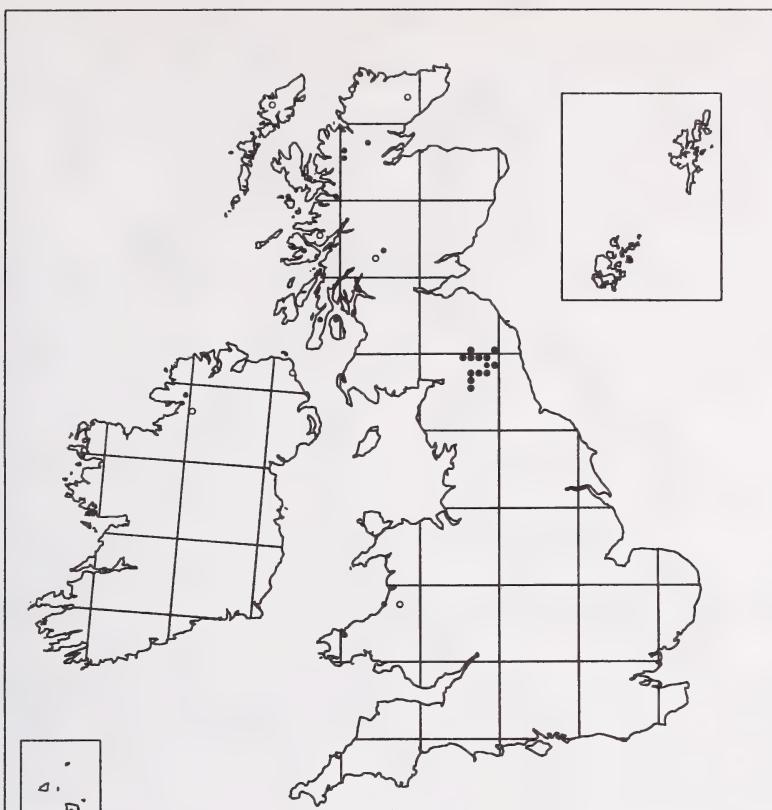


FIGURE 9. The distribution of proliferous *Trichophorum cespitosum* nothosubsp. *foersteri* in the British Isles, based on records by G.A.S. in 1992–1996 (●) and herbarium records (○); and of proliferous subsp. *germanicum* (◎), all herbarium records, except for that at NY/8.8, which is by G.A.S. in 1995.

- v.c. 66, Co. Durham, Widdybank Fell (NY/8.2), 14 July 1905, T. J. Foggitt (**BM**).
- v.c. 67, S. Northumb., Fozy Moss (NY/8.7), 17 May 1957, E. F. Greenwood (**LIV**).
- v.c. 69, Westmorland, flush in blanket bog, 1 mile [1.6 km] S.W. of Moor House (NY/7.3), 1 September 1956, F. Rose (**NMW**).
- v.c. 69b, Furness, Foulshaw Moss (SD/2.7), 10 May 1913, R. S. Adamson (**BM**).
- v.c. 70, Cumberland, Butterburn Flow (NY/6.7), June 1964, F. Rose (**NMW**).
- v.c. 72, Dumfries, Lochmaben Moss (NY/0.8), R. Boyle (**LIV**).
- v.c. 83, Midlothian, Threipmuir (NT/1.6), 31 May 1834; Auchencorth Moss, near Penicuik (NT/19.55), June 1870, W. Evans (**E**).
- v.c. 87, W. Perth, Blair Drummond Moss (NS/7.9), 1 July 1882, F. B. White (**PTH**); bog near the col between Am Binnein and Ben More at 1700 feet [520 m] (NN/4.2), 29 July 1914, E. S. Marshall (**BM, NMW**).
- v.c. 88, Mid Perth, Stuc a' Chroin, above 2800 feet [850 m] (NN/6.1), 16 July 1885, F. B. White (**PTH**); Breadalbane, July 1885, W. B. Waterfall (**K**); Ben Heasgarnich (NN/4.3), 20 July 1886, F. B. White (**PTH**); Rannoch Moor, near station, 950 feet [290 m] (NN/4.5), 26 June 1936, J. E. Lousley (**NMW**); wet moors near Ben Lawers (NN/6.4), 16 June 1946 (**LIV**); Ben Lawers (NN/6.4), 24 June 1950, V. Gordon (**LIV**); Ben Lawers, W side of N ridge, 3400 feet [1050 m] (NN/6.4), 14 July 1954, A. W. Stelfox (**LIV**); Craig Laoghain, N of Meall Ghaordie, with *Carex saxatilis*, *C. nigra* and *Eriophorum angustifolium* (NN/515.406), 700 m, 16 July 1981, A. C. Jermy, K. P. Kavanagh & A. M. Paul (**BM**).
- v.c. 89, E. Perth, Gleann Beag, above 1100 feet [335 m] (NO/1.7), 14 July 1885, A. Sturrock (**PTH**).

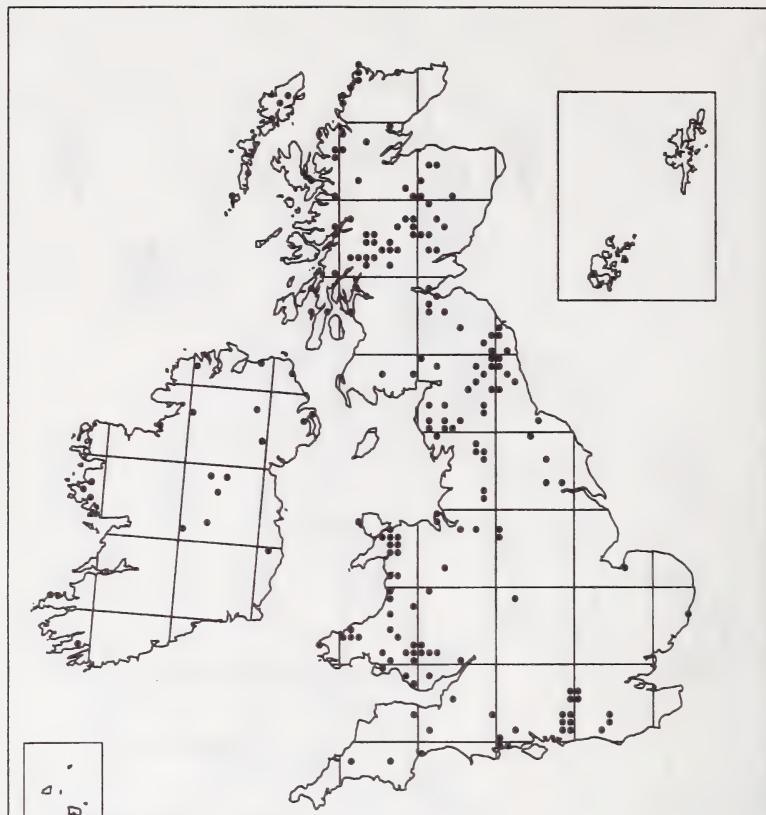


FIGURE 10. The distribution of specimens of *Trichophorum cespitosum* subsp. *germanicum* which were found in the herbaria from which the records in Figs 7, 8 and 9 were derived.

- v.c. 92, S. Aberdeen, end of Loch Callater (NO/1.8), 24 July 1882, *F. J. Hanbury* (**BM**); Linbrig, near Braemar (NO/1.9), 19 July 1885, *F. J. Hanbury* (**BM**).
- v.c. 94, Banffs, Cairngorms, Coire Raibert, 3500 feet [1050 m] (NJ/0.0), 21 July 1966, *E. Rosser* (**E**).
- v.c. 96, Easterness, Glen Affric, N.E. of Loch Beneveian, among *Sphagnum* in wet slope in birch wood, 740 feet [225 m] (NH/2.2), 13 July 1947, *E. Milne-Redhead* (**K**); Cairngorm, peat bog, 2300 feet [700 m] (NJ/0.0?), 23 June 1964, *J. K. Smith* (**LIV**).
- v.c. 97, Westerness, marshes by the wood 3–4 miles [5–7 km] E. of Loch Laggan Hotel (NN/5.8), 15 July 1915, *F. J. Hanbury* (**BM**); Loch Hournhead (NG/9.0), 7 July 1949, *M. S. Campbell & A. R. Clapham* (**BM**); Glen Dubh near Alltachonaich, Morven (NM/7.5), 5 July 1973, *S. S. Hooper & C. C. Townsend* (**K**).
- v.c. 100, Clyde Is., Beinn `a Chliabhain, Arran (NR/9.4), June 1890, *A. Somerville* (**E**).
- v.c. 101, Kintyre, Killean (NR/7.4), 1934, *E. M. Hall* (**E**).
- v.c. 105, W. Ross, small lochan to S of Loch Maree Hotel (NG/9.6), 21 July 1931, *A. J. Wilmott* (**BM**); Beinn Eighe Reserve, Allt Coir `a Laoigh, c. 400 feet [120 m], bog by road (NG 977.580), 30 June 1952, *B. W. Ribbons, R. J. Fenn, J. T. Forrest & T. T. Mac Connell* (**E**).
- v.c. 106, E. Ross, Swordale, moorland, 1100 feet [335 m] (NH/5.6), *A. Meinertzhangen* (**BM**).
- v.c. 108, W. Sutherland, Loch Aisa to Sandwood Loch (NC/2.6), 14 June 1949, *E. B. & J. F. Basdon* (**BM**).
- v.c. 110, Outer Hebrides, Lewis, *R. Vowell* (**DBN**).
- v.c. H18, Offaly, Tullamore (N/34.25), bog, 25 May 1895, *R. L. Praeger* (**DBN**).

- v.c. H20, Co. Wicklow, Wicklow, *R. Barrington* (**DBN**).
 v.c. H25, Co. Roscommon, 1848 (**DBN**).
 v.c. H28, Co. Sligo, Knocknarea (G/50.27), June 1860, *Moore* (**DBN**); Rock Mountain, wet heath, August 1894, *R. L. Praeger* (**DBN**).
 v.c. H39, Co Antrim, Black Mountain, Belfast, 10 June 1878, *S. A. Stewart* (**BEL**). Also in **DBN**.

HERBARIUM SPECIMENS OF THE PROLIFEROUS HYBRID

- v.c. 46, Cards., on a small flush below the forestry road, 500 m W of Bryn Mawr and 1.5 km S.E. of Hafod, with *Rhynchospora alba*, *Carex dioica*, *Drosera* spp. and *Eriophorum angustifolium*, 1100 feet [335 m] (SN/769.721), 31 August 1963, *A. O. Chater* (**NMW**).
 v.c. 87, W. Perth, Monachyle Glen, Balquhidder (NN/4.2), 25 August 1902, *W. E. Evans* (**E**).
 v.c. 97, Westerness, Glen Dubh, near Alltachonaich, Morven (NM/7.5), 5 July 1973, *S. S. Hooper & C. C. Townsend* (**K**).
 v.c. 107, E. Sutherland, hill N.E. of Achentoul Lodge, W. of Kinbrace station, in *Erica tetralix*, *Calluna vulgaris*, *Myrica gale* and *Narthecium ossifragum*, 550 feet [170 m] (NC/8.3), 9 July 1963, *V. B. Summerhayes & P. F. Hunt* (**K**).
 v.c. 108, W. Sutherland, Scourie (NC/1.4), 14 July 1885, *F. J. Hanbury* (**BM**).
 v.c. 110, Outer Hebrides, Lewis (NB/1.2), two sites, *E. F. Warburg* (**BM**).
 v.c. H33, Fermanagh, bog at Shea North (H/0.6), c. 1500 feet [460 m], 14 July 1954, *R. D. Meikle* (**K**).
 v.c. H39, Co. Antrim, Garron Plateau, 14 July 1979, *Dr Ledsham* (**BEL**).

HERBARIUM SPECIMENS OF PROLIFEROUS SUBSP. *GERMANICUM*

- v.c. 45, Pembs., bogs on Prescelly Mountains (SN/0.3), 9 September 1932, *C. I. & N. Y. Sandwith* (**K**).
 v.c. 46, Cards., Rhos Rhudd Bog near Berth Rhys (SN/5.7), July 1958, *G. T. Goodman* (**NMW**).
 v.c. 88, Mid Perth, Killin (NN/5.3), 14 August 1918 (**E**).
 v.c. 97, Westerness, Loch Hournhead (NG/9.0), 3 July 1949, *M. S. Campbell* (**BM**). Specimen unsatisfactory.
 v.c. 100, Clyde Is., Gleann Easan Biorach, Arran (NR/952.475), boggy moorland, 27 August 1951, *R. S. Green* (**E**).
 v.c. 101, Kintyre, Killean, Kintyre (NR/7.4), 1934, *E. M. Hull* (**E**).
 v.c. 103, Mid Ebudes, bog between two small lochans, near Benmore Lodge, Salen, Mull (NM/556.372), 15 July 1965, *H. McAllister* (**BM**).
 v.c. 104, N. Ebudes, W. side of Mullach Mor by Kilmory Glen, Rhum, peat bog on sandstone (NG/3.0), 27 July 1959, *A. C. Jermy* (**BM**).
 v.c. 105, W. Ross, Kinlochewe (NH/0.6), 18 July 1931, and bog above hotel, 22 July 1931, *A. J. Wilmott* (**BM**); above Achnashellach, near the Clair Loch (NH/0.5) 4 August 1936, *S. Sanderson* (**BM**); Allt a' Chiurn, c. 900 feet [275 m], flushed marshy area (NH/003.609), 23 June 1952, *A. L. C. Robertson & D. G. Moulten* (**E**); An Teallach, c. 1000 feet [305 m], boggy ground (NH/0.8), 1974 (**E**).
 v.c. 106, E. Ross, flush by road, Glascarnoch reservoir (NH/3.7), 21 July 1971, *U. Duncan* (**E**).
 v.c. 108, W. Sutherland, S. of Sandwood Loch (NC/2.6), peat bank, 9 July 1948, *P. Marler* (**E**).
 v.c. H35, W. Donegal, Banagher Hill, N. of Donegal town (G/9.8), rough grazing, upland, 15 July 1970 (**DBN**).

OTHER HERBARIUM SPECIMENS

The following proliferous specimen has substomatal cavities like the hybrid (14 µm depth), but has a long sheath-opening, with aerenchyma islands and a petaloid perianth:

- v.c. 69, Westmorland, Swindale, S. side of Swindale Foot Crags (NY/517.138), 360 m, in peat bog with *Eriophorum angustifolium*, *Erica tetralix* and *Sphagnum*, pools with *Utricularia minor*, 3 August 1994, *R. W. M. Corner* (**Herb. G.A.S.**).

The following non-proliferous specimen has substomatal cavities like subsp. *cespitosum*, but has a long sheath-opening:

- v.c. H18, Offaly, Seagull Bog, a few miles S. of Tullamore (N/3.2), May 1895 (**DBN**); see Praeger (1894).

Specimens were found of non-proliferous subsp. *germanicum* from v.cc. H8, 18, 20, 25, 28, 29, 30, 33, 39 and 40 without locality. In addition, very many herbarium specimens are not included because the locality could not be deciphered from the label.

LITERATURE RECORDS

Subsp. *cespitosum* has been recorded in the mire at Tregaron (Godwin & Conway 1939), in Meathop Moss (Ostenfeld 1912) and Flanders Moss (Professor A. Skogen, pers. comm., 1992), but in the absence of voucher specimens, it seems more likely that the plant would be the hybrid, as is the case in the Northumberland mires (M18). In other cases, such as the Silver Flow in Galloway (Ratcliffe & Walker 1958), and mires of Stainmore (Pearsall 1941), Cheshire and Shropshire and Flint (Hardy 1939), the subspecies of the *Trichophorum* is not stated. Moore (1968) allotted subsp. *germanicum* to the association in such mires, but this must surely be an error.

RECENT RECORDS FROM SCOTLAND

Wheeler *et al.* (1983) have described how in Perthshire *Schoenus ferrugineus* grows in base-rich flushes in a mosaic of runnels and stony hummocks. On 4 June 1997, Dr R. A. H. Smith kindly collected (at my request) two specimens of *Trichophorum cespitosum* from one such site in Mid Perth (v.c. 88) (B). One stem, collected from an area which was relatively less base-rich, with *Erica tetralix* and *Myrica gale*, was subsp. *germanicum*. The other stem, from a highly calcareous area, with *Carex hostiana*, *C. panicea*, *Eriophorum latifolium* and *Pinguicula vulgaris* appeared to be subsp. *cespitosum*, although final confirmation awaits finding a fruiting specimen.

On 22 September 1997, Dr Smith collected a fruiting specimen from a second such *Schoenus ferrugineus* site in E. Perth (v.c. 89) (A) and I identified this as subsp. *cespitosum*.

Dr R. W. M. Corner collected a specimen on 26 June 1997 from around the edge of a bog pool, which also had *Drosera longifolia*, *Schoenus nigricans* and *Utricularia intermedia*, on Ceathramh Garbh, W. of Rhiconich (altitude 75 m), in W. Sutherland (v.c. 108) and I identified this as subsp. *cespitosum*. McVean & Ratcliffe (1962) have described a site at Loch Buine Moir, Inverpolly, W. Ross (v.c. 105) which contains *Trichophorum cespitosum* in association with other species of Dr Corner's site.

ABSENCE OF PROLIFEROUS FORMS OUTSIDE THE BRITISH ISLES

The proliferation of the spikelets ("pseudo-vivipary") in British grasses has been studied by Wycherley (1953a, b). True vivipary is the germination of seeds while still attached to the parent plant (Raven & Walters 1956). "Viviparous" grasses such as *Deschampsia cespitosa* subsp. *alpina*, *Festuca vivipara* and *Poa alpina* may be glacial relicts. According to Jeremy *et al.* (1982), there is no record of vivipary in *Carex*.

I found no record of proliferous *T. cespitosum*, with the exception of records of two sites in E. Ross (v.c. 106) (Duncan 1980), evidently referring to proliferous subsp. *germanicum*. According to Professor A. Skogen (Bergen) (pers. comm., 1993 and 1995), "vivipary" in *T. cespitosum* is very rare in Norway. He has seen it only two or three times in the field, and these were stems hanging into wet depressions so that submersion was probably the cause [i.e. possibly true vivipary, rather than floral proliferation, G.A.S.]; all belonged to subsp. *germanicum*. Professor H. C. Prentice (Lund) (pers. comm., 1993) stated that proliferous *Trichophorum cespitosum* was unknown to her and to botanical colleagues (T. Karlsson and J. T. Johansson) in Sweden. Professor H. J. B. Birks (Bergen), (pers. comm., 1995) stated that he had seen the proliferous hybrid only twice, both times in mainland Scotland - in the Cairngorms in 1967 and in Caenlochan Glen in 1976. I have been unable to find a specimen of a proliferous form from outside the British Isles, despite looking through the sheets of *T. cespitosum* in B, M, W and WU.

Festuca vivipara requires a wet climate to enable its propagules to root, so is particularly common in N. W. Scotland. Perhaps the same is (or has been) true of the proliferous *Trichophorum* hybrid and especially proliferous subsp. *germanicum*.

DISTRIBUTION IN GERMANY, HOLLAND AND BELGIUM

Although subsp. *germanicum* is the common and widespread plant in Germany, it is not the only subspecies to occur there. Specimens exist of subsp. *cespitosum* from areas above c. 600 m between Munich and the Zugspitze, such as Oberammergau (BM) and near the Starnberger See and Bad Tölz (M). This subspecies also occurs at low altitude in Prussia and Schleswig-Holstein in the north of Germany. There are specimens (K) from around 1900 from near Königsberg (now Kaliningrad, in Russia), from raised mires, 4 m above sea-level, with *Eriophorum vaginatum*, *Rhynchospora alba*, *Drosera rotundifolia*, *Empetrum nigrum*, *Calluna vulgaris*, *Scheuchzeria palustris* and *Sphagnum* sp.

However, it was Foerster's short paper in 1963 (in which he believed he had found subsp. *cespitosum* growing with subsp. *germanicum* in the Hohes Venn) which led to Oberdorfer's extensive work in Schwarzwald and Vosges. Paradoxically, Foerster's supposed subsp. *cespitosum* from the Pannensterz proved to be the hybrid, as I had already correctly guessed (see section of the present paper, Identification, Fruiting). Nevertheless there is in M a specimen of subsp. *cespitosum*, which Foerster collected in 1964 in the Hohes Venn, but apparently in a different locality, and also one which he collected in Schwarzwald.

Oberdorfer (1969) described various habitats for subsp. *cespitosum*, including flushes and raised mires and one at 1000 m altitude in the Hornisgrinde region of Schwarzwald, where subsp. *germanicum* and subsp. *cespitosum* grew side by side, although sharply separated, the latter in wet depressions in the eroded peat (like subsp. *germanicum* and the hybrid in Northumberland). Oberdorfer's identification of subsp. *cespitosum* was evidently based almost entirely on the sheath-opening/blade length character and Fig. 1 in the present paper shows quite appreciable overlap between subsp. *cespitosum* and the hybrid. He does not mention substomatal cavities or fruiting and I have found no voucher specimen. It is therefore likely that at least some of his records for subsp. *cespitosum* could have represented the hybrid.

Through Dr W. Lippert I received from Dr. E Foerster a copy of a paper which the latter had apparently never completed.

In this paper Foerster stated that in 1969 R. Tüxen had sent him specimens from moors of the Oberharz, of a plant not identifiable as either subsp. *germanicum* or subsp. *cespitosum*, using the key in Foerster (1963), so in 1970 Foerster visited the Oberharz. He found that on moors, on wet paths, and above all in the *Molinia caerulea* phase of the moor, subsp. *germanicum* occurred, but on the intact moor surface there was a population in which the stem anatomy was that of subsp. *cespitosum*, but in which those characters which are recognisable macroscopically were apparently intermediate between those of subsp. *germanicum* and subsp. *cespitosum*. These plants were abundant and often developed in ring-form and with a diameter sometimes well over 1 m. This indicates a very slow or quite stagnant growth of the mire over a long period (standstill complex), or an extraordinarily great age of the individual. In the following year he also found similar plants in the low country of N. W. Germany and in other German highlands.

The occurrence of subsp. *cespitosum* has been claimed in the Netherlands by Kern *et al.* (1947) and Reichgelt (1956). In his paper, Foerster reported that he had investigated the voucher specimens in L on which this occurrence was based and that, according to their macroscopically recognisable characters, they belonged to the same "tribe" as the plants from Harz. He proposed to publish this as a new subspecies: *Trichophorum cespitosum* (L.) Hartman subsp. *hercynicum* subsp. nov.

Foerster's manuscript contains excellent drawings showing the sheath/blade character and stem cross-sections and gives depths of the substomatal cavities in subsp. *germanicum*, *cespitosum* and *hercynicum*. These all agree quite well with those from the corresponding material from Northumberland, the hybrid from the latter corresponding to subsp. *hercynicum*. Surprisingly, there is nothing in his manuscript to suggest that he thought subsp. *hercynicum* might be a hybrid of the other two subspecies, or that it failed to fruit.

I propose that this hybrid be named *Trichophorum cespitosum* nothosubsp. *foersteri*, in view of the plant having been found by E. Foerster in the Harz Mountains.

Although not mentioned by Foerster, the occurrence of subsp. *cespitosum* has been claimed by Dumont (1976) in Haute Ardenne in Belgium, who states "An unequivocal identification in the field requires only an examination of the uppermost leaf and a comparison between the lamina length and the length of the sheath opening". However, in my opinion, this is quite insufficient and Dumont's illustrations of stem cross-section represent the hybrid, rather than subsp. *cespitosum*. The description of habitat given is very similar to that of the hybrid in the Border Mires.

FORMAL TAXONOMY

Trichophorum cespitosum (L.) Hartman

Synonymy

Scirpus cespitosus L.

KEY TO TAXA (FOR NON-PROLIFEROUS PLANTS)

1. Sheath-opening \geq 2 mm; length of sheath-opening/blade length > 0.4 ; fruit produced subsp. *germanicum*
- 1a. Sheath-opening \leq 2 mm; length of sheath-opening/blade length ≤ 0.4 ; fruit produced or not 2
2. Sheath-opening \leq 1 mm (its margin without red colour); length of sheath-opening/blade length < 0.25 ; fruit produced subsp. *cespitosum*
- 2a. Sheath-opening 1–2 mm (its margin possibly red-dotted); length of sheath-opening/blade length < 0.4 ; fruit not produced nothosubsp. *foersteri*

It seems that two taxa of *Trichophorum* sometimes become interwoven in the same tuft of *Trichophorum* and this can lead to confusion in identification.

SUBSPECIES

a) subsp. *cespitosum*

Synonymy

T. austriacum Palla, *T. cespitosum* subsp. *austriacum* (Palla) Hegi, *S. cespitosus* subsp. *cespitosus*, *S. cespitosus* var. *callosus* Bigelow

Description: opening in upper sheath suborbicular, 1 mm in diameter, with blade 5–10 \times as long as opening (length of sheath-opening/blade length < 0.25); plant fruiting; aerenchyma absent; substomatal cavities 20–26 μm deep.

Distribution: Arctic-Alpine

b) subsp. *germanicum* (Palla) Hegi

Synonymy

T. germanicum Palla, *S. cespitosus* subsp. *germanicus* (Palla) Broddeson, *S. germanicus* (Palla) Lindman

Description: opening in upper sheath oblique, 2–3(–5) mm long and 1 mm broad, with blade up to 2 \times as long as opening (length of sheath-opening/blade length > 0.4); plant fruiting; aerenchyma present; substomatal cavities 6–7 μm deep.

Distribution: Atlantic-Subatlantic

Trichophorum cespitosum (L.) Hartman subsp. *cespitosum* \times subsp. *germanicum* (Palla) Hegi = nothosubsp. *foersteri* G. A. Swan, nothosubsp. nov.

Per rationem foraminis vaginae contra longitudinem laminae foliae 0.2–0.35, cavernulae stomatis profunditatem 8–18 μm , fructu sterili parentibus subsp. *cespitoso* (ratio < 0.25 , cavernulae profunditas 20–26 μm , fertilis) et subsp. *germanico* (ratio > 0.4 , cavernulae profunditas 6–7 μm , fertilis) differt.

Differing in the ratio of length of sheath-opening to length of blade 0.2–0.35, the depth of the substomatal cavities 8–18 μm , and sterile fruit, which in subsp. *cespitosum* are ratio < 0.25 , cavities 20–26 μm deep, fertile and in subsp. *germanicum* are ratio > 0.4 , cavities 6–7 μm deep, fertile.

HOLOTYPUS: S. Northumberland, v.c. 67, Gowany Knowe Moss (NY/727.787), raised mire, 20 July 1996, G. A. Swan (BM).

SUMMARY

The hybrid is the predominant plant of raised mires, not only in Northumberland, but also in the Harz Mountains in Germany; it occurs also in S. W. Germany, Holland, Belgium and Norway, as well as elsewhere in Britain and Ireland. In earlier times, subsp. *cespitosum* presumably covered areas which the hybrid does today. The survival of the sterile hybrid is reminiscent of that of *Circaea × intermedia* (Raven 1963) and *Nuphar × spenneriana* (Heslop-Harrison 1953).

Many records for subsp. *cespitosum* represent this hybrid, so populations of *T. cespitosum* in these areas should be re-examined. A plant which has a sheath-opening c. 1 mm and which is producing mature fruits in short, broad heads is likely to be subsp. *cespitosum*. A plant with a sheath-opening 1–1·5 mm and in which the top of the stem becomes more or less bare by July is likely to be the hybrid. In either case, the identification should be confirmed by microscopic examination of the stem-section.

Although subsp. *cespitosum* does not in general require base-rich conditions, in regions where subsp. *germanicum* is also present, subsp. *cespitosum* may be found only in base-rich areas because only there has it escaped hybridisation; attempts should be made to find out whether or not this statement is generally true.

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Genetic differentiation and hybridisation among subspecies of Deergrass (*Trichophorum cespitosum* (L.) Hartman) in Northumberland

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ABSTRACT

A preliminary survey of genetic variation in Northumberland populations of *Trichophorum cespitosum* (L.) Hartman (Cyperaceae) was carried out using isozyme electrophoresis. Isozyme markers were found which differentiated between the two subspecies (subsp. *cespitosum* and subsp. *germanicum*). These markers were also used to show that sterile, morphologically intermediate plants growing in Northumberland are hybrids between subsp. *cespitosum* and subsp. *germanicum*. Based on allelic variation in the parental taxa and the hybrid for the AAT enzyme system, we suggest that the hybrid has arisen on more than one occasion (i.e. it is the product of multiple gamete fusions).

KEYWORDS: isozymes, Cyperaceae, multiple origins, molecular systematics.

INTRODUCTION

In Europe, two different forms of Deergrass (*Trichophorum cespitosum* (L.) Hartman, Cyperaceae) are recognised, namely subsp. *cespitosum* and subsp. *germanicum* (Palla) Hegi. They are primarily distinguishable by sheath morphology and stem anatomy (De Filips 1980). The two subspecies also have somewhat different ranges; subsp. *germanicum* has an atlantic-subatlantic distribution, whereas subsp. *cespitosum* is more circumpolar (Hultén 1962; Meusel *et al.* 1965). In Britain, while subsp. *germanicum* is common and widespread, subsp. *cespitosum* has been considered either a rare plant of uncertain status (Clapham *et al.* 1987), or lacking substantiated records (Sell & Murrell 1996; Stace 1991). Recent studies by G. A. Swan, however, have provided strong morphological and anatomical evidence for the occurrence of subsp. *cespitosum* in Northumberland (Stace 1997; Swan 1999). Furthermore, Swan (1999) reported the presence of sterile, morphologically intermediate plants between subsp. *germanicum* and subsp. *cespitosum* and suggested that these are of hybrid origin (*T. cespitosum* nothosubsp. *foersteri* G. A. Swan (*T. cespitosum* subsp. *cespitosum* × *T. cespitosum* subsp. *germanicum*)).

Both of the subspecies are rhizomatous hermaphrodite perennials (Clapham *et al.* 1987), although some monoecious plants have also been reported (Hegi 1909). Examination of *Trichophorum cespitosum* in Northumberland revealed that some plants of subsp. *germanicum* are also proliferous, with small plantlets formed in the spikelets. The same phenomenon occurs in some populations of the intermediate plants, but it has not been observed in subsp. *cespitosum* in Northumberland (Swan 1999).

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CHROMOSOME NUMBERS

Trichophorum cespitosum subsp. *cespitosum* has a most commonly reported chromosome number of $2n = 104$ (Jörgenson *et al.* 1958; Löve & Löve 1956; Scheerer 1940). We are not aware of any chromosome counts made on *T. cespitosum* subsp. *germanicum*. Cytological studies of *Trichophorum* populations in Northumberland are currently being carried out at the University of Newcastle-upon-Tyne by A. J. Richards. Although at an early stage, and hampered by the technical difficulties of accurately counting numerous small chromosomes, the initial results suggest that individuals of both subsp. *germanicum* and subsp. *cespitosum*, as well as nothosubsp. *foersteri*, may occur at different ploidy levels (A. J. Richards, pers. comm., 1997).

MOLECULAR MARKERS

While the morphological and anatomical studies of Swan (1999) provide strong support for the presence of two subspecies and hybrid plants of *Trichophorum cespitosum* in Northumberland, it is desirable, given the morphologically similarity of the different taxa, to have an additional line of evidence based on molecular data to confirm this.

Molecular markers are now routinely used to study hybridisation among plants and to investigate the delimitation of morphologically similar taxa (Hollingsworth *et al.* 1995b, 1996; Liston *et al.* 1990; Newbury & Ford-Lloyd 1993; Rieseberg & Ellstrand 1993). They can provide powerful insights into the occurrence and frequency of hybridisation, and can be used to examine key evolutionary processes such as introgression and speciation (Abbott 1992; Arnold *et al.* 1991; Ashton & Abbott 1992; Raybould *et al.* 1991a & b; Roose & Gottlieb 1976; Wang & Szmidt 1990). Although a wide array of DNA-based molecular markers are now available and frequently used, isozyme electrophoresis remains a popular choice for biosystematic studies, due to the simplicity with which large numbers of individuals can be screened for genetic polymorphisms. Isozymes represent discrete, non-environmentally malleable markers that show straightforward co-dominant mendelian inheritance. If fixed allelic differences can be identified in the parental species, putative hybrids can be examined for the expected additive inheritance of these markers. The technique has been successfully used to identify the parentage of a number of different hybrid taxa, as well as providing information on the number of times such hybrids may have arisen (e.g. Gallez & Gottlieb 1982; Hollingsworth *et al.* 1995b, 1996; Raybould *et al.* 1991a).

In this study we have used isozymes to show that in Northumberland, *Trichophorum cespitosum* subsp. *cespitosum* is genetically distinct from subsp. *germanicum*, and that the sterile intermediate plants are hybrids between these taxa, and have arisen on more than one occasion.

MATERIALS AND METHODS

Plant material was collected from the localities listed in Table 1. These samples represent a range of populations of subsp. *germanicum* and proliferous and non-proliferous nothosubsp. *foersteri* in the Northumberland area. Additionally, two populations of subsp. *cespitosum* were sampled. Three Scottish populations of subsp. *germanicum* were included in the analysis to provide more geographically distant material for comparison. All samples were analysed for genetic variation using standard starch gel electrophoresis. Eight enzyme systems were investigated: AAT, G6PDH, PGI, PGD, PGM, SKD, MDH and IDH. G6PDH, PGM, PGI, PGD, AAT and SKD were resolved using a lithium borate buffer system (pH 8.1); MDH and IDH were resolved using a morpholine citrate buffer system (pH 8.0). All electrophoretic conditions were as described by Hollingsworth *et al.* (1995a, b) except MDH which was visualised using 50 ml 0.1M Tris-HCl pH 8.5, 750 mg malic acid sodium salt, 10 mg NAD, 10 mg MTT and 3 mg PMS.

Interpretation of enzyme banding patterns in terms of loci and alleles was based on expectations of conserved isozyme number, quaternary structure and sub-cellular compartmentalisation (Gottlieb 1981, 1982; Weeden & Wendel 1989). In the absence of progeny analyses and considering the high chromosome numbers of all of the taxa, as well as the potential for intra-taxon euploid variability (see Introduction), locus and allele designations remain putative and we avoid interpretations of the data that are ploidy-level dependent. Numerical codes to indicate multi-locus genotypes have been given to all samples (two samples sharing a multi-locus genotype have the same banding pattern for all enzyme systems).

TABLE 1. SAMPLE LOCALITIES OF *TRICHOPHORUM CESPITOSUM* (L.) HARTMAN

	Population	Code	V.c.	Grid ref.	Sample size
a. Subsp. <i>germanicum</i>	Ottercops Moss	a	67	NY/946.893	3
	Nr Gowany Knowe	b	67	NY/735.789	1
	Langleeford	c	68	NT/945.233	1
	Padon Hill (1)	d	67	NY/817.924	1
	Padon Hill (2)	e	67	NY/816.928	5
	Battle Hill	f	67	NY/950.915	1
	Creag nan Gall, Balmoral	Sco 1	92	NO/271.916	5
	Buailteach, Balmoral	Sco 2	92	NO/277.932	5
	Gleann Beag	Sco 3	89	NO/137.756	5
b. Nothosubsp. <i>foersteri</i> (non-proliferous)	Ottercops Moss	n	67	NY/948.896	1
	Greenleighton Moss	g	67	NZ/016.923	1
	Gowany Knowe	h	67	NY/731.789	2
	Felecia Moss	j	67	NY/722.775	3
	Blackheugh End	k	67	NY/827.915	1
c. Nothosubsp. <i>foersteri</i> (proliferous)	Ottercops Moss	n	67	NY/948.896	2
	Felecia Moss	j	67	NY/722.775	3
d. Subsp. <i>cespitosum</i>	Margin of Gowany Knowe	m	67	NY/727.788	4
	Blackheugh End	k	67	NY/827.915	6

TABLE 2. ISOZYME VARIATION IN EIGHT ENZYME SYSTEMS IN *TRICHOPHORUM CESPITOSUM* (L.) HARTMAN

Uppercase letters correspond to zymograms in Fig. 1. Population codes refer to Table 1.

	A	G6	M	I	P	P	P	S	M	Sample size
Code	A T	P D	D H	D H	G D	G I	G M	K D	L G	
a. Subsp. <i>germanicum</i>	a	A	A	A	A	A	A	A	A	1
	b	A	A	A	A	A	A	A	A	1
	c	A	A	A	A	A	A	A	A	1
	d	A	A	A	A	A	A	A	A	1
	e	A	A	A	A	A	A	A	A	1
	f	A	A	A	A	A	A	A	A	1
	Sco1	A	A	A	A	A	A	A	A	1
	Sco2	A	A	A	A	A	A	A	A	1
	Sco3	A	A	A	A	A	A	A	A	1
b. Nothosubsp. <i>foersteri</i> (non-proliferous)	n	A	A	B	B	B	A	A	2	1
	g	A	A	B	B	B	A	A	2	1
	h	A	A	B	B	B	A	A	2	2
	j	B	A	B	B	B	A	A	3	3
	k	A	A	B	B	B	A	A	2	1
c. Nothosubsp. <i>foersteri</i> (proliferous)	n	A	A	B	B	B	A	A	2	2
	j	B	A	B	B	B	A	A	3	3
d. Subsp. <i>cespitosum</i>	m	C	A	C	C	C	A	A	4	2
	m	A	A	C	C	C	A	A	5	2
	k	A	A	C	C	C	B	A	6	3
	k	B	A	C	C	C	A	A	7	3

MLG = multi-locus genotype.

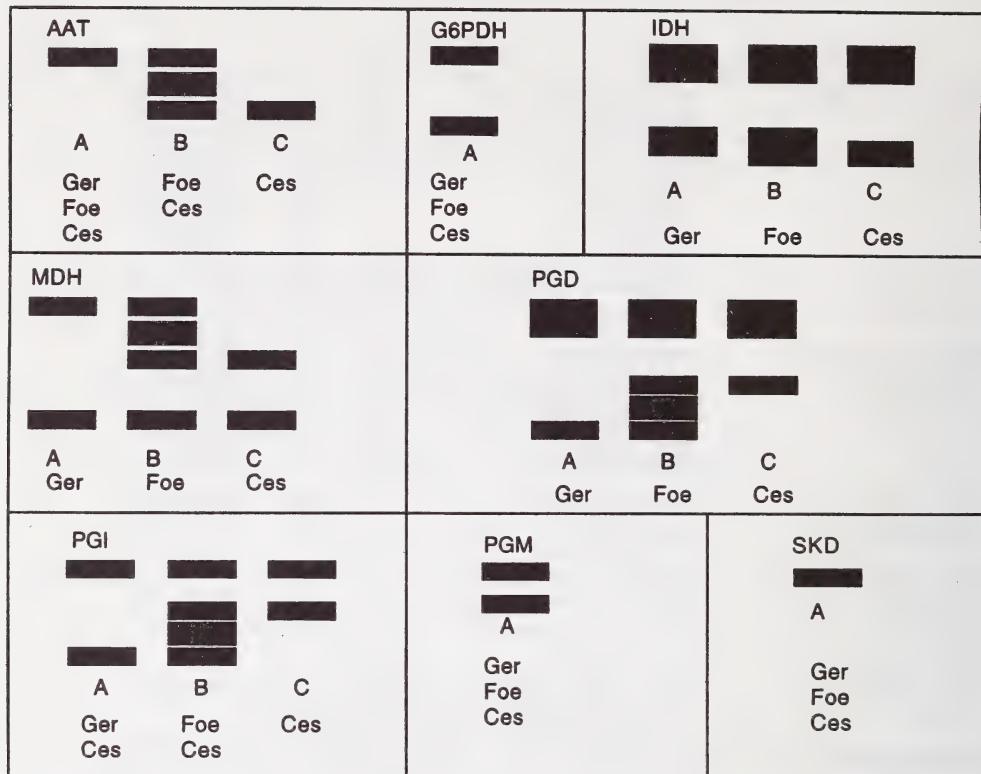


FIGURE 1. Zymogram representing banding patterns in *Trichophorum cespitosum* (L.) Hartm. in Northumberland (anode towards the top of the figure). Letters below the banding patterns represent a single enzyme genotype, the distribution of these among samples are given in Table 2. Ger = subsp. *germanicum*, Foe = nothosubsp. *foersteri* and Ces= subsp. *cespitosum*.

RESULTS

ENZYME PHENOTYPES

From the eight enzyme systems examined, a minimum of eleven anodally migrating loci was clearly resolved (Fig. 1 and Table 2). These are described in turn below.

AAT - a single putative locus was resolved, although there was a faint trace of a second faster migrating locus on the gel. At the locus that was clearly resolved, all samples of subsp. *germanicum* were homozygous for a fast allele, nothosubsp. *foersteri* was either homozygous for this fast allele, or heterozygous for this and a slower allele. Subsp. *cespitosum* showed all possible combinations of the two alleles.

G6PDH - two putative loci were resolved with both being homozygous and uniform in all three taxa.

IDH - two putative loci were resolved with the most anodally migrating locus being uniform across all samples. The other locus was variable, although resolution was poor. All individuals of subsp. *germanicum* have a fast moving zone of activity, all individuals of subsp. *cespitosum* have a slow moving zone of activity, and all individuals of nothosubsp. *foersteri* have a smear which corresponds to both zones of activity.



FIGURE 2. MDH evidence for hybridisation between *Trichophorum cespitosum* subsp. *cespitosum* and subsp. *germanicum* in Northumberland (anode towards the top of the figure). Two loci are shown with all taxa being homozygous and uniform for the least anodally migrating locus. At the most anodally migrating locus, all individuals of subsp. *germanicum* (from left to right, lanes 1–12) are homozygous and uniform for a fast moving allele (marked A), all individuals of subsp. *cespitosum* (lanes 26–35) are homozygous and uniform for a slow moving allele (marked B), and all individuals of nothosubsp. *foersteri* (lanes 13–25) show a heterozygous genotype (including a heterodimer) for these two alleles. Bands present just behind these two different alleles are considered to be artifactual and do not represent additional alleles or loci.

MDH - two putative loci were resolved with all taxa being homozygous and uniform for the least anodally migrating locus. At the most anodally migrating locus, all samples of subsp. *cespitosum* were homozygous and uniform for a slow moving allele, all individuals of subsp. *germanicum* were homozygous and uniform for a fast moving allele, and all samples of nothosubsp. *foersteri* showed a heterozygous genotype for these two alleles (Fig. 2).

PGD - two putative loci were detected, the most anodally migrating was invariant across all samples. At the second locus, all samples of subsp. *cespitosum* were homozygous for a fast moving allele, all samples of subsp. *germanicum* were homozygous for a slow moving allele and all samples of nothosubsp. *foersteri* were heterozygous for these two alleles.

PGI - two putative loci were detected with the most anodally migrating locus being poorly resolved but apparently uniform. At the least anodally migrating locus, all samples of subsp. *germanicum* were homozygous and uniform for a slow moving allele, all samples of nothosubsp. *foersteri* were heterozygous for this and a fast moving allele. Subsp. *cespitosum* showed all possible combinations of the two alleles.

PGM - all taxa were monomorphic for two bands. As PGM is a monomeric enzyme it is not clear whether this represents all samples being homozygous and uniform for two separate loci, or fixed heterozygosity at a single locus.

SKD - One putative locus was detected at which all taxa were homozygous and uniform.

VARIATION BETWEEN TAXA

Subsp. *cespitosum* and subsp. *germanicum* in Northumberland are clearly distinguishable by fixed genetic differences for three enzyme systems MDH, PGD and IDH. For all of these enzyme systems, nothosubsp. *foersteri* shows apparent direct additive inheritance of these taxon-specific markers.

VARIATION WITHIN TAXA

All individuals of subsp. *germanicum* showed the same multi-locus enzyme genotype, and at the loci where allelic designations could be made, all samples were homozygous.

Subsp. *cespitosum* showed diallelic variation for two enzyme systems (AAT and PGI). A total of four different genotypes was identified, two from each of the two populations sampled (Fig. 1, Table 2). For these variable loci, both homozygous and heterozygous genotypes were recovered, although the small sample sizes and our cytological ignorance preclude tests for deviations from random mating based on the Hardy-Weinberg principle.

A total of two different genotypes of nothosubsp. *foersteri* was detected based on variation at one enzyme system (AAT). No intra-population variation was detected, with four of the populations having one of the genotypes, and the other genotype being confined to the fifth population (Fig. 1, Table 2). It should be borne in mind, however, that for two populations, only one individual plant

was sampled and the sample sizes for the other populations are small. No genetic markers were found that distinguished between the proliferous and non-proliferous plants.

DISCUSSION

TAXON DIFFERENTIATION AND HYBRIDISATION

The sample sizes used in this study are low and we stress that the following conclusions remain tentative. Nevertheless, the initial findings are quite striking. Isozyme evidence suggests there is a clear genetic differentiation of subsp. *germanicum* and subsp. *cespitosum* in Northumberland, with three loci (MDH, IDH, PGD) showing apparently fixed genetic differences. The data also provide strong support for nothosubsp. *foersteri* being of hybrid origin from the two subspecies (Figs 1 & 2). The absolute concordance of data from these loci between populations (including comparisons with Scottish populations) suggests that these samples are representative for British plants, although of course further verification including wider geographic sampling is desirable.

Given the fixed genetic differences between the subspecies (based on this sample) and the sterility of the hybrid, this raises the question as to whether the subspecies should be raised to specific rank. We cannot commit ourselves to this based on such a small sample, but point out that if more intensive studies support the conclusions from this work, namely a. that there are clear fixed differences between the two sub-species, and b. that the hybrids are sterile, then specific rank for subsp. *germanicum* and subsp. *cespitosum* should be considered. However, it is worth stressing that the question of the sterility of nothosubsp. *foersteri* remains open for discussion. Although no mature fruits have ever been seen on plants of nothosubsp. *foersteri*, Swan (1999) noted that there is often high stainability of its pollen; he also reported the presence of *Trichophorum* plants growing in Northumberland that appear to be intermediate between nothosubsp. *foersteri* and subsp. *germanicum*. These may represent backcrosses and there is an obvious need to study these plants to determine whether their isozyme profiles support this suggestion.

Any possibility of trace fertility in nothosubsp. *foersteri* potentially complicates interpretations of the number of origins of the hybrid. AAT variation between plants of nothosubsp. *foersteri* could indicate that the hybrid has arisen on at least two occasions, i.e. it is the product of more than one successful gamete fusion (Fig. 1). We feel that this, rather than hybrid fertility, is the most likely explanation for the genetic variation in the samples of the hybrid examined in this study, as (a.) no disruption of the taxon specific markers (MDH, IDH, PGD) was detected amongst the hybrids, and (b.) the variation for AAT is exactly as would be predicted based on crosses between the fixed fast band of subsp. *germanicum* and both the fast and the slow alleles from subsp. *cespitosum*. In this respect it is noteworthy that the homozygous slow condition is not detected in nothosubsp. *foersteri* due to the invariant fast allelic constitution of subsp. *germanicum*.

Variation of PGI in subsp. *cespitosum* indicates that the nothosubsp. *foersteri* plants in this study result from a cross involving a subsp. *cespitosum* plant or plants with the fast PGI allele, as no individuals of nothosubsp. *foersteri* homozygous for the slow allele were observed.

Our inability to distinguish between the proliferous and the non-proliferous forms of nothosubsp. *foersteri* using isozymes may simply be a result of not sampling enough loci, and these different forms may represent additional origins of the hybrid. The difference in spikelet morphology between the two forms is quite striking, with the bristles in the non-proliferous plants being replaced by a membranous perianth in the proliferous plants. However, environmentally induced variation in spikelet morphology and function is far from unknown, and the transition from non-prolifery to prolifery is well documented (e.g. as in *Deschampsia cespitosa* (L.) P. Beauv.; Briggs & Walters 1984). The proliferous plants sampled here showed identical multi-locus genotypes with their sympatric non-proliferous counterparts (Table 2). In the absence of information from more molecular markers, and given our lack of understanding of what the mechanism would be if prolifery was under genetic control, it is difficult to comment further.

VARIATION WITHIN TAXA

The uniformly homozygote genotype detected within subsp. *germanicum* precludes us from distinguishing between clonal growth and sexual reproduction (be it self-pollination, mixed mating or outcrossing) as the major reproductive mode. The presence of hybrids with subsp. *cespitosum*, however, indicate that reproduction is probably not purely asexual or purely autogamous.

Large-scale sexual reproduction by nothosubsp. *foersteri* is considered unlikely based on the results of this isozyme survey and the fact that mature fruits have never been found (as discussed above). A more probable explanation is that nothosubsp. *foersteri* persists via a combination of clonal propagation and recurrent origins from the parental subspecies. Further sampling is required, however, to substantiate this.

Diallelic variation and the presence of both homozygote and heterozygotes for AAT and PGI in subsp. *cespitosum* provides good evidence for sexual reproduction with at least some outcrossing in this taxon. That more variation was detected in subsp. *cespitosum*, which is local and rare in Britain, than in the common and widespread subsp. *germanicum* is surprising and we as yet have no explanation for this apparent paradox. A greater sampling of both individuals and loci, set in the context of a firm cytological framework, may offer further insights into the reproductive biology and population biology of these taxa.

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Towards a simplified taxonomy of *Capsella bursa-pastoris* (L.) Medik. (Brassicaceae)

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ABSTRACT

Capsella bursa-pastoris (L.) Medik. is a species with a cosmopolitan distribution which shows considerable morphological variation. Numerous authors have recognised widely differing numbers of varieties, microspecies or other infraspecific subdivisions (segregates) of this species. In an attempt to clarify this situation, we grew British material of the species under controlled conditions through to the F₃ generation to remove environmental variation, and assessed the plants on the basis of a range of morphological criteria, namely leaf shape, capsule size and also length of time taken to flower. Analysis of these characteristics consistently produced four basic groups, which had been previously described. Herbarium specimens could also nearly always be assigned to one of these groups. Limited chromosome counts suggest that two of these groups are diploid and two are tetraploid. We suggest this fourfold division into broad groups reflects the major genetic separations within the species, but that there is also considerable phenotypic plasticity shown by *C. bursa-pastoris* in response to factors such as shade or trampling. These four groups appear to differ in their geographical distribution in Britain.

KEYWORDS: Shepherd's Purse, morphological variation, leaf characters, capsule characters, chromosome counts, infraspecific groupings.

INTRODUCTION

Capsella bursa-pastoris (L.) Medik. (Shepherd's Purse) (Brassicaceae) has a cosmopolitan distribution, and is a colonising species of disturbed ground. Being found in a broad range of conditions, up to 5900 m (Wilson 1949; Mani 1978) and in almost all countries of the world from tropical to subarctic habitats (Holm *et al.* 1979), the species is known to exhibit considerable morphological variation.

Capsella bursa-pastoris has been described by numerous authors since the late 19th century, and has been divided taxonomically into many species, subspecies, varieties, microspecies and segregates. Jordan (1864), one of the earliest workers, described five species in France, namely *Capsella agrestis*, *C. virgata*, *C. ruderalis*, *C. sabulosa* and *C. praecox*, none of which are recognised today. Hopkirk (1869) considered the variation in Belgium to consist of subspecies derived from one common type, and he went on to describe six subspecies based primarily on the character of the capsule. Mott (1885) described eight varieties for Leicestershire and Rouy & Foucaud (1893) listed seven varieties and four subspecies based on the fruit characteristics in France. Almquist (1907) described 70 elementary species and later (Almquist 1921) examined British *Capsella bursa-pastoris* and listed 16 species. His descriptions were based on fine distinctions of leaf and capsule shape and size. Two years later, Almquist (1923) had recorded twelve classes of *Capsella* containing almost 200 microspecies. His microspecies were again based on minute differences in capsule shape and size, differing leaf shapes and position of leaf lobes. More recently, but only in Cyprus, Meikle (1977) recognized two species based on capsule size whilst Clapham *et al.* (1987) record *Capsella bursa-pastoris* as "very variable with a strong tendency for distinctive populations to arise because of self-pollination. Many of these have been named", but they do not specify any of these. The first edition of *Flora Europaea* (Chater 1964) comments that numerous variants have been described by Almquist, whilst the second edition (Chater 1993) states that "there is extreme

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polymorphism within the four species listed" and that "*Capsella bursa-pastoris* is especially polymorphic and its variants incorporate many of the characteristics of the other three species". Most recently, Stace (1997) describes *C. bursa-pastoris* "as extremely variable in leaf and fruit shape; c. 25 segregates have been recognized in the British Isles". No details of these are given, nor is any information on them provided by the specialist *Crucifers of Great Britain and Ireland* (Rich 1991).

The problems of taxonomy at the infraspecific level, relevant to a very variable species such as *C. bursa-pastoris* which is largely inbreeding yet has many phenotypic variations, are discussed, for example, by Stace (1989). This author notes that such phenotypic modifications would not be given taxonomic status by most taxonomists and that when such variations are recognised as phenotypic, they are relegated to synonymy. *Capsella bursa-pastoris* certainly shows phenotypic variation as a direct result of a wide range of environmental factors including temperature, shading, altitude, latitude and season; for example, Almquist (1923) found that leaves developing in autumn and spring were mostly lobed, whereas mid-summer leaves tend to be poorly lobed or entire. Hurka (1990) found pronounced ecotypic variation in time to flowering between early Scandinavian and late Alpine populations; he also found early and late ecotypes in North America. Aksoy (1996) observed the effects of shading on leaf shape, Steinmayer *et al.* (1985) recorded correlations between leaf form and temperature and rainfall, and Neuffer (1989) investigated the effects of temperature on variables such as leaf shape and flowering times. However, it is possible that not all the complex variations observed in this species can be reduced to phenotypic variation superimposed on one single species complex.

Shull (1909) collected seeds of *C. bursa-pastoris* from different sites in North America, where the species is introduced but now widely naturalized, and grew these under standard conditions for several generations, by self-pollination. He found that the majority of his plants could be fitted into four basic groups based on the characters of the rosette leaf shape. He referred to these four groupings ("biotypes" *sensu* Shull) as *Capsella bursa-pastoris* and used these names for them: rhomboidea, simplex, heteris and tenuis.

Steinmayer *et al.* (1985) examined 29 populations of *C. bursa-pastoris* from the Alps to northern Scandinavia, from Iceland and also a population from the Hindu Kush Mountains in Afghanistan, while Neuffer (1989) worked with populations of *C. bursa-pastoris* collected from southern to northern Europe (including three from Britain), two populations from Egypt and one from Israel. Their populations were grown under standard conditions either in glasshouses or in field trials for varying periods of time. Analyses of leaf shapes and capsule size allowed the authors to classify most of their plants into one of the four basic groups proposed by Shull (1909).

This paper seeks to expand on the work of Neuffer (1989) by examining populations of *C. bursa-pastoris* from a variety of habitats and geographical areas in Britain, to determine how well Shull's four basic groups are generally recognizable in the field, and from herbarium specimens; to germinate and grow seed from the different populations under standard conditions, and to observe whether, when environmental variation is removed, the plants can be classified according to Shull's groups; and, finally, to determine whether or not this classification is maintained in their progeny.

If Shull's groupings are substantiated then a step will have been made towards simplifying the taxonomic classification of *C. bursa-pastoris* from 200 microspecies, or 25 segregates, or no attempt at all to sub-divide this variable species, to producing four useful groups, which can be recognized as having a distinct genetic basis underlying the environmentally modified phenotype.

Although Shull's work was concerned only with examining leaf morphology, other workers, mentioned above, have used capsule size and shape as identifying characters and these have also been examined in the present paper; chromosome numbers have also been assessed. Chromosome numbers are usually tetraploid with $2n = 32$ (Davis 1965; Löve & Löve 1956; Svensson 1983; Clapham *et al.* 1987). Chater (1993) records both $2n = 32$ and also $2n = 16$; Svensson (1983) also records diploid specimens with $2n = 16$ from Greece.

MATERIALS AND METHODS

Seed samples from locally available populations were collected from 20 different habitats in Bradford and district, and from 14 other locations throughout Britain, between April and July 1993.

These were germinated in potting compost in a glasshouse and grown on until they set seed. Cross pollination was assumed to be prevented by keeping each of the populations in a different place in the glasshouse, with sliding separating doors to aid isolation, and by the fact that the species is primarily adapted for self-pollination. Subsequent seed collection and growing was continued through to the F₃ generation.

In each generation the rosette leaf shape was assessed for 15 plants, randomly selected from each population, according to a four-fold categorisation on the basis of Shull (1909) as follows:

Capsella bursa-pastoris group A ("simplex" sensu Shull (1909))

Leaves with mostly simple, rounded or triangular, acutish lobes.

Capsella bursa-pastoris group B ("rhomboidea" sensu Shull (1909))

Leaves divided to the midrib; possessing a more or less rhombic terminal lobe, set off by deep sinuses from the nearest lateral lobes.

Capsella bursa-pastoris group C ("heteris" sensu Shull (1909))

Leaves divided to the midrib; the terminal lobe usually separated from the nearest lateral lobes by deep, clean-cut incisions.

Capsella bursa-pastoris group D ("tenuis" sensu Shull (1909))

Sinuses relatively shallow, rarely extending to the midrib; the terminal lobe is not separated from lateral lobes by deep incisions; lateral lobes are generally slender, elongated and acute.

The original parent plants had also been evaluated on this categorisation. While most of these could be fitted to one of the groups a number were of intermediate status and could not be classified at the time of collecting.

For each of the F₃ plants, the lengths and widths of 30 seed capsules were measured to provide an indication of shape. The number of days elapsed between germination and the production of the first flower by each plant was recorded for each group.

The somatic chromosome number was determined for 15 plants of the F₃ generation of each group from root-tip squashes. The root tips were pretreated for 2 hours in a solution of 0.1% colchicine and 2 mM 8-oxychinoline (1:1), fixed in Carnoy's fluid and stained in aceto-orcein.

In addition to the fresh material collected during this study, herbarium material from The Natural History Museum, London (BM) was consulted to obtain further information on the relative frequencies and geographical distribution of the groups in Britain, wherever the groups could be recognized from herbarium specimens. Two hundred specimens were examined, of which 189 could be allocated to one of Shull's four basic groups.

RESULTS

Although the field populations showed phenotypic variation, the F₁ generation, produced by self-pollination, gave rise to F₂ and F₃ generations which exhibited no phenotypic variability from the F₁ generation. Observations and measurements from the F₃ generation are presented in Figs 1 & 2 and Table 1, divided into the leaf morphology groups shown consistently from the F₁ generation.

The chromosome studies reported in this paper indicate that there are diploid as well as tetraploid populations of *C. bursa-pastoris* in Britain. Groups A and B (simplex and rhomboidea) are tetraploid while groups C and D (heteris and tenuis) are diploid. The results indicate that the rate of growth was greater for the tetraploid groups, which produced larger capsules (Fig. 2). Capsule

TABLE 1. MEASUREMENTS OF VARIOUS PARAMETERS (MEAN \pm STANDARD ERRORS) FOR THE DIFFERENT GROUPS (A-D) (SENSU SHULL (1909)) OF *CAPSILLA BURSA-PASTORIS* GROWN UNDER STANDARD GREENHOUSE CONDITIONS

Group	A (simplex)	B (rhomboidea)	C (heteris)	D (tenuis)
Chromosome number	2n = 4x = 32	2n = 4x = 32	2n = 16	2n = 16
Capsule length (mm)	7.81 \pm 0.15	7.58 \pm 0.15	6.56 \pm 0.11	6.29 \pm 0.11
Capsule width (mm)	7.34 \pm 0.11	6.47 \pm 0.11	4.85 \pm 0.07	4.25 \pm 0.06
Days to first flowering	32 \pm 4.26	40 \pm 5.12	65 \pm 6.24	70 \pm 7.54

30 capsules from 15 plants for each group were measured.

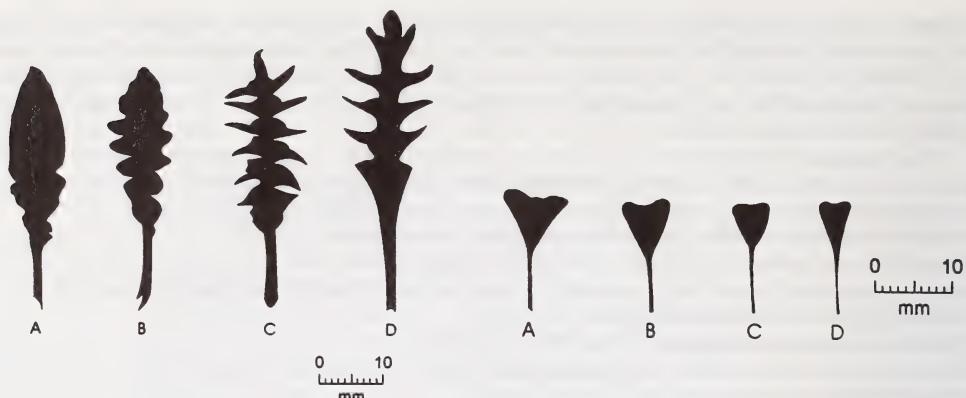


FIGURE 1. Comparison of leaf morphologies for F_3 *Capsella bursa-pastoris* groups A–D, grown under standard conditions: A - simplex; B - rhomboidea; C - heteris; D - tenuis (sensu Shull (1909)).

FIGURE 2. Comparison of capsule size and shape for F_3 *Capsella bursa-pastoris* groups A–D, grown under standard conditions: A - simplex; B - rhomboidea; C - heteris; D - tenuis (sensu Shull (1909))).

lengths for groups A (simplex) and B (rhomboidea), the tetraploids, were significantly different based on t-tests (at $p < 0.001$) from those of group C (heteris) and D (tenuis), the diploids. Capsule lengths were not significantly different between A and B nor between C and D. However, capsule widths were significantly different (at $p < 0.001$) between all four groups. Days to flowering was also examined and, as for capsule length, the differences between A and B were not significant, nor those between C and D, but the differences between the tetraploids and diploids were significant, based on t-tests, at $p < 0.001$ with the tetraploids flowering earlier (Table 1). Observations, however, suggest that the diploid groups tended to flower over a more extended period and to survive longer than the tetraploids.

From observations of 289 individual plants (both herbarium and fresh) from Britain, the relative frequencies of the four groups were found to be: A (simplex) 23%; B (rhomboidea) 39%; C (heteris) 33% and D (tenuis) 5%. Based on this relatively restricted sample, the distribution of the four groups appears to vary geographically (Fig. 3); from the material (fresh and herbarium) available, groups B and C were found throughout Britain but group A was not recorded from northern Scotland and group D (based on a small percentage of records overall) was only found in material from England.

DISCUSSION AND CONCLUSIONS

The classification of *C. bursa-pastoris* in the field has been hampered by the polymorphic variation in leaf shape and size resulting from gene-environment interactions, particularly as the species is of such widespread geographical and altitudinal distribution and is found in a wide variety of habitats. Neuffer (1989), working with a large number of populations of *C. bursa-pastoris*, showed that the genotypes defining leaf type are easily modified by environmental parameters and that the degree of phenotypic plasticity varies from provenance to provenance. This variation has led to widely differing attempts to classify *C. bursa-pastoris* in terms of microspecies based on either leaf shapes and/or capsule shape and size.

If systematic botany relies solely on descriptions of plants in the field then the problems of classifying polymorphic species such as *C. bursa-pastoris* will remain. However, if collateral cultivation methods are adopted in lieu of comparative field morphology, as has been carried out in this study, then a useful step forward may be made.

Because genotype-environment interactions are very pronounced then the use of herbarium specimens in classifying *C. bursa-pastoris*, although also of considerable value, may have limitations owing to the presence of intermediate leaf shapes. It is not always possible to classify these into the basic groups, although in the current work only 5% of the herbarium specimens

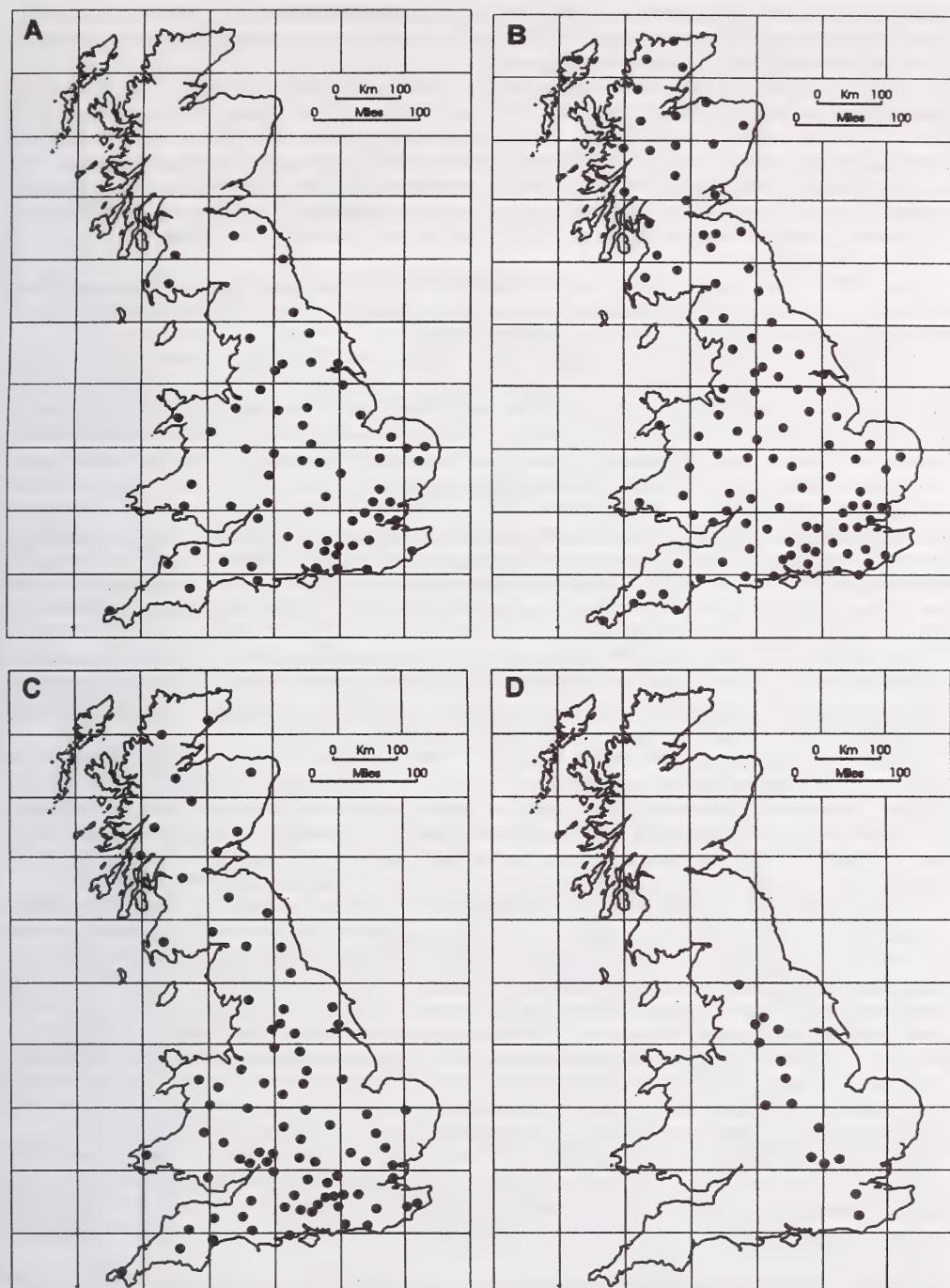


FIGURE 3. Distribution of *Capsella bursa-pastoris* groups A-D in Britain, based on collected samples and herbarium material: A - simplex; B - rhomboidea; C - heteris; D - tenuis (sensu Shull (1909)).

examined could not be so classified. It nevertheless remains a possibility that some misclassification of specimens might have occurred because of phenotypic variation mimicking the characteristics of a different genetically-determined grouping.

The glasshouse experiment carried out here shows that the original four-fold grouping of Shull, extended and defined by Steinmayer *et al.* (1985) and Neuffer (1989), also appears to hold good for British *C. bursa-pastoris* and although in the field a number of intermediates were collected, which could not be immediately classified into one of the four basic groups, on cultivation through to the F_3 generation all progeny derived from the intermediates could be placed into one of the four groups. The leaf morphology of these groups is easily recognisable and because these have a recognised genotype (Steinmayer *et al.* 1985) this seems a sensible sub-division on which to classify *C. bursa-pastoris*.

Shull (1909) based his groupings only on leaf shape but in this paper capsule dimensions have also been examined and this additional work provides a further means of determining to which of the four groups individuals of *C. bursa-pastoris* belong.

The differences in geographical distribution in Britain of the groups shown in Fig. 3 may possibly be a reflection of the restricted sample for which material has been examined and more sampling needs to be done to clarify this. However, differences in distribution of the groups, and in the relative abundance of the different groups, have also been suggested by other work elsewhere. Preliminary observations on plants in Turkey (not presented here) indicated that the same groups were recognisable there, although in that smaller sample only groups A, B and C were recorded. Group A was found only along the Mediterranean coast, while groups B and C were found both along the coast and also at inland sites. Neuffer (1989), in her more extensive studies throughout Europe, recorded 57% of her plants as belonging to group C (heteris), 41% as group B (rhomboidea) and 2% as group A (simplex). Group D (tenuis) again was not recorded. Confirmation of such differences would obviously be important for assessing the ecological significance of differential adaptations of these groups.

The tetraploids (groups A and B) flowered earlier than the diploids (Table 1) under glasshouse conditions, as did those in the field trials of Neuffer (1989), and also those recorded during field observations by Svensson (1983) for *C. bursa-pastoris* in south-eastern Europe. This suggests that cross-pollination between the diploid and tetraploid groups is unlikely.

Capsella bursa-pastoris flowers are adapted to both self- and cross-pollination although the former seems to be by far the more common method. This method is favoured by the fact that the stigma is receptive to pollen on both its under and upper surfaces and the anthers dehisce while they are held in contact with the under surface of the stigma by the partially-closed petals (Shull 1909). After the anthers begin to dehisce the petals open fully and pollen is available to be transported to other plants. *Capsella bursa-pastoris* is visited by a variety of small flies and bees (Shull 1909).

Stebbins (1951) commented that self-pollinating annual species, in addition to showing genetic similarity, have a relatively high degree of phenotypic plasticity compared with perennials, so that the individual genotype can be modified considerably depending on whether the environment is favourable or not. It is the variable expression of this plasticity which has led to the confusion in the classification of *C. bursa-pastoris*. However, *C. bursa-pastoris* has not lost its capacity for forming new gene combinations and Hurka *et al.* (1989) estimated outcrossing rates, based on allozymes, as between 3 and 12%. They found that cold and rainy weather seems to support self-pollination, whereas dry and sunny weather seems to favour cross-pollination. Thus this predominantly autogamous, yet flexible mating system, coupled with polyploidy and extreme polymorphism, may contribute to the colonising ability of *C. bursa-pastoris*, and its widespread distribution.

Shull did not present his names for the four types of *Capsella bursa-pastoris* as formal taxonomy. Indeed he states "in adopting the names used in this paper I have been governed entirely by the demands of present utility and not by any thought that these names will be accepted by taxonomists as having proper standing in the nomenclatural system now recognized by them" (Shull 1909).

However, he goes on to record that a large number of plants of "the fourth pedigree generation and a few of the fifth under observation" retained "easily recognized differentiating marks, which, except in one form, show no transgression of the characteristic features of any other form studied. These forms are therefore distinct elementary species, or biotypes, each characterized by certain constant features and each with its own range of fluctuating variability." (Shull 1909). Shull

comments that he was at first inclined to use binomial names, leaving the Linnaean species name - *bursa-pastoris* - as the valid name for the aggregation of the infraspecific forms, having the same habit and triangular or obcordate capsules. But the fact that a corresponding series of infraspecific forms may occur in different related species led him to use the trinomial system, and he used the same infraspecific names for the two closely related species *Bursa* (= *Capsella*) *bursa-pastoris* and *Bursa* (= *Capsella*) *heegeri*.

The authors are of the opinion that Shull's (1909) interpretation of this taxon is based on sound characters underlying the complex phenotypic variability, and that consideration might be given to the establishment of subspecific nomenclature to describe these four groups of *C. bursa-pastoris*.

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Conservation of Britain's biodiversity: *Filago lutescens* Jordan (Asteraceae), Red-tipped cudweed

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ABSTRACT

This paper summarizes the conservation work being carried out on *Filago lutescens* L. (Asteraceae), Red-tipped cudweed, a rare, statutorily protected species in Britain. It is a winter or spring annual, germinating mainly in the autumn, and flowering from June to October. Its habitats are mainly arable fields, tracks and path sides, open sandy ground, sand pits and commons or heathland usually in *Thero-Airetalia* vegetation. It has been recorded in a total of at least 212 sites in 86 10-km squares in south-eastern England, but has been seen in only 14 sites in ten 10-km squares since 1990. It appears to have declined in arable field habitats owing to changes in agricultural practices, and in tracks and heathland owing to reduced disturbance. Much of the decline took place before the 1960s. Population counts for all extant sites between 1993 and 1996 show marked variation from year to year and marked differences between sites. The best conservation management is currently thought to be annual disturbance by digging or rotovation in early autumn. This species is still under severe threat in Britain; only two extant sites have statutory protection and the two largest populations are unprotected.

KEYWORDS: population size, ecology, distribution, habitat management, rare species.

INTRODUCTION

Filago lutescens Jordan (*F. apiculata* G. E. Sm. ex Bab.; Asteraceae), Red-tipped cudweed, is a rare species in Britain. It is one of five species of *Filago* native to Britain all of which occur in open skeletal habitats, and all of which are declining. *F. pyramidalis* L. is very rare and statutorily protected; its conservation is described by Rich (1999a). *F. gallica* L., recently reassessed as a native species (Rich 1994), has subsequently been reintroduced from native stock to mainland Britain from where it has been extinct since the 1950s (Rich 1995a). *F. vulgaris* Lam. and *F. minima* (Sm.) Pers. have also shown significant declines between 1930 to 1960 and 1987 to 1988 (Rich & Woodruff 1996).

Although *F. lutescens* has been known to be declining in Britain for over 20 years (e.g. Perring & Farrell 1983), virtually nothing was known about its ecology or the reasons for the decline. In 1994, the wild-plant conservation charity Plantlife became concerned that *Filago lutescens*, *F. gallica* and *F. pyramidalis* were amongst the most threatened plants in Britain. The species were therefore included in their 'Back from the brink' project, which aims to conserve critically endangered plant species through research and management work. About 20 rare plant species have been included in this project between 1992 and 1996, which represents a significant contribution to the conservation of biodiversity in Britain by the voluntary sector. The aim of this paper is to summarize and update the conservation work carried out on *F. lutescens* up to 1996; full details can be found in Rich (1995b, 1996) and Rich & Davis (1996). Further details about the 'Back from the brink' project can be obtained from Plantlife.

DISTRIBUTION

DISTRIBUTION IN BRITAIN

As *Filago* species have often been confused in Britain, a review of the historical records was first carried out. *F. lutescens* is relatively easily distinguished from the other species by the red tips to

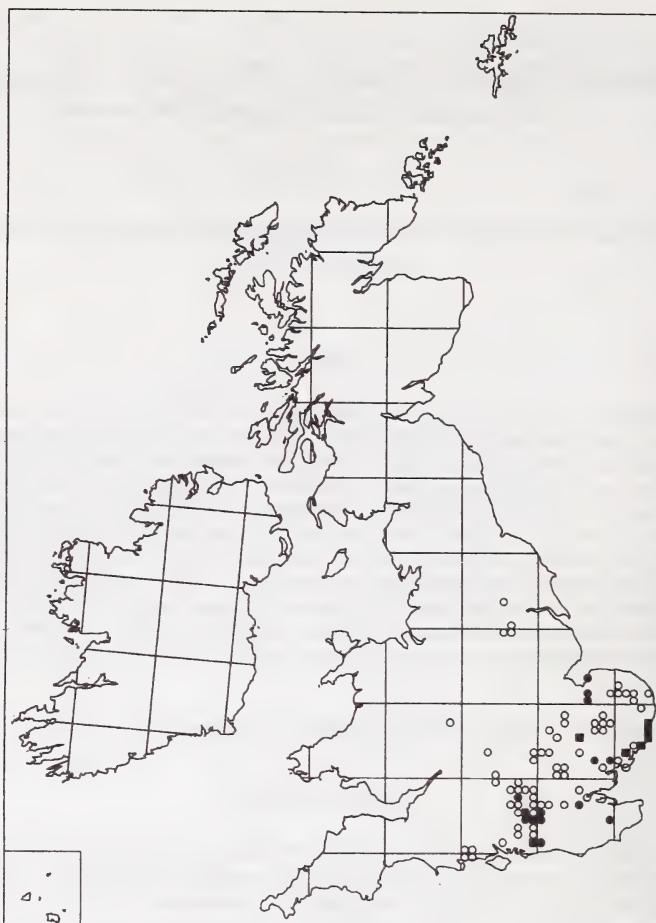


FIGURE 1. Distribution of *Filago lutescens* in the British Isles. ■ 1990 onwards. ● 1950–1989. ○ Pre-1950 and undated records.

the young phyllaries – in older flowers these fade to straw-coloured, resulting in confusion with *F. vulgaris* and *F. pyramidata*. There are two subspecies of *F. lutescens* (Holub 1976): subsp. *lutescens* is widespread and occurs in Britain and Europe, and subsp. *atlantica* Wagenitz occurs in Portugal and the Azores.

F. lutescens was first reported in Britain by Smith (1846) from sandy borders of fields, hedgebanks and roadsides in Yorkshire. Watson (1848) clarified the distinction between it and the other species, and it was subsequently quite widely recorded (not always correctly) in southern England. It has slowly declined, and is now very rare and unknown to most British botanists.

Records have been compiled from the literature, herbaria (BM, BRISTM, BTN, CGE, E, GL, GLAM, IPS, K, LIV, LTR, MNE, NMW, NWH, OXF, RAMM, RNG, SLBI, TTN and US; abbreviations following Kent & Allen 1984), field survey, correspondence with botanists and from information held by English Nature and the Biological Records Centre, Monks Wood. Most of the records are supported by herbarium specimens determined by T. C. G. Rich or J. Holub. Doubtful records have been rejected. About 400 records have been traced, representing at least 212 localities in 86 10-km squares in 24 vice-counties.

A distribution map distinguishing 1990 to 1996, 1950 to 1989 and older records is shown in Fig. 1. The species has been fairly widely recorded in south-eastern England. All the records are accepted as native as there are no records of any introduced localities. Note that a number of the records in Perring & Walters (1962, 1990) have been revised here and many more added.



FIGURE 2. Distribution of *Filago lutescens* (redrawn from Meusel & Jäger 1992). The distribution of subsp. *atlantica* is enclosed by a dotted line.

WORLD DISTRIBUTION

The world distribution is shown in Fig. 2; it is widely recorded in western Europe, with scattered records in the former Yugoslavia (Holub 1976; Meusel & Jäger 1992).

It is still reasonably widespread in Spain, Portugal and France but becomes rarer eastwards in Europe. In Holland, it has been long-neglected and is probably extinct (Adema 1976), and there is no known reason for its disappearance (Mennema, Quene-Boterendrood & Plate 1980). In Belgium and Luxembourg, it was recorded 18 times before 1930, and only once since (van Rompaey & Delvosalle 1972). In Germany, it is scattered and rare, mainly in the south and also in an area around the Baltic; there are relatively more pre-1945 records suggesting that it has declined (Haeupler & Schonfelder 1989). In Switzerland, there are 28 historical records mainly in the north-west of the country (Welten & Sutter 1982). In the Czech Republic, it is very rare and is statutorily protected. In the former U.S.S.R., it is treated as a variety of *F. vulgaris*, and is described as rare (Smol'yaninova 1990). It is extinct in Sweden (Holub 1976).

STATUS IN BRITAIN

CHANGES IN THE NUMBER OF RECORDS WITH TIME

A conservative approach has been taken to analysing the records to determine changes in the status with time, due to the inherent inconsistencies of the records and the recorders. Some records lack dates, some localities cannot be traced, and it is unclear if some records refer to the same or different sites. Whilst the general quality of most post-1950 records allows individual sites to be identified, this becomes increasingly difficult with older records. A site with the same name is assumed to be the same locality unless the habitats are obviously different (e.g. arable field or gravel pit). The absence of a record from a locality does not necessarily mean that the plant did not

TABLE 1. SUMMARY ANALYSIS OF RECORDS OF *FILAGO LUTESCENS* IN BRITAIN BY DECADE. THE OVERALL NUMBER OF RECORDS IS 25% UNDER-ESTIMATED DUE TO UNDATED RECORDS

Decade	Total no. of records	No. of 10-km squares	Extrapolated number of extant localities per decade
1840–49*	26	12	21
1850–59*	5	5	7
1860–69*	11	6	8
1870–79*	15	12	16
1880–89	26	15	20
1890–99	29	16	25
1900–09	14	8	23
1910–19	24	15	23
1920–29	8	7	14
1930–39	17	10	19
1940–49	9	6	16
1950–59	23	8	19
1960–69	20	10	17
1970–79	12	10	12
1980–89	17	5	9
1990–1996	40	10	14
Undated	59	18	52

* = Probably significant under-estimates due to lack of recording.

Table 1 summarizes the records by decade, 10-km square and locality. Note that because a quarter of the historical sites have no date information, the number of records is under-estimated. The total number of records per decade varies according to the botanical activity of recorders rather than changes in the frequency of the plant, as is well known for other plants (e.g. *Thlaspi perfoliatum*; Rich 1999b). The publication of the first record in 1846 stimulated many other records from the Botanical Society of London, which was very active at the time, but the records drop in the 1850s when the Society collapsed. Collecting by its successor, the Botanical Exchange Club, in the 1860s and 1870s again resulted in many records with a peak in the 1890s, by which time the main features of the distribution were known. The troughs in the 1920s and 1940s may be due to the Depression and Second World War respectively. The influence of the agricultural revolution in the 1950s and 1960s is seen with a subsequent decrease in the number of records, the rise recently being due to field work for the Nature Conservancy Council in the late 1980s and the survey work in the 1990s reported below.

The number of 10-km squares recorded is a widely-used measure of relative frequency in Britain (e.g. Perring & Farrell 1983). The number of 10-km squares recorded per decade shows a similar pattern (Table 1); note that because not all sites persist there is a considerable turnover of 10-km squares each decade.

A better measure of change than the number of 10-km squares is the change in the number of sites with time. As not all sites will have been continuously recorded, the number of sites present has been extrapolated by assuming the species was present at each site for all decades between the first and last record. The number of sites present for each decade was then totalled (Table 1). There is a decline in the number of sites to the current 14 by gradual loss of sites randomly across the whole range, and most of the decline appears to have taken place by the 1960s. The plant has been recorded since 1990 in 14 out of at least 212 localities (6.6%), and many of the remaining populations are so small that they could be threatened in poor years (see below). Further losses are to be expected unless the remaining populations are conserved.

REASONS FOR THE DECLINE

The reasons for the decline have been investigated by analysing changes in the habitats in which the plant has been recorded (Table 2). Whilst some records do not indicate exactly in which habitat the plants were growing, the main trends can be discerned.

TABLE 2. HABITATS OF *FILAGO LUTESCENS* IN BRITAIN COMPILED FROM RECORDS WITH HABITAT DATA. REPEATED RECORDS FROM THE SAME SITE ARE NOT INCLUDED. 114 RECORDS (43% OF ALL HISTORIC RECORDS) HAVE NO HABITAT NOTED

Habitat	Number (%) of records up to 1989	Number (%) of records 1990–1996
Fields or arable	65 (43%)	4 (29%)
Roadsides, lanes, paths, tracks	24 (16%)	3 (21%)
Gravel and sand pits	12 (8%)	2 (14%)
Commons and heathland	12 (8%)	1 (7%)
Sandy or gravelly ground	12 (8%)	1 (7%)
Fallow or stubble fields	7 (5%)	1 (7%)
Railways	6 (4%)	1 (7%)
Gardens	3 (2%)	0
Woods (presumably on tracks)	2 (1%)	0
Chalk pit	2 (1%)	0
Meadow	1 (0.7%)	0
Clay pit	1 (0.7%)	0
Golf links	1 (0.7%)	0
Rubbish tip	1 (0.7%)	0
Market garden	1 (0.7%)	1 (7%)
Total	150 (100%)	14 (100%)

Historically, *Filago lutescens* was most commonly reported from arable fields, associated with a wide range of crops including rye, corn, barley, wheat, clover, sainfoin, roots and potatoes (Table 2). Often the fields are described as sandy, and sometimes as gravelly. Interestingly, it was much less commonly reported from fallow or stubble fields than its two rare relatives, *F. pyramidalis* and *F. gallica*, perhaps owing to the plant's growing and flowering earlier than the other species. The decline in records from arable fields is striking.

It was also widely reported from paths, tracks and roadsides (Table 2). Before roads were paved and covered with tarmac, road and tracks were regularly disturbed by carts and animals which must have created suitable habitats. Most road verges today tend to support unsuitable tall, closed grassland communities. Some unpaved tracks and paths still maintain suitable short, open habitats.

The next most suitable habitats are sand or gravel pits, sandy ground, and commons and heathland. These reflect the suitability of the soils and the disturbance created by grazing or small-scale mineral extraction. The railway habitats include a range of sites from cuttings to tracks and station yards. The plant is only rarely recorded from other habitats, and has only occasionally been recorded from closed communities where it does not persist.

The main reason for decline is undoubtedly the loss of populations in arable fields, probably due to the use of selective herbicides, fertilisers and changes in the timing of agricultural operations (Wilson 1992). This is a similar story to many other arable weeds in Britain such as *Scandix pecten-veneris* and *Agrostemma githago*. Loss of other habitats such as roadsides, and the decline in grazing and disturbance on heathlands, possibly coupled with the decline of rabbits through myxomatosis, have also taken their toll.

POPULATION SIZES 1993 TO 1996

The population sizes of all post-1990 sites were monitored between 1993 and 1996 (Table 3; the population at Suffolk 5 was last seen in 1991). In addition, a considerable amount of time has been spent by many volunteers and the author searching old sites across the country (Rich 1995b). During this search one old site was rediscovered and two new sites found, and it is probable that there are still a few more undiscovered sites.

The number of plants differs markedly between sites, with four sites holding on average over 90% of the plants (Table 3). The number of plants also varies markedly between years at some sites,

TABLE 3. ESTIMATED POPULATION SIZES OF *FILAGO LUTESCENS* AT ALL KNOWN SITES IN BRITAIN 1993–1996. SITES ARE LOCATED ONLY TO COUNTY

Site	Population size			
	1993	1994	1995	1996
Cambridgeshire 1	'frequent'	'frequent'	Unsurveyed	Unsurveyed
Essex 1	25	59	20	7
Hampshire 1	114	135	26	11
Suffolk 1	10	0	0	0
Suffolk 2	30	3	0	0
Suffolk 3	1 seedling	0	0	0
Suffolk 4	-	5	1000	5700
Suffolk 5	0	0	0	0
Surrey 1	17	35	10	110
Surrey 2	2000	2000	2000	2000+
Surrey 3	2000	1000	5000	61
Surrey 4	1000	23142	No access	No access
Surrey 5	-	-	300	100000
Sussex 1	200	500	40	20
Total	5397+	26879+	8400+	107909+
Number of sites	11	10	10 (+2?)	8 (+2?)

while staying relatively stable at others. Although some increases were responses to conservation management others were not, and there is no obvious link between population size and general management or climate; the only consistent pattern appeared to be an increase on arable fields in the second year of fallow. Were it not for exceptional increases in populations at two sites, the total British population in 1996 would be a matter of significant concern.

ECOLOGY

LIFE CYCLE

Filago lutescens is an annual, as are all its close relatives. Observations in the field and in cultivation show that seeds germinate throughout the autumn, winter and spring (Rich 1995b). Moss carpets provided a good micro-site for germination in Essex, but plants were later more prone to drought (C. Gibson, pers. comm. 1994). Müller (1995) studied germination at different temperatures, and found 100% germination at 15, 18, 20 and 22°C, without and with chilling (8 days in a freezer) treatments. Significant germination was found in all treatments within 6 days. Germination was a little slower at cooler temperatures, while treatment with Gibberellic acid resulted in enhanced rates of germination. No seeds in the dark at 15°C had germinated after 7 days, but once given light they germinated rapidly. Subsequently, seedlings not given the chilling treatment appeared to survive significantly better than seedlings given the chilling treatment; why is not known but it may reflect some aspect of the species' ecology as it is noticeably western in distribution in Europe (cf. Fig. 2).

Seeds thus seem to have little innate dormancy, and there is rapid germination of all viable seed when they grow in suitable conditions. There is unlikely to be a large, long-term seedbank. However, after clearance of *Ulex europaeus* scrub at the Hampshire site plants re-appeared after an absence of six years (C. Hall, pers. comm. 1995), and its appearance in arable fields in Surrey (J. E. Smith, pers. comm. 1996) also suggests that a small seed bank may be present in some sites.

The plants over-winter as small rosettes, the stems elongating from about May onwards. The main flowering period is July to October. Plants in cultivation in Sussex flowered in the last week of June with *F. vulgaris*, a week after *F. gallica* and a week before *F. pyramidata*. On a still sunny July day, the heads of cultivated plants smelled sweet but no insects were observed to visit them.

Plants are very variable in size in the field, perhaps related to time of germination and soil

conditions. Plants observed severely droughted in July 1994 in Sussex were noted to have 'greened up' again in August 1994 after rains (C. Murray, pers. comm. 1994). Plants which had flowered in autumn 1993 in Essex were still present in December 1993 and over-wintered but died the following spring and did not set more seed (C. Gibson, pers. comm. 1994).

VEGETATION AND SOILS

Historically in Britain, *F. lutescens* would have primarily been a species of weedy fields, but due to its decline in such habitats, it now appears to be a member of the annual communities of sandy, open places. The sites are usually disturbed and variable in composition. It is usually associated with species like *Aira praecox*, *Myosotis discolor*, *Filago minima*, *F. vulgaris* and strikingly, in most sites, *Scleranthus annuus*. In at least two British sites it has also been associated with both *F. pyramidalis* and *F. gallica*.

The vegetation is typically the *Thero-Airetalia* as it is in central Europe (Ellenberg 1988). This is a short-lived hairgrass community, one of a number of communities of heaths and grassland determined by human and animal activity. Other species characteristic of this vegetation type in Europe are *Aira caryophyllea*, *Filago arvensis*, *Hypochaeris glabra*, *Moenchia erecta*, *Nardurus lachenalii*, *Ornithopus perpusillus* (a weak associate), *Scleranthus polycarpos*, *Teesdalia nudicaulis*, *Trifolium striatum*, *Tuberaria guttata*, *Vulpia bromoides* and *V. myuros*. The species does not tolerate shade.

Most of the sites have fine, sandy, well-drained soils. pH measurements ranged from pH (5.1–) 5.7 – 6.7 (–8.0), neutral to basic in terms of plant growth (Rich 1995b). Interestingly, in Hertfordshire, Webb & Coleman (1849) described it as occurring on "light but moister soil than its congeners". All of the current sites are freely drained, and now only *F. pyramidalis* can be found on moister clays.

CLIMATE

The distribution in south-eastern England suggests a requirement for warm summers and low rainfall. Most of the sites fall in the area with a mean daily July air temperature of above 16°C, and an annual rainfall of less than 800 mm (sites in Sussex and Hampshire may have up to 1000 mm a year). In Europe it is mainly distributed to the west of the 16°C July isotherm north to Denmark, with a sharper cut-off in distribution in central Europe and only minor extensions to the east (Meusel & Jäger 1992).

In wet years it is likely that plants will dampen off as happens with other *Filago* species. Seedlings over-watered in a greenhouse in spring 1995 damped off (P. Angold, pers. comm. 1995). Plants were observed to have survived snow for a period of at least one week during the winter of 1995/1996. Further observations are required.

HERBIVORY

Plants do not seem to be systematically grazed by rabbits, although the young inflorescences may be nibbled off, and they also tolerate minor damage from horse and cattle grazing. It is possible that the plants are distasteful and are avoided by large herbivores. Slug damage appears uncommon.

CONSERVATION MANAGEMENT

SITE MANAGEMENT

It is essential that sites are appropriately managed each year to maintain open conditions as the plant appears to have only a limited seed bank. Traditionally, disturbance occurred during cultivation of the fields, but sites may now need rotavating on an annual basis. The best conservation management is currently thought to be annual disturbance by digging or rotavation in early autumn, but further research is required. Some of the current sites are unmanaged and the fact that the plants survive in some of them is amazing.

Digging or rotavation of sites has been successful at the sites Sussex 1, Surrey 1 and Essex 1 (see Table 3), but attempts to resurrect ailing or recently extinct populations using this technique at Suffolk 1, 3 and 5 have failed. Some preliminary data for Surrey 3 suggest that in arable field situations harrowing is a better option than ploughing, presumably because it creates the open ground necessary without burying seeds too deeply in the soil. Clearance of *Senecio jacobaea* has been carried out at Sussex 1 and Suffolk 4 to eliminate the need for weed control by herbicide. The Surrey 1 site was nearly destroyed by unauthorized spraying of the protected roadside verge.

An experiment designed to determine the best time for management work was carried out in the Sussex site in 1994–1995 by C. Murray, S. Dipper and T. C. G. Rich (Rich 1996). Replicated 1 m² squares were dug over by hand at monthly intervals from September 1994 to April 1995 and the number of plants counted in each plot in July 1995. Plants of *F. lutescens* appeared in plots dug over in all months. An analysis of variance showed that there were no significant differences ($p = 0.07$) between plots dug over in different months, indicating that the timing of management work is not critical. However, to ensure maximum population potential it is suggested that management work should be carried out in August or September depending on the season and occurrence of existing healthy populations.

Calculations have shown that a minimum sample size of 172 plants is required to preserve all, or very nearly all, polymorphic genes with frequency over 0.05 in a population (Lawrence, Marshall & Davies 1995a, b). It is thus proposed that conservation management should aim to achieve at least 172 *F. lutescens* plants at each site each year. On this basis, five sites have populations with long-term averages consistently above this minimum size but the others are distinctly threatened (Table 3).

This species is still under severe threat in Britain. It is desirable that all populations of over 1000 plants, and at least one population in each county, should be given statutory protection to maintain local biodiversity.

STATUTORY PROTECTION

Filago lutescens is statutorily protected under Schedule 8 of the *Wildlife and Countryside Act 1981* (as amended), which should prevent plants at all sites being picked or uprooted. The current protection of and threats to sites are summarized in Table 4. The Suffolk 2 and Surrey 3 sites are protected as statutory Sites of Special Scientific Interest (S.S.S.I.) specifically for *F. lutescens*, though it is currently extinct at one of these. Another S.S.S.I. designated for its bird populations has had two *F. lutescens* populations in the recent past (Suffolk 3 and 5). Surrey 1 and Sussex 1 have non-statutory nature conservation designations. The other seven sites, including the two largest, have no protection and are currently have no conservation management which is a particular cause for concern.

MONITORING AND RESEARCH

It is essential that populations are monitored each year, not only to establish new threats, but also to determine the results of the conservation work and assess natural variation due to weather. Between 1993 and 1996 monitoring was carried out cost-effectively by simple counts of plants, photographs and observations on management. Further research work into the factors controlling population size is urgently required.

TABLE 4. SITE PROTECTION AND THREATS TO *FILAGO LUTESCENS* SITES IN 1996

Site	Site protection and threats
Cambridgeshire 1	No protection. Privately owned; owner aware of plant.
Essex 1	No protection; threatened by fly-tipping and encroachment of vegetation. Management working.
Hampshire 1	Local designation only; managed appropriately by local Wildlife Trust.
Suffolk 1	No protection; appropriate management not working.
Suffolk 2	S.S.S.I.; inappropriately managed.
Suffolk 3	S.S.S.I.; appropriate management not working.
Suffolk 4	No protection; co-operative owner.
Suffolk 5	S.S.S.I.; appropriate management not working.
Surrey 1	Protected road verge subject to regular catastrophes but otherwise sympathetically managed.
Surrey 2	No protection; co-operative owner.
Surrey 3	S.S.S.I.; appropriate management not working.
Surrey 4	No protection and no access to assess threats.
Surrey 5	No protection; horse grazed with potential threat of 'improvement' of grass.
Sussex 1	Local designation only; co-operative owners

S.S.S.I. = Site of Special Scientific Interest.

EX-SITU CONSERVATION

Seed from five extant sites and one extinct site is held at the Royal Botanic Gardens Seed Bank at Wakehurst Place (J. Terry, pers. comm. 1997). Collections from the other sites are urgently required to ensure conservation of the genetic diversity and allow for reintroduction programmes if needed.

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Juniper in the Lake District National Park. A review of condition and regeneration

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ABSTRACT

Juniperus communis L. (Common Juniper) (Cupressaceae) is a native British species of evergreen dioecious conifer, threatened by extensive grazing, competing tree species and lack of sites to colonise. This study assesses the present status of juniper in the Lake District. Ten large stands recorded as in good condition in 1975 were compared to five smaller stands, and a reference stand protected from grazing for 70 years. Recorded values of the number of berries produced by large stands and seed viability of these berries were combined as a seed viability index. Analysis showed that the seed viability indices of large stands were significantly higher than the small stand values, but significantly lower than the reference stand. These results suggest low reproductive potential may be indicative of a senescing population, and that grazing pressure is limiting reproduction. The absence of regeneration is attributed to stands becoming substantially moribund at a similar time without replacement. Seedling propagation and planting in fenced areas is suggested as the best strategy for juniper conservation.

KEYWORDS: reproductive potential, seed viability index, stand size, grazing pressure.

INTRODUCTION

Juniperus communis L. is a characteristic shrub of varied morphology. It is one of three native species of Coniferae in the British Isles (Humphries 1981), well established in the Lake District where it is mainly found on scree slopes and exposed regions. Throughout the country *J. communis* exhibits variation in population structure existing sometimes as large stands, sometimes as individual bushes, and has been observed to show differences in life history, genetic constitution and morphology, particularly between southern and northern Britain. The north/south divide is also apparent from the distribution map of the species (see Fig. 1).

Two subspecies of *J. communis* are recognised, *J. communis* subsp. *nana* Syme which is usually prostrate, small and slow growing, and *J. communis* subsp. *communis* the commoner, larger subspecies. However there is some doubt as to the distinction between subspecies due to the highly variable morphology (Ward pers. comm.).

Evidence from Upper Teesdale Nature Reserve, North Pennines and Tynron Juniper Wood, Dumfries and Galloway shows that there has been active management of *J. communis* in this country for a considerable period (Piggott 1956). By continuously disturbing the ground over a large area, substantial quantities of *J. communis* have been maintained which would otherwise have been outshaded by successional species such as *Betula pendula* (Clifton, Ranner & Ward 1997). In the Lake District particularly, the wildly fluctuating mining and quarrying industries which were a feature of the area for several hundred years up until this century (Gilbert 1980), and the lack of any regulated grazing regime are thought to have encouraged colonisation by continuous disturbance of the ground (Milner 1992). The large quantity of *J. communis* in the Lake District is therefore thought to be due to two main influences: (1) active management and (2) conditions which are conducive to repeated colonisation.

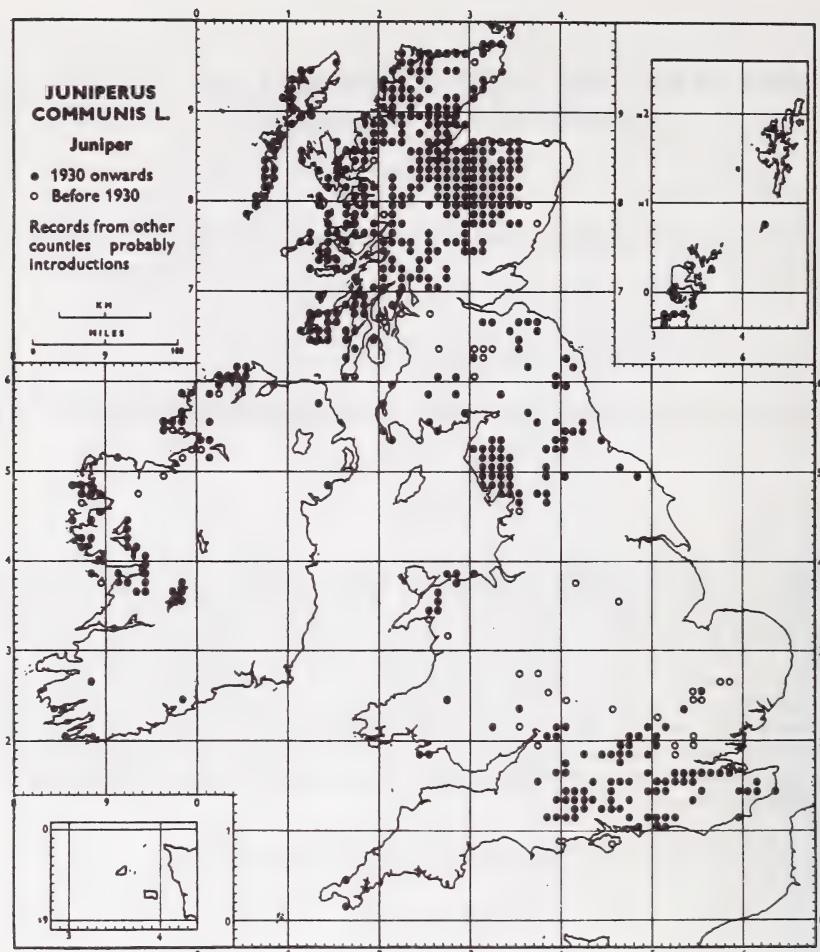


FIGURE 1. National distribution of *Juniperus communis*

The vast majority of research into British *J. communis* has been carried out in Southern England. As far as we are aware there are no published papers relating to *J. communis* in the Lake District, and while Miles & Kinnard (1979a; b) have researched *J. communis* in the Scottish Highlands, and Ward has made maps of distribution over the Lake District (Ward pers.comm.), there remains a gap in our knowledge of *J. communis* in this region. It is recognised however that *J. communis* is declining in the area and has been for most of this century, as it is over the majority of the country (Ward 1973).

There has been speculation over the reasons for the present decline in *J. communis* but Ward (1977), Gilbert (1980) and Clifton, Ranner & Ward (1997) have all suggested that lack of suitable sites to colonise and intensive grazing of any regeneration are the principal causes. Ward (1982) has conducted surveys of the age of *J. communis* and results show that most stands have a very even age structure. This is taken as evidence of the colonising nature of *J. communis* and also suggests that without further colonisation, individual stands will tend to become universally moribund at a particular age. Evidence that *J. communis* declines in seedling viability with age of parent means that if stands are allowed to become moribund, the potential for natural regeneration will also decline (Raatikainen & Tanska 1993).

In the Lake District particularly, the grazing and mining regimes used until the end of the last century, are thought to have been beneficial for recolonisation. At present any mining is done on a

more long term basis and is less disturbing to the local community. The widespread change of farming practice from arable to livestock following the agricultural depression of 1870–1940 seems to coincide with the start of the *J. communis* decline in the area (Milner 1992). Grazing would appear to play an important role in *J. communis* colonisation, as noted by Thomas (1960; 1963) when the widespread outbreak of myxomatosis in the 1950s was followed by an unprecedented period of regeneration. Rabbit grazing seems to bare the ground sufficiently to allow *J. communis* growth, if the grazing pressure from rabbits and other herbivores is then reduced. However Fitter & Jennings (1975) found that the removal of grazing altogether allows other species to overshadow *J. communis* seedlings within three years. Thus some grazing appears to be essential.

Several other suggestions have been made as to the conditions necessary for regeneration, including fire to bare the ground, death of other plants, trampling by farm animals and disturbance by moles (Miles & Kinnard 1979a; 1979b), which all assist the colonising nature of *J. communis*. Few experiments have been conducted to test these theories, with the exception of sheep grazing experiments by Fitter & Jennings (1975).

This paper presents the results of a 1995 survey of *J. communis* in the Lake District. The aims were (1) to assess the status and (2) to propose recommendations for future management. As this survey did not record variables over a period of time, substantial sites of juniper were compared with smaller sites, to discover whether there were differences in seed viability and berry abundance. Results of the present survey are compared with others carried out in 1975 (Ward pers. comm.) and in 1995 (Sear 1995), which had similar aims to the present study.

METHOD

Ten substantial stands > 1000 of *J. communis* were chosen which were in good condition in 1975. As these large stands were recognised as worth conserving in 1975, but had not been actively managed since this time, any change in their condition was likely to be apparent in September 1995 when the survey was conducted (see Table 1). The ten large stands were compared with five smaller stands of < 1000 bushes (small stands). The stands selected for this survey encompass the range of habitats occupied by *J. communis* throughout the Lake District (Table 1).

An area of *J. communis* which had not been recorded in 1975 known as Juniper Scar was also examined. This had been documented for several years and more importantly, surrounded by a sheep proof fence for the last seventy years. This stand was therefore examined to assess how protection from grazing might influence the ecology of *J. communis*.

Three 100 m² quadrats per stand were examined. The quadrats were distributed over the stand at three points, representing the variations in physical condition and exposure of the site. Notes were taken on the general appearance of each stand, and appearance of individual quadrats.

Perhaps the most useful variable which could have been recorded in this survey was the age of stands. However *J. communis* is a notoriously difficult species to age without cutting live samples of the stem, for two reasons. The first is that the stem diameter of *J. communis* is not closely related to age. The second is that *J. communis* stems are usually eccentric in shape and therefore their girth is difficult to record with any accuracy; this also precludes accurate core sampling (Fitter & Jennings 1975).

Seed viability has obvious implications for the reproductive potential of a stand of *J. communis*, and is therefore an important indicator of present and future condition which may not be obvious to the eye. Ten mature, purple berries were collected in each quadrat using random number tables to select the nearest female bush to given co-ordinates. Viability was determined by sectioning berries. Seeds are viable "where the internal tissues fill the seed completely and are white/off white in colour" (Ward 1989). Viability was then recorded as a mean of the three samples out of a possible thirty seeds. A seed production index was obtained using the abundance of berries on bushes at each site. This was calculated by multiplying the number of bushes with a limited number of berries by one, the bushes with abundant berries by ten, and the bushes with very abundant berries by one hundred. Together these values gave the mean seed production index for each site (from Sear 1995).

The seed viability index is the mean proportion of a possible 30 seeds at each site which were viable, multiplied by the seed production index to show how many of the seeds produced were viable, as sites may have produced many berries but these may have contained very few viable seeds. This value demonstrates the condition of the stand and the likely regeneration potential, as far

TABLE 1. SITES STUDIED WITH GRID REFERENCES

Site	Grid Reference	Habitat	Altitude m	Geology
<i>Large sites</i>				
Place Fell	NY/396.180	Rough fell	210	Volcanic
Mardale Banks	NY/482.124	Grazing	290	Volcanic
Carrock Fell	NY/329.327	Grazing	310	Volcanic
Dovedale	NY/380.116	Scree	610	Volcanic
Blind Tarn Moss	NY/314.070	Fell	270	Volcanic
Blea Tarn	NY/295.037	Grazing	350	Volcanic
Thwaites Fell	SD/177.904	Grazing	190	Volcanic
Yew Barrow	SD/354.871	Woodland	230	Volcanic
Bradleyfield	SD/489.921	Grazing	190	Carboniferous limestone
Whitbarrow	SD/442.893	Grazing	200	Carboniferous limestone
<i>Small sites</i>				
Whitbarrow N.	SD/443.889	Fell	140	Carboniferous limestone
Lingmore Oak	NY/300.057	Fell & grazing	190	Volcanic
Broad Hollins	SD/299.914	Bog	150	Valley bog
Blea Tarn S.	NY/298.836	Fell	320	Volcanic
High Harsop	NY/393.105	Fell & grazing	410	Volcanic
<i>Reference site</i>				
Juniper Scar (Staveley Head Fell)	NY/476.012	Nature reserve	260	Volcanic

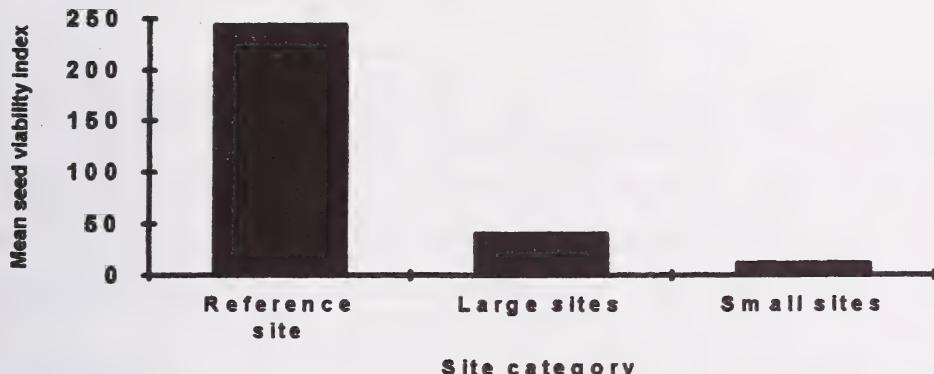
TABLE 2. SEED VIABILITY INDICES OF JUNIPERUS COMMUNIS IN THE THREE SITE CATEGORIES

Site	Seed Viability	Seed Viability Index
<i>Large sites</i>		
Place fell	14.00	29.73
Mardale Banks	15.00	83.84
Carrock Fell	16.67	200.25
Dovedale	12.33	9.86
Blind Tarn Moss	15.33	5.47
Blea Tarn	15.00	2.65
Thwaites Fell	14.33	6.05
Yew Barrow	9.33	0.52
Bradleyfield	10.00	18.67
Whitbarrow	11.67	3.90
<i>Small sites</i>		
Whitbarrow N.	5.33	1.24
Lingmore Oak	15.00	13.49
Broad Hollins	11.33	5.67
Blea Tarn S.	11.67	4.67
High Harsop	17.33	7.32
<i>Reference site</i>		
Juniper Scar (Staveley Head Fell)	17.33	243.39



FIGURE 2. Berry abundance on bushes at each site category.

None - No berries. Limited abundance - Few berries on some branches. Abundant - Berries on most branches, some in clumps. Very abundant - Bushes laden with berries, most in large clumps.

FIGURE 3. Mean seed viability of *Juniperus communis* L. at each site category.

as seed production and viability are concerned. Values are recorded in Table 2. The seed viability index for each site category were then compared using a one-way ANOVA test.

RESULTS

The null hypothesis that there is no difference in seed viability index between the site categories was rejected at the 5% significance level. The average seed viability indices were: Small Sites = 6.478, Large Sites = 36.094 and Reference Site = 243.39. The calculated F value was greater than the tabulated F value as $F_{\text{calc}} = 8.6063 > F_{\text{tab}} = 4.75$ for 2 degrees of freedom between groups and 13 error degrees of freedom within groups.

As the large sites had significantly higher seed viability indices than the small sites, there is a $> 95\%$ probability that large sites produce more viable seeds than small sites. Large sites also produce significantly less viable seeds than the reference site (Juniper Scar). Berry abundance and seed viability indices at each category of site are illustrated in Figs 2 & 3 respectively.

In addition to the 16 sites recorded in this survey, an example of attempts to encourage *J. communis* regeneration was visited at Greenside Mines. Although the ground was heavily

polluted with lead, *J. communis* seedlings were growing well within protective tubes. However, these will have to remain protected for at least eight more years before they are able to resist grazing (Ward & Lakhani 1977), particularly from sheep which occupy the surrounding land. This regeneration experiment provided a useful example of how conservation measures could be implemented to propagate *J. communis* in the Lake District.

DISCUSSION

The seed viability indices found in this survey are consistent with data obtained by Ward (1989) at Teesdale National Nature Reserve, which showed that the maintenance of a high seed viability is important for the conservation of *J. communis*. This suggests that the sites recognised as good in 1975 producing adequate quantities of berries, are still in a more reproductively viable condition than the small sites in this survey. However the much higher viability index recorded at Juniper Scar may be an indication of the seed reproductive potential and berry production necessary to maintain regeneration, as recommendations for the maintenance of viability such as disturbance and fencing (Miles & Kinnard 1979a) are found at this site. In this case the ten large sites may be in worse condition than in 1975, but have experienced a viability decline in parallel with the small sites. Without long-term experimental evidence that seed viability and berry production correlates with regeneration, it is not possible to suggest a limit at which regeneration is endangered, but the evidence from these three categories of sites would seem to suggest a decline over the last 20 years at least.

CONSERVATION AND FUTURE RECOMMENDATIONS

The situation at Greenside mines is characteristic of the problems of conservation schemes in the Lake District. Such is the need for plant cover on steep slopes of the area, that the National Parks have sometimes had to implement emergency action to stop intense erosion (Harding, pers. comm.), but long term schemes are often restricted by land ownership complications. Several authors have drawn attention to the need for long term surveys to be conducted into the causes of declining *J. communis* in Britain including Ward (1987) and Ranner (1994), who also used Ward's 1975 survey as a baseline for his own study. With the exception of regeneration experiments at Teesdale National Nature Reserve (Findley, pers. comm.) which are at present unpublished, there have been few studies which have been conducted thoroughly enough and over a long enough period to suggest techniques which may be employed to encourage regeneration.

The problem with long term experiments at present is that the decline of *J. communis* may be extremely severe before conclusions can be put into practice. Also, the range of morphologies and possibly genealogy of *J. communis* in the Lake District alone, may mean that *J. communis* varies in the conditions needed for regeneration between regions, and possibly between stands. Milner (1992) underlines that *J. communis* propagation should use cuttings from local sources as the species has a wide genetic diversity. Although historical aerial or terrestrial photographs were not used for our study, this source of information on past populations and colonisation could be invaluable for rapidly establishing changes in population density in other regions.

As intense grazing seems to be one of the central causes of *J. communis* decline, controlled grazing regimes should be put into practice as soon as possible, perhaps using the collapsible fences recommended by Miles & Kinnard (1979a). These authors suggest other means of encouraging regeneration such as felling mature trees and sowing seed, but these are experimental techniques not yet investigated for the conservation of *J. communis*. Propagating seedlings and planting in fenced areas seems to be the best immediate approach to *J. communis* conservation. The National Parks Centre at Brockhole have found that propagating cuttings is an effective way to grow stock. Roughly 60% of Greenside Mines cuttings were successfully grown in greenhouse conditions (Tasker, pers. comm.), which also preserves genetic diversity.

Long term studies of reproductive condition in parallel with planting are urgently required. Unless these are instigated, young or small populations of *J. communis* face great danger through population fluctuation in the near future.

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Correlations between higher-taxon richness and species richness in the British Isles flora

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ABSTRACT

It has been suggested that the biodiversity of areas may be compared using the number of higher taxa present rather than by compiling full species lists. This would reduce sampling problems especially in the tropics with their high species richness. Data from British Isles regional Floras are used to examine the relationship between species richness and higher taxa richness for flowering plants. Positive correlations were found between species richness and genus richness ($r_s = 0.97$) and species richness with family richness ($r_s = 0.89$). Richness of species in a small number (15) of the most species-rich genera was highly correlated with total species richness ($r_s = 0.91$) and could be used as an alternative to higher taxa in comparing sites. Such relationships, validated on the well studied British flora, could be of great use in less well studied areas such as tropical forests. The study also illustrates the importance of regional Floras as a data base for use in studies of biodiversity.

KEYWORDS: regional Floras, biodiversity, higher taxa, species richness.

“The ultimate task of the systematist is not merely to describe the diversity of the living world but also to contribute to its understanding.” Mayr (1997).

INTRODUCTION

One of the key problems of conservation biology is how to identify the most important areas for biodiversity so that they can receive protection (Williams & Gaston 1994; Wilson 1992). An ideal data set on which to base such a decision would include full species lists for all areas under discussion. However, even for biologically well known countries such as Britain, this has not been achieved for many groups. The problem is much greater in the tropics, the home of the greatest terrestrial biodiversity (Wilson 1992); here estimates of the total number of species are very large. For example, estimates of the number of insects based on extrapolation from beetle data (reviewed by May (1988) and Gould 1996)) give values of up to 50 million species. Studies based on extrapolation from other insect orders give smaller, but still very large numbers (Hodkinson & Casson 1991). Whatever the true number, it is clear that full species lists will not be achieved, even for the apparently less diverse flowering plants, which have an estimated 250,000 species (Holdgate 1991).

This raises the question of how areas can be compared when full species lists are not available. A number of approaches have been described, including: i. use of correlation between biodiversity and environmental variables (e.g. soil or water chemistry); ii. relationships between indicator groups and total biodiversity; iii. using higher taxa to compare sites (Williams & Gaston 1994); and iv. combining data from groups of widely differing organisms (Vane-Wright *et al.* 1994). This paper concentrates on the use of higher taxa, based on the idea that relationships between species richness and number of higher taxa can be used to compare sites. Such an approach has been widely used in palaeontology, where making comparisons at the species level is often difficult (Gaston & Spicer 1998). This approach, if successful, would be in many cases logically more realistic and more cost-effective than compiling full species lists (Andersen 1995; Gaston & Williams 1993; Williams & Gaston 1994).

This paper aims to investigate the relationship between species richness and higher taxon (family

TABLE 1. NUMBERS OF FAMILIES, GENERA AND SPECIES RECORDED IN 20 BRITISH AND IRISH REGIONAL FLORAS

Area	Reference	Number of:			
		families	genera	species	species in large genera
Suffolk	Simpson, 1982	118	622	1643	221
Kent	Philp, 1982	119	657	1643	216
Dorset	Good, 1984	110	585	1473	223
Glamorgan	Wade <i>et al.</i> , 1994	126	570	1460	213
Jersey	Le Sueur, 1984	120	585	1448	201
Durham	Graham, 1988	113	546	1421	220
Somerset	Roe, 1981	110	572	1413	223
Angus	Ingram & Noltie, 1981	105	491	1192	212
Leicestershire	Primavesi & Evans, 1988	98	505	1171	189
East Yorkshire	Crackles, 1990	104	476	1133	184
Shropshire	Sinker <i>et al.</i> , 1985	110	475	1089	186
Derbyshire	Clapham, 1969	101	478	1089	186
South Lancashire	Savidge <i>et al.</i> , 1963	103	479	1063	185
Staffordshire	Edees, 1972	98	436	1017	171
Anglesey	Roberts, 1982	102	450	1004	188
Cheshire	Newton, 1971	100	427	913	152
Radnorshire	Woods, 1993	99	387	871	157
Connemara & Burren	Webb & Scannell, 1983	94	387	818	160
Outer Hebrides	Pankhurst & Mullin, 1991	81	321	696	148
Shetland	Scott & Palmer, 1987	79	300	627	93

and genus) richness, for the well studied British flora, to test the correlation between species and higher taxa richness. It also considers the importance of the more species-rich genera in such relationships.

METHODS

The long history of biological recording in Britain, often carried out by non-professional biologists (Allen 1976) makes it one of the best studied countries in the world. This provides data sets which can be used to test relationships between species richness and higher taxon richness. This study used data on flowering plants from a subset of the regional Floras produced for Britain and Ireland (Table 1), most of which cover a single Watsonian vice-county. This system dates from 1852 and divides Britain into 112 vice-counties (Ireland is covered by an additional 40). The idea was to create a set of areas of more equal size than the administrative counties, into which the country could be divided for biological recording. These vice-counties are still somewhat unequal in size with between three and six per 100 km² (Vincent 1990). While such sizes are large by the standard of British reserves they are more comparable in size with some existing and proposed tropical protected areas (Janzen 1994; Wilson 1992).

In 20 such regional Floras the numbers of species, genera and families of flowering plants were counted. As Ratcliffe (1984) pointed out, humans have introduced a large number of non-native species to Britain and altered the distribution of many native plants. No attempt was made to distinguish native from non-native species, all species listed in a given Flora as growing in the area were counted. The coverage of apomictic microspecies of *Rubus* and *Taraxacum* is very variable between different Floras, and therefore in this study they were counted as two species *R. fruticosus* agg. and *T. officinale* agg. The apomictic microspecies of the genus *Sorbus* were also excluded from the calculations. Such microspecies are really clonal lineages and can be regarded as single

TABLE 2. LARGE GENERA, DEFINED AS ONES WITH 20 OR MORE SPECIES IN BRITAIN
AND IRELAND LISTED BY STACE (1991)
Excluding *Sorbus* with its many apomictic microspecies

Genus	Number of species
<i>Carex</i>	74
<i>Cotoneaster</i>	45
<i>Salix</i>	35
<i>Trifolium</i>	32
<i>Ranunculus</i>	31
<i>Potamogeton</i>	29
<i>Juncus</i>	28
<i>Chenopodium</i>	27
<i>Veronica</i>	26
<i>Geranium</i>	24
<i>Rumex</i>	23
<i>Saxifraga</i>	22
<i>Euphrasia</i>	21
<i>Allium</i>	20
<i>Rosa</i>	20

evolutionary individuals rather than good species (Janzen 1977); as such they should probably not be considered as important as other species in biodiversity surveys (see Gould (1996) for an alternative view of microspecies).

Species are not evenly distributed between higher taxa; for example a small number of plant genera are unusually species-rich (Cronk 1989; Webb 1991). A good example is *Carex* in the British Isles (Table 2). To investigate this, the numbers of species in large genera were recorded for each Flora; large genera are defined as those with 20 or more species listed by Stace (1991). It should be noted that one of these genera, *Cotoneaster*, is composed almost entirely of introduced species.

RESULTS AND DISCUSSION

Data from 20 regional Floras are shown in Table 1. There are significant correlations (using the non-parametric Spearman rank correlation coefficient) between species richness and genus richness ($r_s = 0.97$, $p < 0.001$) and species richness and family richness ($r_s = 0.89$, $p < 0.001$). Both higher taxon levels investigated are therefore highly correlated with species richness, with variation in genus richness accounting for more of the variation in species richness ($r^2 = 0.94$) than is accounted for by family richness ($r^2 = 0.79$). These patterns are found even though the regional Flora data are potentially "noisy", with different levels of accuracy and detail between different Floras. This suggests that this approach may work with data sets from areas of the world where "noise" is introduced due to the local flora being incompletely known.

The results of this study provide an example of a data set with a good positive correlation between higher taxon richness and species richness. Other published examples include relationships between family and species richness for: British ferns and British butterflies among 100-km squares, Australian passerine birds using $5^\circ \times 5^\circ$ grid squares and northern and central American bats using grid squares of c. 611,000 km² (Williams & Gaston 1994). However, Anderson (1995), working on genus richness as a surrogate for species richness in Australian ants, found that "except in limited circumstances, genus richness ... appears to be an unreliable surrogate for species richness in local Australian ant faunas. This may apply more generally to taxa in which relatively small numbers of genera can contribute a large proportion of species."

When the number of species in large genera are compared with total species richness in this British Isles data set a very strong positive correlation was found ($r_s = 0.91$, $p < 0.001$). This means

that if data were only collected on numbers of species in these 15 genera it would be almost as useful a predictor ($r^2 = 0.83$) for comparing areas as a full species list. If such a relationship holds for richer floras which are less well known taxonomically it suggests an option of just recording data from a subset of all genera i.e., the large ones. In the British Isles data set, removing the large genera has little effect on the relationships between higher taxa as, with the exception of the mainly non-native *Cotoneaster*, all large genera occur in each of the regional Floras studied.

The only approach to validating such heuristic rules is an empirical one, testing these rules at a variety of sites and with a variety of taxa. It is hoped that relationships such as this, tested on the British flora, will also work on tropical forest vegetation. These forests are thought to contain some 40% of the world's flora (Archibald 1995); mean values of over 230 plant species per 0.1 ha have been described for some of these forests (Crawley 1997). For such areas, comparing lists of higher taxa is a much more realistic possibility than attempting to compile full species lists. The British flora would suggest that comparing sites at the family level could be a good guide to their relative species richness. Comparison at the genus level would provide greater accuracy but would also require more taxonomic work.

This study also highlights the importance of regional Floras as biodiversity data sets. Such Floras contain a wealth of data which can be used in many different studies. An attempt to replicate these results using tropical Floras would be of great interest if/when enough data are available.

The quotation from Ernst Mayr at the start of this paper suggests that data from plant systematics (and biogeography) can add to our understanding of the world as well as merely describing its variety. It can also contribute to its preservation by providing ways of evaluating the biodiversity of different sites as illustrated by this study.

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***Urtica galeopsifolia* Wierzb. ex Opiz (Urticaceae) confirmed for Britain by its chromosome number**

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ABSTRACT

The ‘stingless’ Fen Nettle from Wicken Fen, Cambridgeshire, England and similar nettles from elsewhere in southern England are found to be diploid ($2n = 26$) and a new character, non-stinging hair-base diameter of less than $25 \mu\text{m}$, is given to distinguish this diploid *Urtica galeopsifolia* Wierzb. ex Opiz from the tetraploid *U. dioica* L.

KEYWORDS: Stingless nettle, *Urtica dioica*, key, Wicken Fen.

INTRODUCTION

The ‘stingless’ Fen Nettle (*Urtica* sp.) which grows at Wicken Fen, Cambridgeshire, was thought to be the eastern European *U. galeopsifolia*, by Geltman (1992). This suggestion stimulated considerable interest and there have since been several reports of *U. galeopsifolia* at other British locations (Last 1995; Showler 1995; Bull 1995; Killick *et al.* 1998). Geltman suggested that as *U. galeopsifolia* was known to be diploid in E. Europe (Geltman 1984), a chromosome count should be made on the Wicken Fen plant.

In studies of the Wicken Fen population, Pollard & Briggs (1982) concluded that it was distinct, although other populations had individuals that tended towards the characteristics of the form found at Wicken. They showed that shaded plants tended to have a much lower density of stinging hairs than plants grown in full sun. However, they found that the density of stinging hairs was genetically based and heritable, and was the best character for distinguishing the Wicken Fen variant.

Although Geltman (1984, 1993) records both diploids and tetraploids in *U. galeopsifolia* and *U. dioica*, Geltman (1992) regards the former as largely diploid and the latter as largely tetraploid. Given the difficulties of distinguishing between the species on the basis of morphology and the possibility of diploid to tetraploid gene transfer, atypical counts could be the result of misidentification. Accordingly I carried out chromosome counts on a range of *Urtica* plants to assess the ploidy level and to determine suitable characters for distinguishing between the cytotypes.

MATERIALS AND METHODS

Living specimens were obtained from Wicken Fen and from three other localities where *U. galeopsifolia* had been reported (Table 1). These plants were grown in pots and root tips removed for chromosome counting. Counts were made by a modification of the method described by Dyer (1963). The chief modifications to the method were (a) the omission of rinsing following pretreatment and (b) the squashing of the root tips in a mixture of equal parts of lactic and propionic acids.

TABLE 1 COLLECTION LOCALITIES AND CHROMOSOME COUNTS OF *URTICA DIOICA*
AND *U. GALEOPSIFOLIA*

Species	Locality (with grid reference for English localities)	Chromosome number
<i>Urtica dioica</i>	England, Kew, Richmond, Surrey; woodland. TQ/17.76	2n = c. 52
<i>Urtica dioica</i>	England, Norfolk, Surlingham, footpath (more stinging hairs than marsh plant), TG/322.068	2n = c. 52
<i>Urtica dioica</i>	England, Norfolk, North Tuddenham, Dirty Lane, TG/042.148	2n = c. 52
<i>Urtica dioica</i>	England, Wiltshire, Wlye, SU/01.37	2n = c. 52
<i>Urtica dioica</i>	Scotland, Ayr, R. Ayr walk, woodland	2n = c. 52
<i>Urtica dioica</i>	Germany, Mecklenburg, Rugen, Wissender Klinker, <i>Fagus</i> wood on chalk	2n = c. 52
<i>Urtica dioica</i>	Netherlands, Doorn, Gimborne Arboretum, wet ditchside in shade	2n = c. 52
<i>Urtica galeopsifolia</i>	England, Berkshire, Woolhampton, Froud's Bridge, N. side of river, SU/580.665	2n = c. 26
<i>Urtica galeopsifolia</i>	England, Cambridgeshire, Wicken Fen, TL/55.70	2n = c. 26
<i>Urtica galeopsifolia</i>	England, Norfolk, Surlingham, Coldham Hall Marsh (very wet with <i>Glyceria maxima</i>), TG/324.071	2n = c. 26 ($\times 2$)

RESULTS

Chromosome counts made on nettles collected as *U. galeopsifolia* or superficially similar morphologically (Table 1) show a clear separation into two cytotypes, *U. galeopsifolia* as diploid and *U. dioica* as tetraploid. Observations made in the field confirm that the two cytotypes grow in different habitats, for example at Surlingham the diploid plants were collected from a marsh dominated by *Glyceria maxima* (Hartman) O. Holmb., while the tetraploid grew in a drier situation close by near a footpath (Bull 1995). The diploid had many fewer stinging hairs than the tetraploid, this being particularly noticeable on the upper surface of the leaf. This observation confirms the view of Pollard & Briggs (1982) that the stinging hair density variation is more or less discontinuous, the Wicken Fen population having a much lower density than any other in their samples. Taken together, these observations suggested that stinging hair density might be the best, if not the only, character to reliably distinguish between the two cytotypes.

The morphology of the plants collected in this study showed that all diploids had narrower leaves with many fewer stinging hairs, especially on the upper surface of the leaves, than the tetraploids. It was very difficult to find qualitative characters to distinguish between them though the two cytotypes differ considerably in general appearance and under the microscope. The diploids always look much more delicate and have a much lower density of stinging hairs.

The two characters, pubescence density and lowest node of inflorescence, given by Geltman (1993), either did not distinguish between the cytotypes or could be difficult to assess. The pubescence density does not differentiate between the *galeopsifolia*-like tetraploids and the diploids and the lowest node can be difficult to determine. Known diploids and morphologically similar tetraploids were examined very carefully to see if any other characters could consistently differentiate between them. Under a hand lens or dissecting microscope the indumentum of the tetraploids always seemed to be much coarser than that of the diploids. The difference is due to the greater width of the non stinging hairs in *U. dioica* giving a much coarser appearance to the indumentum. In diploids the base of these hairs are 20–25 µm (0.02–0.025 mm) in diameter whereas in the tetraploids the hair bases are 25–35 µm (0.025–0.035 mm) in diameter. The hairs taper gradually from base to apex and are finely patterned with protuberances, but no consistent differences in length or pattern was found. Perhaps the easiest way to identify the diploid would be

by comparison with the common stinging nettle which is usually available. A $\times 20$ hand lens is adequate to observe the difference in hair diameter when comparison is possible.

DISCUSSION

The detection of two cytotypes which can be separated on morphological grounds means that the diploid growing at Wicken Fen and elsewhere is therefore a distinct biological species.

In contrast, superficially morphologically similar specimens from elsewhere are tetraploid ($2n = 52$). They are not quite so stingless as the Wicken Fen plant but looked rather similar with elongated, narrow, upper leaves.

The following key was developed to distinguish between *Urtica dioica* and *U. galeopsifolia*.

Leaves relatively long and narrow with very few stinging hairs, especially on upper surface of leaf; not flowering till mid July; lowest flowering on 13th to 22nd node; tomentum of non-stinging hairs appearing fine with hair bases 20–25 μm across (detectable by comparison with *U. dioica* using 20 \times hand lens)..... *U. galeopsifolia*

Leaves very variable but with some conspicuous stinging hairs on the upper surface of the leaves; flowering from June; lowest flowering on 7th to 14th node; tomentum of non-stinging hairs appearing coarser with hair bases 25–35 μm across *U. dioica*

Most *U. dioica* plants are of course very distinct and easy to identify but nettles in deep shade and fenlands may greatly resemble *U. galeopsifolia* and only be identifiable with careful observation.

Pollard & Briggs (1992, 1983) concluded that intermediate individuals between the Wicken Fen and 'ordinary' nettles occur. This is supported by results here and their possible mode of origin is exemplified by the reported crossing of a Wicken Fen plant with an 'ordinary' nettle. Pollard & Briggs (1982) reported six progeny from a single cross between a Wicken Fen and a normal nettle. Of the six offspring they report five varying from intermediate to resembling an 'ordinary' stinging nettle. This suggests that hybridization between the ploidy levels occurs readily, producing either triploids or perhaps some tetraploids. Their conclusion of "high interfertility of the Wicken variant with ordinary weedy plants" may be correct but the mechanism needs to be studied now that it is known that two ploidy levels are involved. Hybrids would be expected to be largely triploid with the occasional tetraploid as a result of a non-reductional meiosis in the diploid. Any such tetraploids would be likely to be freely interfertile with tetraploid *U. dioica* and would result in one way gene transfer from the diploid to the tetraploid (Anamthawatt-Jonsson & Tomasson 1990). Such gene transfer can also occur through triploids (Bielawska 1964). However, because of the ploidy level difference, there is unlikely to be any gene transfer to the diploids, which will therefore remain pure, though gene transfer from tetraploid to diploid is possible and has been documented in *Betula* (Anamthawatt-Jonsson & Tomasson 1990).

The hybrid most similar to *U. galeopsifolia* would be a tetraploid arising from the union of an unreduced gamete from *U. galeopsifolia* and a normal reduced gamete from *U. dioica*. The genome of such a hybrid would have received half of its chromosomes from each parental species. However, repeated interbreeding of such hybrids with *U. dioica* could result in tetraploid plants more closely resembling *U. dioica*.

It would be very instructive to repeat such diploid *U. galeopsifolia* \times tetraploid *U. dioica* crosses and examine the ploidy level and fertility of the offspring. The reported intercrossing of Wicken Fen plants yielded only similar progeny, confirming the distinctness and true breeding nature of what we now know to be the diploid.

Pollard & Briggs (1982) noted that plants fairly similar in appearance to those at Wicken were found at both Woodwalton Fen, Cambridgeshire, TL/230.840 and South Tawton, N. Devon, SX/655.947 and this suggests other possible sites for the diploid *U. galeopsifolia*. Dr. J. Edmondson has also drawn my attention to two specimens in the herbarium of the National Museums and Galleries on Merseyside (LIV) which have been identified by Geltman as *U. galeopsifolia*: v.c. 59, Cheshire: Eastham on the Wirral, collected by J. A. Wheldon in 1894; v.c. H2, North Kerry: Muckross, one mile (1.5 km) N. of Killarney, collected by M. Goodfellow in 1961.

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***Lysimachia punctata* L. and *L. verticillaris* Sprengel (Primulaceae) naturalised in the British Isles**

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ABSTRACT

Four species of *Lysimachia*, *L. punctata* and *L. verticillaris*, and to a lesser degree *L. ciliata* and *L. vulgaris*, are much confused in gardens and when naturalised. *L. punctata* is easily distinguished from *L. verticillaris* by the absence of an orange area at the petal base, the leafy nature of all bracts, the leafy continuation of the inflorescence axis beyond the inflorescence, the more elongate rhizomatous habit and, in Britain, the absence of viable seed. These distinguishing characters seem not to have been previously noticed. *L. vulgaris* is native but is also found as a garden escape. The other three species are found occasionally as escapes from cultivation though *L. verticillaris* has not previously been recognised as distinct from *L. punctata*. *L. punctata* and *L. verticillaris* have chromosome numbers of $2n = 30$ while *L. ciliata* has $2n = c. 96$.

KEYWORDS: yellow loosestrife, chromosome number.

INTRODUCTION

This note was prompted by difficulties encountered in identifying yellow loosestrifes (*Lysimachia* spp.) both in cultivation and naturalised in the British Isles. I was very familiar with *L. punctata* L. naturalised and as a garden plant in Argyll where it is often found in ditches near abandoned crofts. However, at Ness Botanic Gardens on the Wirral a quite different plant was labelled *L. punctata*. The orange spot at the petal base, branched inflorescence branches, absence of continuation of the leafy axis beyond the inflorescence and the fact that it produced seed, easily distinguished this species from what I knew as *L. punctata* - which I had never seen to produce seed and therefore assumed to be self-incompatible. There were, therefore, two quite distinct taxa commonly being grown under the same name.

Originally I identified the plant in cultivation at Ness as *L. ciliata* L. because of the presence of the orange spot at the petal base (Ferguson 1972), but this identification was questioned by a visitor who provided a living specimen of *L. ciliata* which was clearly distinct from either of the two species already in cultivation and was named correctly.

There was clearly confusion in the literature. Huxley (1992) mentions *L. verticillata* (sic) as being very similar to *L. punctata*. Ferguson (1972) regards *L. verticillaris* Sprengel as synonymous with *L. punctata*, but Leblebici (1978) describes *L. punctata* and *L. verticillaris* as distinct, distinguishing them primarily on petiole length.

Accordingly a morphological study has been made of the upright *Lysimachia* species likely to be encountered native or naturalised in the British Isles and the following key devised, a summary of distinguishing characters being given in Table 1.

DISCUSSION

L. vulgaris is distinct with its terminal, paniculate inflorescence, *L. ciliata* equally so with its flat flowers on long pedicels and its ciliate petioles and *L. terrestris* (L.) Britton with its smaller spotted flowers and bulbils. The other two species are much confused and usually grown under the name *L. punctata*. However, they are easily distinguished by the characters mentioned in Table 1. No previous mention seems to have been made of the orange area at the petal base in *L. verticillaris*, its

TABLE 1. DIFFERENTIAL CHARACTERS AMONG FOUR UPRIGHT SPECIES OF *LYSIMACHIA*

	<i>L. vulgaris</i>	<i>L. ciliata</i>	<i>L. punctata</i>	<i>L. verticillaris</i>
Petal base	pale	orange	pale	orange
Bracts at extreme tip of inflorescence	leafy	leafy	very leafy	subulate or leafy
Bracts in upper inflorescence	subulate	leafy, ovate	leafy, ovate	subulate
Inflorescence	panicle	panicle-raceme	raceme	raceme-panicle
Axillary branching in inflorescence	raceme - single flower	single flower or reduced raceme with bracteoles	2 flowers on ebracteolate pedicels	2 flowers or reduced raceme with bracteoles
Flower shape	campanulate	flat	campanulate	campanulate
Pedicel length	<2.5cm	>2.5cm	<2.5cm	<2.5cm

absence in *L. punctata*, or the fact that the inflorescence is usually terminal in *L. verticillaris*, lacking the leafy apical rosette to the racemose inflorescence which is always so conspicuous in *L. punctata*. All the bracts in *L. punctata* are leafy whereas only the lower and very rarely the extreme uppermost are leafy in *L. verticillaris*; the bracts in most of the upper part of the inflorescence are subulate and inconspicuous. This results in a much less leafy appearance to the inflorescence of *L. verticillaris*. On vigorous stems both species can produce lateral inflorescences similar to the primary one. *L. verticillaris* always produces axillary reduced racemes in the axils of bracts on the lower part of the raceme whereas bracts of *L. punctata* always bear paired flowers in their axils. These flowers are borne on ebracteate pedicels though the pedicels are often fused for part of their length. The inflorescences of *L. verticillaris* may therefore sometimes look almost paniculate or be a panicle of racemes. Another very evident difference in cultivation is that *L. verticillaris* forms clumps of stems which do not spread laterally to any great extent while *L. punctata* is strongly rhizomatous and forms dense, extensive patches.

The most obvious distinguishing character in living flowering specimens is the orange spot at the petal base in *L. verticillaris*. This character is much less obvious in herbarium specimens. However, some of the other characters mentioned, perhaps especially the nodal red coloration in *L. verticillaris*, may not be present in all specimens in the wild, only in the material introduced to cultivation. Many of the other distinguishing characters mentioned above are also much less evident on herbarium specimens though very obvious when living material is studied.

Difficulties of identification may also be encountered, with both herbarium and living material, because of the state of maturity of the specimens. In immature specimens, or those taken early in the flowering period, the state of the bracts in the upper parts of the inflorescence will not be evident. Supplementary characters given both in the key and table should, however, allow the correct identification of such specimens. Leblebici (1978) describes the two species as having non-overlapping ranges, *L. punctata* occurring in Europe and Western Turkey while *L. verticillaris* is found in north and east Turkey, Caucasia, Crimea and N. Iran.

L. verticillaris always produces liberal quantities of viable seed whereas *L. punctata* has never been seen to produce any seed, even when grown in close proximity to *L. verticillaris*. Therefore it seems that *L. verticillaris* is self-compatible while *L. punctata* is self-incompatible and that the two species do not normally interbreed. This lack of interbreeding supports the retention of the two taxa as distinct species. Both *L. verticillaris* and *L. punctata* have chromosome numbers of $2n = 30$ while *L. ciliata* has $2n = c. 96$ (counts made in the course of this study). *L. vulgaris* is recorded as having $2n = 56, 84$ (Ferguson 1972).

HABITAT REQUIREMENTS

It is interesting that Leblebici (1978) describes *L. punctata* and *L. verticillaris* as occupying wet

habitats in the wild and it is nearly always in wet situations that they are found naturalised. In gardens they are usually grown in herbaceous borders where they grow more or less satisfactorily as long as they are free from competition. At Tighnabruaich, Argyll in Scotland naturalised populations of *L. verticillaris* occur between the road and the shore (Grid ref. NR/990.738) alongside naturalised plants of *Persicaria campanulata* (Hook. f.) Ronse Decraene (*Polygonum campanulatum* Hook. f.), *Geranium × oxonianum* Yeo, and *Rumex pseudoalpinus* Hoefft, all species of wet habitats in their native ranges and when naturalised in Britain often found growing in flushes.

Voucher specimens of *L. verticillaris* are deposited in LIV, E and BM. This is the first record of the species for the British Isles; it is not mentioned in Clement & Foster (1994) but many records of *L. punctata* are likely to be *L. verticillaris*.

KEY TO FOUR CONFUSED SPECIES OF *LYSIMACHIA* FOUND IN THE BRITISH ISLES

- 1a. Petiole ciliate; leaves glabrous, mostly opposite; pedicels more than 2.5 cm; open flower flat..... *ciliata*
- 1b. Petiole not ciliate; leaves pubescent, mostly verticillate; pedicels less than 2.5 cm; open flower campanulate 2
- 2a. Inflorescence paniculate; flowers borne singly in axils of bracts; stem leaves usually in whorls of three *vulgaris*
- 2b. Inflorescence racemose or a panicle of racemes; flowers paired in axils of bracts; stem leaves usually in whorls of more than three 3
- 3a. Petals with orange flush at base; some axillary branches in inflorescence themselves branched and bearing several flowers subtended by bracteoles; some bracts subulate and shorter than or equal to pedicel; petiole more than 5 mm; nodes and leaf bases purplish; inflorescence racemose to a panicle of racemes *verticillaris*
- 3b. Petals paler towards base; axillary branches in inflorescence single or 2-flowered but pedicels lacking bracteoles; all bracts leafy and much longer than pedicel; petiole less than

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Notes

A TERRESTRIAL FORM OF *CALLITRICE TRUNCATA* GUSS. SUBSP. *OCCIDENTALIS* (ROUY) BRAUN-BLANQUET (CALLITRICHACEAE)

The distribution and ecology of the Callitrichaceae (water-starworts) is poorly understood in Britain, due mainly to difficulties in identification caused by their high morphological plasticity (Wigginton & Graham 1981; Preston & Croft 1997; Lansdown 1998). The taxonomy of the genus in Europe was clarified by H. D. Schotsman in a series of articles (e.g. Schotsman 1967; Schotsman 1972; Schotsman & Andreas 1974; Schotsman 1977). However, most identification features are microscopic and without ripe fruit it is difficult to identify some specimens without counting the chromosomes. Seven taxa have been reliably recorded in Britain: *Callitriche brutia* Petagna, *C. hamulata* Kütz. ex W. D. J. Koch, *C. hermaphroditica* L., *C. obtusangula* Le Gall, *C. platycarpa* Kütz., *C. stagnalis* Scop. and *C. truncata* Guss. subsp. *occidentalis* (Rouy) Braun-Blanquet (Preston & Croft 1997).

Most of the British *Callitriche* species have two distinct growth forms: an aquatic form generally growing in water (but sometimes exposed by falling water levels) and in some species, producing a rosette of coriaceous leaves if the shoot reaches the surface; and a terrestrial form with short, rigid leaves, generally growing on damp mud (although it can be re-submerged e.g. in tidal reaches of rivers or after heavy rain).

Of the British taxa, two (*C. hermaphroditica* and *C. truncata* subsp. *occidentalis*) were separated into a distinct group (Group 1) by Schotsman (1967) and have frequently been described as having common features which are not shared by other members of the genus. They have translucent submerged leaves, floating rosettes are not produced and there is no known morphologically distinct terrestrial form. In all the *Callitriche* species, stomata are only produced on rosette and terrestrial leaves; as a consequence, stomata have not been recorded on either species.

HABITAT

I found the terrestrial form of *C. truncata* subsp. *occidentalis* in the Cerisières on the Tour du Valat estate in the eastern part of the Camargue, Bouches du Rhône, southern France in November 1996. The Camargue represents the delta of the River Rhône with fine, sandy calcareous soils grading southwards into sand dunes. The Cerisières are a complex of small pools up to 0.8 m deep, which dry out during the summer and within which there is a high degree of water level fluctuation during the autumn. Although the pools derive from fresh rainwater, the soils in the area are saline and, over time, standing water becomes mildly brackish as salts are released from the soil (Molina 1996). The vegetation surrounding the pools is mainly *Salicornia* heath, with scattered scrub dominated by *Phillyrea angustifolia* L., and stands of *Tamarix gallica* L. bordering many of the pools. *C. truncata* subsp. *occidentalis* is abundant to dominant in the water, with *Zannichellia pedunculata* Reichenb., *Potamogeton pusillus* L., *Myriophyllum spicatum* L., *Chara vulgaris* L. and *Tolypella glomerata* (Desv.) Leonh. The pools are surrounded by an expanse of wet mud with the aquatic form of *C. truncata* subsp. *occidentalis* and scattered herbs such as *Oenanthe lachenalii* C. C. Gmel. and *Ranunculus sceleratus* L. Where the border of the wet mud grades into *Salicornia* heath, there is a zone 2–3 m wide with abundant plants of the terrestrial form of *C. truncata* subsp. *occidentalis*.

Plants toward the wetter edge of this zone show basal leaves characteristic of the aquatic form, with the apical leaf pairs characteristic of the terrestrial form, while those furthest from the water have fairly uniform small, coriaceous leaves.

In July 1997 I visited Anglesey (v.c. 52) with A. M. Walker and J. E. Smith. We located abundant *C. truncata* subsp. *occidentalis* in its aquatic form in the lake and a stream flowing into the lake from the north-west, which constitute the first records for v.c. 52. In addition, we located a number of plants in the terrestrial form on the margin of a small pond adjacent to the N. W. corner of the lake (grid reference SH/383.701). The plants were very sparse on bare mud with scattered plants of *Ranunculus hederaceus* L. and *Juncus articulatus* L.

MORPHOLOGY

The following description is based on fresh material collected from the Cerisières on the Tour du Valat estate and from near Llyn Coron, Anglesey. (Specimens from Anglesey are lodged at NMW.) Roots silvery white, to 16 mm long, adventitious at all except 3–5 apical nodes and arising from the nodes immediately below and between the leaf bases. Stems creeping and flattened, to 35 mm long ($n = 10$), with only the apical 3–5 nodes held away from the substrate; similar to aquatic form, in that it has few major branches (Barry & Wade 1984), but with more frequent shoots arising in the leaf axils bearing 1–3 pairs of leaves. Leaves opposite, short and truncate to bluntly emarginate, 1.7–4.7 × 0.5–1.2 mm ($n = 22$), opaque, more or less rigid, with abundant stomata. Axillary hairs abundant, as described by Schotsman (1967), complex, fan-shaped, 2–3-seriate, composed of two basal cells and a number of lines 5–6 cells high; irregularly arranged. Leaf and stem hairs absent. No flowers located. A plant grown in an aquarium where the water level gradually declined through evaporation produced broader leaves at the surface but no rosette and subsequently produced a pair of emergent, terrestrial leaves.

IDENTIFICATION OF THE TERRESTRIAL FORM

The terrestrial form of *C. truncata* subsp. *occidentalis* can be distinguished without difficulty from all previously described terrestrial forms of western European *Callitrichace* species, on microscopic examination, by the lack of leaf and stem hairs and the multi-seriate axillary hairs. All other terrestrial forms of *Callitrichace* species have leaf and stem hairs, while the axillary hairs are in the shape of a fan of a single row of linear cells supported by a short stalk composed of two cells (Fig. 1). In the field, identification may be more difficult; *C. truncata* subsp. *occidentalis* appears to have darker green leaves which are not attached at the base, whereas all the material which I have seen of the terrestrial forms of other *Callitrichace* species suggests that the leaves are connate at the base (Fig. 1).

If *C. hermaphroditica* is also found to adopt a terrestrial form, then it is likely to resemble *C. truncata* subsp. *occidentalis* in all these aspects. The only reliable feature distinguishing plants of *C. hermaphroditica* from *C. truncata* subsp. *occidentalis* in the field is the broad wing on the fruit of the former, while the fruit of the latter lacks a wing and is distinctly rounded. As both species are described as only having submerged pollination (Schotsman 1967) and therefore terrestrial plants are unlikely to fruit, it is unlikely that it will be possible to separate the terrestrial forms of these two species in the field.

DISCUSSION

Schotsman (1967) separated the European *Callitrichace* species into five distinct groups, based on their morphology and reproductive biology. One aspect cited in this separation is the lack of a known terrestrial form in those species assigned to Group 1 (which includes *C. truncata*, *C. hermaphroditica*, *C. pulchra* Schotsman and *C. fassettii* Schotsman, an American species). Although there is no reason to doubt the validity of the grouping, discovery of a terrestrial form of *C. truncata* subsp. *occidentalis* suggests that, in suitable circumstances, the other species in this group may also adopt a terrestrial form.

Until recently, *C. truncata* subsp. *occidentalis* had only been recorded from permanent waterbodies (Barry & Wade 1984) and it is not surprising that the terrestrial form had not been recorded. However Grillas *et al.* (1989) note that in the Carmargue this species is adapted to temporary marshes with an early drying date, in shallow waters where flooding often lasts less than 30 weeks. Grillas (pers. comm., 1996) noted that terrestrial forms of *Callitrichace* occur adjacent to waterbodies which support *C. truncata* although the identification of terrestrial plants has not previously been confirmed. Until now, the geographical distributions of *C. hermaphroditica* and *C. truncata* subsp. *occidentalis* were thought to be virtually vicarious. However, *C. hermaphroditica* has been known to occur on Anglesey since at least 1867 (Hegelmaier 1867) and has been collected from Llyn Coron on a number of occasions including as recently as 1975 (R. H. Roberts specimen in NMW). In view of the potential confusion of these two species in the field, recorders are therefore encouraged to submit material of plants of these two species for confirmation by the author.

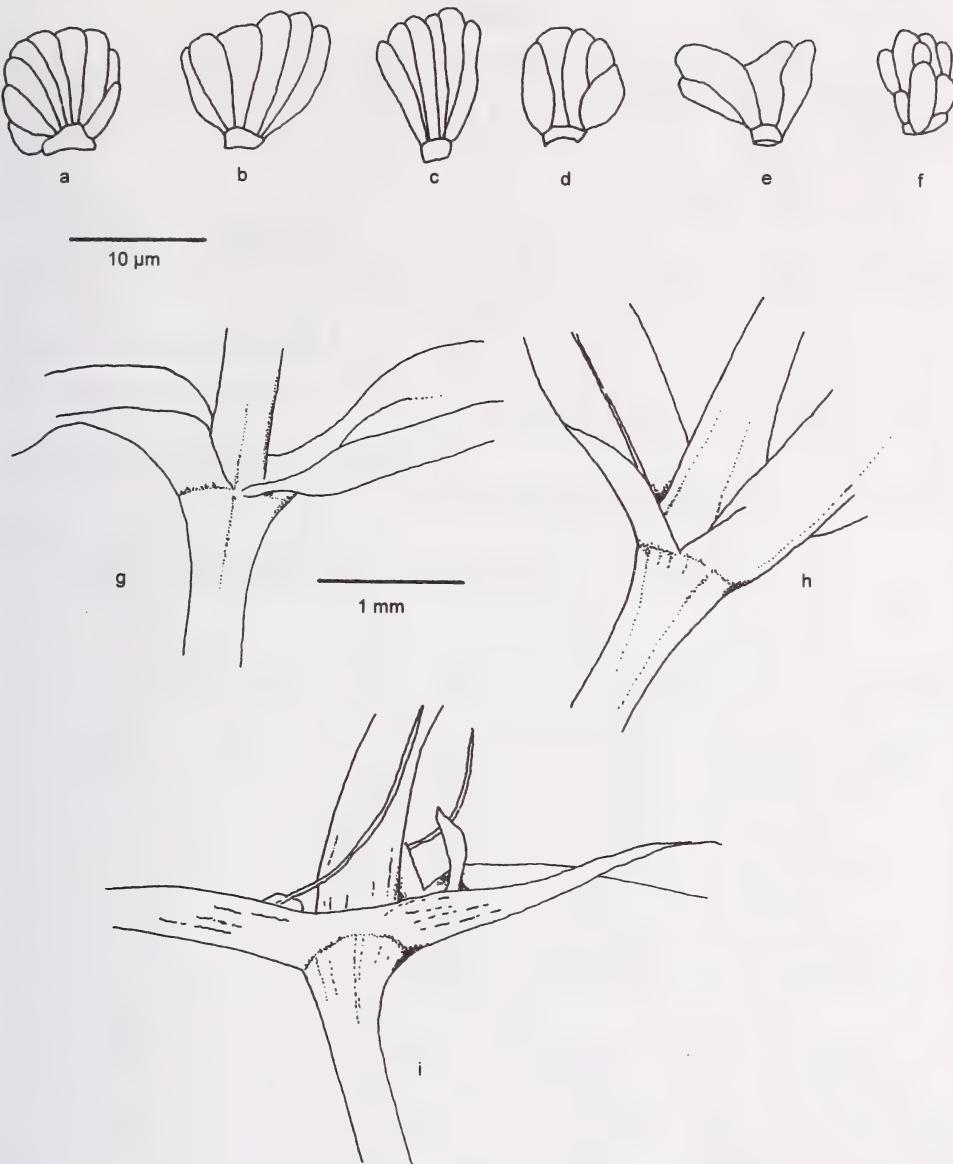


FIGURE 1. Axillary hairs (a-f, scale bar = 10 µm) and leaf-bases (g-i, scale bar = 1 mm) of British *Callitriches* species. a: *C. hamulata*; b: *C. brutia*; c: *C. obtusangula*; d: *C. stagnalis*; e: *C. platycarpa*; f: *C. truncata*; g-h: *C. truncata*; i: *C. stagnalis*.

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Book Reviews

Between seasons and science. P. Faasse. Pp. viii + 124. S.P.B. Academic Publishing, Amsterdam. 1995. Price Dfl. 53.00. ISBN 90-5103-100-9.

This slender paperback celebrating the sesquicentenary of the Royal Botanical Society of the Netherlands might be thought of interest to Dutch botanists only – or even just to the membership of that society itself. That, however, would be a mistake. Of all their Continental neighbours, The Netherlands is surely the one with which Britain and Ireland have most in common, with a similar flora, shared experiences in the past, a minimal language barrier and, not least, a kindred sense of humour. More to the point, though, it has a botanical society with almost as long a history as the B.S.B.I., which at once suggests that the two bodies may present some parallels or contrasts in their development from which some enlightening lessons might be learnt. Although the B.S.B.I.'s own sesquicentennial history features in the bibliography, disappointingly there are no comparisons with counterparts in other countries to be found in the text. This review must accordingly attempt to make up for that deficiency to some extent.

The Dutch society was founded in 1845 (though not formally constituted till one year later), at a time when botany in that country was just awakening from a fifty years' slumber. By no coincidence the Dutch Entomological Society had its birth almost simultaneously – much as the Entomological Society of London only shortly anticipated its botanical sister – and the two events can be seen as part of a general resurgence in the nation's intellectual life. The founding group of 20 were almost all amateurs and collectors and interested in the flora of The Netherlands exclusively, the producing of a comprehensive, high-quality account of which was one of their agreed aims at the outset. Others were the holding of field meetings, the formation of a herbarium and library, and the exchange of correspondence and specimens with botanists in other countries. The forming of a herbarium was rendered the more necessary by the policy of the director of the national herbarium in Leyden of keeping its doors permanently locked, a practice which ended only with his death in 1862. Though nothing as ambitious as the large-scale exchange schemes operated by the two contemporary British botanical societies was attempted, every member was required under the rules to donate to the Society's herbarium a specimen of every noteworthy new discovery, in return for which they were entitled to take duplicates from it for their own personal collections. Reports of the Society's activities were regularly published in two independent periodicals.

Unexpectedly, the leading figures in the early years were all cryptogamists. Dominant among these was R. B. van den Bosch, a small-town physician who held the Presidency for 17 years. The Vice-President was a former class-mate of his with the unfortunate name (to English eyes) of Dozy – though seemingly an appropriate one, for according to the author he "suffered from ... inertia and needed some stimulation once in a while".

For many years the Society was evidently content to remain a tiny coterie, with still only 44 subscribing members six years into its life. At the same stage the Botanical Society of London, by contrast, had an estimated 125. Following the death of van den Bosch in 1862 and of most of the rest of the founding group in quick succession not long afterwards, a period of discord and decay set in, work on the proposed national Flora came to a halt and the subscribers dwindled to a low of just 19.

At that point a series of important changes were fortunately put in hand. In contrast to H. C. Watson's unsuccessful attempt in 1866 to interest J. D. Hooker in accommodating the Botanical Exchange Club at Kew, the Dutch national herbarium agreed to both house and curate the Society's collection. The *Nederlandsch Kruidkundig Archief* was taken over to serve as the Society's official journal, in place of the previously informal relationship analogous to that between the Botanical Society of London and Newman's *Phytologist*. And the scientific remit was broadened and winter lectures introduced, with a view to gaining recruits among the now increasingly numerous biologists in the universities. But the potential friction between the latter and the field botany amateurs, which in Britain was accidentally side-stepped thanks to the privilege of its larger population which made it possible for separate societies for the two to flourish in parallel, had been underrated, and a growing hostility culminated in 1904 in a splitting of the Society into two

self-contained parts, each with its own journal. That failed to still the unrest, though, and in 1909 a further reorganisation was tried, this time into five autonomous sections. That proved a workable solution at last and the sectional structure has continued ever since. Of the six which exist today, three cover floristics-cum-conservation, vegetation science, and plant systematics and geography. The Society has not ended up, however, as the single national unitary body that this might suggest, for it does not embrace all aspects of botany and other societies exist today in The Netherlands which also cover ecology and phytopathology, for example.

Like the B.S.B.I., the Dutch society has had a continuing struggle since the Second World War to sustain the cost of publishing two journals. In 1952 it was forced to retreat to having just one, *Acta Botanica Neerlandica*, together with a yearbook to take less formal matter, just as the B.S.B.I. had to retrench in 1969 by sacrificing its *Proceedings*. With a membership with much more heterogeneous interests, however, the Dutch society could not hope to have a journal with the relative uniformity of contents enjoyed by *Watsonia* and there was scant room in the new combined journal for papers on taxonomy and distribution. Worse, at the same time page charges were introduced and in order to ensure an international readership it was stipulated that papers must be in English. These changes so infuriated the systematists that they successfully put up a rival candidate as President. As a result the journal was remodelled and a supplement, *Wentia*, introduced into which all lengthier papers were siphoned off. But that compromise eventually proved financially unsustainable too and *Wentia* had to be abandoned in its turn. Finally, in 1981, the Society decided that to hand over this side of its activities to a commercial publisher was the best solution.

Meanwhile plans to produce a national Flora had been revived in the 1930s. Only the first part of that had been completed, however, before the War intervened and though work on the project was subsequently resumed and further parts appeared, by the mid-1980s not only was commitment flagging but publication was questionably still affordable. The funds set aside for that purpose were therefore used instead to support the Society's journal.

A second major project on that front had a happier ending. This was the Instituut voor het Vegetatie-Onderzoek in Nederland (or I.V.O.N., for short), the Dutch predecessor, and in part inspirer, of the B.S.B.I.'s own Distribution Maps Scheme of the 1950s. Older members who attended the historic conference which gave rise to the latter will recall the long-bearded figure of Dr A. W. Kloos and the highly instructive (and encouraging) account he gave on that occasion of the methods developed and by then long in use for mapping the flora of The Netherlands. Formally an independent initiative, which began in 1930, I.V.O.N. had a similar effect in mobilising the energies of the country's field botanists and in so doing substantially supplanted for a period the work of the Dutch society's floristics section. Like the B.S.B.I. scheme, that one also culminated in being taken over and carried on by the State – in the Dutch case by that now-traditional saviour, the national herbarium in Leyden, of which in 1954 I.V.O.N. became a new and permanent department. In 1988 that story became even happier, when the role of that department was broadened to incorporate the Society's library, archive and herbarium as well. Under the title of FLORON this now assumed responsibility for co-ordinating all floristic work in The Netherlands flora (except for field meetings, which the Society continues to organise). It is as if 'Monks Wood' had been absorbed by a merged British Museum and Kew and then provided the B.S.B.I. with a full-time secretariat. Though the book curiously plays down this very remarkable dénouement, any readers on this side of the North Sea will surely find it hard to suppress some forceful pangs of envy. Sometimes it pays to be a smaller country.

D. E. ALLEN

Wicken Fen. The making of a wetland nature reserve. Edited by L. Friday. Pp. xvi + 306. Harley Books, Colchester. Hardback £37.50, ISBN 0-946589-33-X. Paperback £24.50, ISBN 0-946589-58-5.

There are two Wicken Fens: one is the story of the struggle to maintain a scrap of wild fenland in the midst of an arable prairie; the other is that of an outdoor laboratory, one of the most closely documented ecosystems in the world. Wicken Fen has been a nature reserve for nearly 100 years, since a few acres of it were purchased in 1899 and later handed over to the National Trust. When the Trust first acquired it, the Fen was regularly cut for peat, or cropped for sedge-thatch. When

these activities ceased, much of the open fen turned into a thicket. During the Second World War part of it was requisitioned by the Ministry, cleared and drained with great difficulty and turned into a farm. Today it is one of the most popular nature reserves in the country, with some 30,000 paying visitors each year. Wicken's is a story of changing human aspirations and expectations. Its managers have to juggle with the competing claims of tourism, education, research and preservation together with those of species and habitats, and all on a tight budget. It is not a story of unrelieved success - species like Fen Orchid (*Liparis loeselii*) and Swallowtail butterfly have died out for want of the right management - but it is an interesting story, and experience of Wicken has a relevance far beyond the boundaries of this small fen in Cambridgeshire. For many years it has been used as a classic example of nature conservation in practice, of habitat management, species monitoring and recording and, above all, of vegetation dynamics. It is important for itself but it is also important because it is famous.

This admirable book, produced to his usual impeccable standards by Basil Harley, charts the history and wildlife of Wicken Fen in considerable detail. It opens with a short introduction to Wicken and its Fenland neighbours by Norman Moore, followed by well-balanced sections on habitats and communities, flora and fauna, and the human dimension or the uses which the Fen has served during the twentieth century. Each chapter is written by a different author or group of authors, which leads to some unevenness of writing, but they have been edited into a book very competently by Laurie Friday, chair of the management committee, who herself contributes to no fewer than six chapters. Max Walters' chapter on botanical studies includes fascinating accounts of Wicken's well-studied plants, including *Viola persicifolia*, *Lathyrus palustris*, *Taraxacum palustre* and the reintroduced *Senecio paludosus*. The sections on history, by Terry Rowell, and the management of the fen, by Laurie Friday, Mike Lock and Tim Bennett, could be read with profit by the managers of any nature reserve in the land, and not just fenland ones. I am a firm believer in learning from detail (generalisations are always misleading). If you understand a place like Wicken, you are well on the way to understanding nature. If I had a criticism it is that the broader picture is often lost in the detail, and it is also not as easy to look something up as it should be. I also think that the authors have been a little too kind and understanding to their scientific predecessors, who sat back while the Fen dried out, or to farmer Bloom, who burned, dredged and ploughed Adventurers' Fen in the 1940s. The human dimension is described here more in terms of policies than personalities. But the book is a model of good natural history writing, and is well-illustrated throughout with diagrams and photographs, with a panel of 16 colour plates in the middle. The only book about a nature reserve that comes near it in my view is that by O. Rackham on Hayley Wood, also in Cambridgeshire, published over 20 years ago. The authors and publishers have done Wicken Fen proud and, as they say, established "a benchmark against which future generations may measure progress....and a blueprint for all those who are striving to maintain a viable Fenland environment." For such a book, it is fairly priced, and deserves to be widely read. A checklist of the flora and fauna is in preparation and will be published separately.

P. MARREN

Red data book for Cornwall and the Isles of Scilly. Edited by A. Spalding. Pp. viii + 479. Croceago Press, Camborne. 1997. Price £15.00. ISBN 1-901685-00-4.

Cambridgeshire's Red data book including Huntingdonshire, Old Cambridgeshire & The Soke of Peterborough. A. Colston, C. Gerrard & R. Parslow. Pp. 69. The Wildlife Trust for Cambridgeshire, Cambridge. 1997. Price £5.00. ISBN 0-952078-81-4.

The closure of the Cornish Biological Records Unit in 1996 was one of the disastrous consequences of the previous government's cost-cutting policies and this volume only goes to demonstrate what Cornwall and the UK as a whole might have lost as a result. What should have been one of the proudest products of that Unit 24 years after its foundation in 1972 had to be published privately by a federation of biological recorders in Cornwall and the Isles of Scilly after the records had been rescued from the Exeter University Centre in Redruth.

This remote, but very special, area of the British Isles has been wonderfully successful in producing or attracting an incredible biodiversity of biological recorders so that this Red data book

not only covers the marine environment as well as the terrestrial but deals with almost every taxonomic group omitting only, somewhat apologetically, Ephemeroptera, Plecoptera, Neuroptera, Megaloptera, Mecoptera and part of the Diptera. So, if your interest is booklice, bristletails, bumblebees, bats or Bryozoa, you will find them all here as well as the major plant and animal groups.

The result is that no less than 346 Red Data Species and 657 Nationally Scarce Species are listed and, though the book is in part a warning to the general public that wildlife is in danger in Cornwall, it is also a celebration of the enormous biological richness of the area – long appreciated by field botanists.

For the threatened Red Data Species there are sections on international, national and regional (v.c. 1) distribution; habitat and ecology; degree and type of threat; and suggestions for conservation with species listed in *Biodiversity: The UK Steering Group Report. Volume 2: Action Plans* given special prominence. There are brief accounts of Nationally Scarce Species and a list of additional species of particular interest in Cornwall.

The vascular plants are given very up-to-date treatment by Rose Murphy, ably assisted by Colin French and Rosemary Parslow (Isles of Scilly), with details of the number of 1-km squares, post-1980, from which each of the Red Data Species has been recorded.

It is good to know that the work of the dedicated team will continue to flourish in collaboration with the Cornwall Wildlife Trust and now forms a major part of the Environmental Records Centre for Cornwall. There can be few if any other areas of the British Isles which have been so thoroughly recorded and this publication is a credit to all concerned: it seems remarkably free of errors though the inclusion of *Centaurium scilloides* within the umbellifers is a curious lapse.

Cambridgeshire's Red data book covers the same ground as the Cornish model but, perhaps because the county lacks a Records Centre, it lacks the same thoroughness and, to judge by the vascular plant account alone, is prone to error – authors of three of the four Floras of Cambridgeshire cited have their names spelt wrongly!

The entries for each species are minimal and often give less information than is available in *A Checklist of the Flora of Cambridgeshire* (1983) e.g. “*Hernaria* (sic) *glabra* Dry sandy ground in vc29”. In contrast the entries for the vertebrates are extensive and informative, including Cambridgeshire and UK status and proposed conservation action where needed. Though English names from *English names of wild flowers* have been used their punctuation is chaotic with a random use of capital letters and hyphens.

The selection of plants does not distinguish clearly between native, established and casual species and one questions the value of including “*Cynodon dactylon* Still occurs as a rare casual in vc29?” in the “Near Threatened species” category between those special native Cambridgeshire plants *Cirsium tuberosum* and *Phleum phleoides*. The former has the curious distinction of appearing twice as it also occurs (as *tuberososum*) amongst the Nationally Scarce Species (an error) – with different dates of last record/extinction! One wishes that the strong editorial hand of Adrian Spalding in Cornwall, which ensured the high standard of accuracy and uniformity of coverage between groups, had also been available in Cambridgeshire.

F. H. PERRING

The phytogeography of northern Europe (British Isles, Fennoscandia and adjacent areas). E. Dahl. Pp. xii + 297. Cambridge University Press, Cambridge. 1998. Price £60.00. ISBN 0-521-38358-7.

It is a pleasure to review a book that recalls the personality and individuality of a friend and colleague. I first met Eilif Dahl 50 years ago and shortly after this we visited Teesdale together, where, as always, his energy and enthusiasm were immediately evident. We walked to High Cup Nick and back on a day when the temperature rose to 25°C and, even though the arctic-alpine flora may have kept cool by evaporation or heat transfer from narrow leaves, we did not, perhaps because we scarcely stopped talking all the way. Whether one agreed or disagreed with particular explanations which Dahl advanced for what we saw, his ideas were challenging and inspiring, and he could never be faulted on bad science. His knowledge of the Norwegian flora was profound and extended to bryophytes and lichens (then neglected groups in Britain). The war had brought Dahl to

Britain and the knowledge of the British flora which he rapidly acquired is displayed throughout the book. We must thank Gro Gulden and John Birks for completing the unfinished manuscript.

I share with Dahl a basic philosophy of biogeography which is set out on p.10 in the first chapter. Correlations between distributions of species and environmental conditions are important indicators but cause has to be sought in terms of physiological and ecological mechanisms, and, I would add, confirmed by experiment. Chapters two and three discuss climatic and edaphic controls of plant distribution. One of my few criticisms is that the account of the influence of soil is too brief. For example, the response of plants to calcium is treated but surprisingly not the influence of limestone (calcium carbonate). Chapter four considers the historical events since the Tertiary which affect the distribution of species. It includes a summary of Dahl's fascination with the geological evidence for the existence of ice-free (unglaciated) areas, close to the Atlantic but far to the north of the southern limits of glaciation, where some species may have 'over-wintered'.

The following chapters are then devoted to each of the main geographical elements of the European flora and the analysis includes examples of Dahl's conversion of climatic data, either into measurements which are directly related to particular geographical elements (for example, maximum temperatures at the highest altitude in each 50 × 50 km square of the *Atlas Flora Europaea* grid for comparison with the distributions of arctic-alpine species), or into parameters which represent physiological responses of plants. Chapter nine examines the intriguing problems of endemics and of highly disjunct species.

There are several appendices, of which the second (72 pages) lists all the species of vascular plants in northern Europe, their status and, where possible, the relevant climatic parameters which may influence their distribution.

This is a book of special interest to members of the B.S.B.I. who have contributed so much to the raw material on which such studies are based. The subject is directly relevant to predicting the consequences of global warming but maps which show striking correlations are all too often interpreted simplistically. Dahl shows that the physiological controls are not simple, neither are ecological responses: for example, the geographical limits of many species were determined at a time when conditions other than climate were very different from the present. Human influence has been very potent causing fragmentation of habitats, erosion of soils, changes in plant communities and animal populations etc. We must expect such factors to interact with climatic change and the outcome may be very different from what has happened in the past, or from predictions based simply on adjusting isotherms.

C. D. PIGOTT

Obituaries

WILLIAM MORETON CONDRY (1918–1998)

Bill Condry was widely known and loved as a naturalist through his lectures and broadcasts, his many books and his Country Diary for *The Guardian* which he wrote for 42 years. He was born in 1918 in Birmingham, his parents being Clarionites, pacifists and active members of the Independent Labour Party. His love of the Welsh countryside began on family holidays to Cardigan Bay, and he was first taken up Cadaid Idris at the age of six. His university degrees at Birmingham, London and Aberystwyth were variously in French, Latin and History. During the war he worked as a conscientious objector in forestry in Herefordshire. In 1946 he married Penny, herself a good botanist and a brilliant gardener, and they made a succession of homes mostly in north Cardiganshire, moving always closer to the Dyfi estuary which Bill's writings made so much his own and which he did so much to conserve. The same year they went to Pembrokeshire to seek out Ronald Lockley, and began their long involvement with what was then known as the West Wales Field Society and which later became the Dyfed Wildlife Trust.

From 1947 to 1956 Bill was the W.W.F.S. Nature Warden, Mid Wales, and edited their *Field notes*. The 19 numbers of these, from 1950 to 1954, inspired and became incorporated into *Nature in Wales* in 1955, Bill being co-editor with Lockley and others for the first six issues. Although far from being a committee man by nature, he sat on many, most importantly the Nature Conservancy Committee for Wales, and was closely involved in setting up some of the early National Nature Reserves as well as the Bardsey Bird and Field Observatory and, with Captain and Mrs Vaughan, the Kite Committee. He became the first warden of the R.S.P.B. Reserve at Ynys-hir in 1969, and retired in 1982 to devote himself to writing. His first book had been *Thoreau* (1954). The New England philosopher and prophet of self-sufficiency, with his passion for close observation of nature and his belief in the "tonic of wildness", had a great influence on Bill.

He joined the B.S.B.I. in 1963 and was immediately elected on to the Welsh Region Committee which had been set up the previous year, and remained on it until 1971. He had already contributed many records to the *Atlas of the British flora*. His interest in, and considerable knowledge of ecology came about chiefly through his friendships with Hugh Chater, lecturer in Botany at Aberystwyth, and Evan Price Evans, the schoolteacher who had been a friend of Tansley and introduced ecology into the school curriculum. Bill, partly in preparation for his many books, visited every part of Wales. His especial interest became the distribution of the mountain plants of Caernarvonshire and Merioneth, their relationship to the geology, and the history of their discovery by the botanists of the past. It gave him the greatest pleasure to set out with friends on expeditions to refind some Snowdonian rarity where Edward Llwyd or James Backhouse had recorded it. In this age of increasingly desk-bound conservationists, the quantity and quality of information on the detailed history and localities of rare plants possessed by dedicated field naturalists of Bill's calibre has become ever more valuable, and he used his immense store of knowledge to help numerous research workers and recorders. Much of this knowledge fortunately went into his writings, and for the botanist the best are his magnificent New Naturalist books, *The Snowdonia National Park* (Collins, 1966), and *The Natural history of Wales* (Collins, 1981). Among his dozen other books the autobiographical *Pathway to the wild* (Faber, 1975) and *Wildlife my life* (Gomer, 1995) are outstanding. He was a brilliant photographer, especially in black and white, and took many memorable photos of plants. A long friendship with Mary Richards of Dolgellau, co-author with Peter Benoit of *A contribution to a Flora of Merioneth*, and from the age of 66 one of Kew's greatest plant collectors in Africa, led to his last book, *Wildflower safari, the life of Mary Richards* (Gomer, 1998). This was the fulfilment of a promise Bill made to her that he would record her life, and is based largely on her diaries. It is one of the few biographies of a B.S.B.I. member that we have.

The cumulative effect for conservation of Bill's lifelong output of books, talks, broadcasts and articles was immense, and for many of us he was a touchstone in his attitude to the natural world.

A. O. CHATER

ALFRED A. P. SLACK
(1913–1998)

Alfred Slack (Alf to his many friends and acquaintances) died on 6 March 1998 following a severe stroke. His passing deprives Scottish field botany of one of its most active workers. A Londoner, he attended school in the capital and was a graduate of London University. In the 1930s however he moved to Scotland and, having remained there ever since, may justly claim to have been an 'adopted Scot'! During the war years Alf worked in agriculture and forestry in Argyll and afterwards took up teaching as a profession. For many years he was a teacher, and latterly Principal of the Glasgow Tutorial College. No doubt nurtured by his experience in the hill country of Argyll during the war, Alf's great interest in natural history subjects, particularly botanical, led him in 1948 to join the Andersonian Naturalists of Glasgow (now the Glasgow Natural History Society) of which he was a member until his death. He was its President from 1970 to 1973.

In 1952 Alf joined the B.S.B.I. and was soon much involved in field work for *Atlas of the British Flora*, published in 1962. Weekends and holidays were generally spent away from Glasgow, either camping or living in a car-caravan with his wife Mattie and children Alan and Christine, often in places seldom if ever visited by other botanists, although 'classic' localities such as the Clova Mountains and the Braemar area also received attention. A good supply of B.S.B.I. field recording cards was always to hand on these occasions and the *Atlas* project benefitted accordingly. In the 1960s the tenancy of a holiday cottage in Argyll enabled more ready access to points north, and soon the acquisition of an old cabin cruiser named *Fulmar* made it possible to explore some of the off-shore islands and to visit the Hebridean islands.

In his younger days Alf was a climber of no mean ability, and he never lost his love of the hills and their fascinating arctic-alpine flora. He will perhaps be best remembered for his rediscovery of the Purple Colts-foot (*Homogyne alpina*) in the Clova Mountains in 1951 (one of George Don's 'lost' plants). Alf was very secretive about the location of this rarity and only revealed it to a privileged few, of which I feel very honoured to have been one. I recall the occasion when a small party gathered at Glen Doll Youth Hostel to be taken by Alf to the rock ledge where the *Homogyne alpina* grew. He had decided that Ursula Duncan, the then v.c. Recorder, had better be shown the site, and the others present were myself, Grant Roger and David McClintock. On another occasion Alf and I were in Clova to check on the *Homogyne* when we happened to meet the late Dr Humphrey Milne-Redhead who was camping in the area. The conversation inevitably turned to the subject of the *Homogyne* and it was very obvious that the doctor would dearly love to have directions to the spot; but it was equally obvious that the discoverer had no intention of divulging the information! Another of Alf's notable achievements was his confirmation of the 18th century records of *Dryas octopetala* and *Oxytropis halleri* on the limestone of Beinn Sguilaird in Argyll.

Alf Slack was not a prolific writer on botanical subjects. His published articles include an account of *Pinguicula lusitanica* in the *Glasgow naturalist*, notes on the limestone flora of Beinn Sguilaird in the same journal and, as joint author, notes on the flora of the Kishorn limestone in Wester Ross. He was one of the main organisers of the field work resulting in the publication of *A Map Flora of Mainland Inverness-shire* in 1985. He led many of the meetings in connection with that project and was largely responsible for the text, although this was never adequately acknowledged. His interest in the Rev. John Lightfoot was well known, and in 1986 he was invited to a symposium in Edinburgh to speak on that gentleman's travels in Scotland with Thomas Pennant. Alf possessed a first edition of Lightfoot's *Flora Scotica*.

After teaching in Glasgow and at Keil School in Dumbarton, Alf and the family moved to Campbeltown in Kintyre on his taking up a post there. When he retired they moved to Kentallen, near Ballachullish, in a house with magnificent views across Loch Linnhe to Ardgour and Kingairloch. If any part of Scotland attracted Alf Slack more than another it was the western part of Inverness-shire and that bit of Argyll which is included in v.c. 97. He was Recorder for that vice-county up to the time of his death.

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A. McG. STIRLING

Report

ANNUAL GENERAL MEETING, 9 MAY 1998

The Annual General Meeting of the Society was held at the Reardon Smith Lecture Theatre, National Museum and Gallery of Wales, Cardiff, at 11.45 a.m. The President, Mr D. A. Pearman took the Chair in the presence of 109 members.

Apologies for absence were read and Minutes of the 1997 Annual General Meeting, published in *Watsonia* 22: 139–141 (1998), were accepted as correct, approved and signed by the President.

REPORT OF COUNCIL

The President took members through the Report of the Council, which had been previously circulated to members, commenting on the main achievements of the Society during the year. He also mentioned the post of Co-ordinator and reported on C. S. Crook's impending resignation from the post and the possible appointment of a part-time, temporary replacement. The Treasurer then reported that, as only summary accounts had been published in the Annual Report, full sets of accounts were available at the meeting and on application to him. He further reported that he had found the accounts in good order when he took office and then gave a short account on the Society's financial activities and income. He was pleased to report a small surplus for the year but thought this could be considerably increased if more members took out Deeds of Covenant. Finally he thanked all those who worked so hard for the Society on a voluntary basis. Mr R. G. Ellis was congratulated on producing the Annual Report and Mr M. E. Braithwaite on his first Treasurer's Report and Accounts. The adoption of the Annual Report was proposed by Mr E F. Greenwood, seconded by Mrs A. P. Daly and accepted unanimously.

PRESIDENTS' AWARD

David Bellamy (President Wild Flower Society) and David Pearman (President B.S.B.I.) had both recommended Mr P. R. Green, Mr I. P. Green and Miss G. A. Crouch for their *Atlas Flora of Somerset*. Although there were other strong contenders, both Presidents thought the breadth of coverage, especially of aliens, was quite outstanding. The award would be presented at the Wild Flower Society's A.G.M. in November.

ELECTION OF PRESIDENT

Mr D. A. Pearman, in proposing Mrs M. E. Briggs as President, commented on her great qualities so admirably demonstrated during her 25 years as Hon. General Secretary and was certain that she would bring the same qualities to her new appointment. He was also delighted to welcome our first lady President. The election of Mary Briggs as President of the B.S.B.I. was approved by acclamation.

In response, Mrs Briggs reported that the B.S.B.I. had been a large part of her life and had been very dear to her heart for more years than she cared to remember and was quite overcome by the honour bestowed on her and was almost (but not quite!) speechless with emotion. As her first task as President she was pleased to thank David Pearman for the tremendous amount of work he had undertaken during his three year Presidency. She mentioned in particular *Atlas 2000* and reported that he would continue to oversee the project. Under his leadership we had also taken the great leap forward of appointing paid staff and he would continue to play a pivotal role with our Co-ordinator post.

ELECTION OF HON GENERAL SECRETARY

Council had nominated Mr R. G. Ellis. His election was carried unanimously by acclamation.

ELECTION OF HON. TREASURER

Council had nominated Mr M. E. Braithwaite. His election was carried unanimously by acclamation.

The President then praised the work of the Editors of *Watsonia* and *B.S.B.I. news*, the compiler of *B.S.B.I. abstracts*, and all Representatives on Council and other Committees for the hard work they carried out, voluntarily, on behalf of the Society. She gave special thanks to Dr B. S. Rushton, who was retiring after 14 years as an Editor, and since 1991 the Receiving Editor, of *Watsonia*. This was greeted by applause.

ELECTION OF COUNCIL MEMBERS

In accordance with Rule 11 nominations had been received for Miss A. Burns, Mr A. O. Chater and Mr T. J. James. Profiles had been published with proposers and seconders, and election of these members was proposed by Mr M. Walpole, seconded by Mr C. R. Boon and approved unanimously.

ELECTION OF HONORARY MEMBERS

The President mentioned that two members had been nominated for Honorary Membership of the Society this year. Both had made outstanding contributions to the Society and to field botany in general in the British Isles and Europe. Sponsors for both gave short appreciations of their respective candidates (to be published in *B.S.B.I. news*) and their election was carried unanimously with warm applause.

The two new Honorary Members (and sponsors) were: Mr R. S. R. Fitter (D. McClintock represented by D. A. Pearman) and Dr B. E. Jonsell (Dr F. H. Perring).

ELECTION OF HONORARY INDEPENDENT EXAMINER

The President warmly thanked Mr J. Coats, of Greaves West & Ayre, Chartered Accountants, Berwick-upon-Tweed for his exemplary examination of our accounts. His re-election was proposed by Mr M. E. Braithwaite, seconded by Mr D. A. Pearman and carried unanimously.

There being no other business, the meeting closed at 1.15 p.m.

GWYNNE ELLIS

FIELD EXCURSIONS HELD IN CONJUNCTION WITH THE A.G.M.

Four field meetings were held over the weekend; all were well attended, and we have to thank our leaders, Miss G. Barter, Mr M. Hampton and Mr J. Woodman for their sterling work. One meeting, on Sunday 10 May, was to the National Botanic Garden of Wales, Middleton Hall, Carmarthen, where over 40 members and guests were shown around the site of this exciting new venture by the director, Prof. C. Stirton. After lunch members were taken to see some of the delights of Pembrey Burrows, Llanelli, by Dr R. Pryce and we thank both him and Prof. Stirton for a very interesting day. A report of the visit to Pembrey Burrows will appear in *B.S.B.I. News*.

FRIDAY 8 MAY, FLAT HOLM

Forty members and guests gathered on Barry Island to embark for Flat Holm. The weather had improved after a wet and windy week, and this enabled the excursion to proceed, as the *Lewis Alexander* would not have taken passengers in winds in excess of force five. In fact, the sea was calm and the weather good, with only an occasional light shower.

On arrival, we were welcomed by the warden, Libby Robinson, who gave us an introductory talk. The island is managed by the Flat Holm Project, which was initiated by the former South

Glamorgan County Council and is now run by Cardiff County Council. The Project staff are working to restore grassland, having cleared much of the bracken and scrub which took over following the cessation of agriculture in the 1940s. Part of the island is now grazed by sheep, and the remainder is dominated by a colony of lesser black-backed gulls.

The Project Officer, Kevin Hogan, and the warden then each led a tour of the island, answering questions but allowing plenty of time for the study of plants and photography. One of the first specialities of the island to be found was *Trifolium ornithopodioides* (Bird's-foot Clover) which favours trampled turf on the paths. *Arum maculatum* (Lords-and-Ladies) was frequent in the recently restored grassland and rosettes of *Carduus tenuiflorus* (Slender Thistle) were abundant. Cliff-top turf included *Erodium maritimum* (Sea Stork's-bill), *Cochlearia danica* (Danish Scurvygrass), *Plantago coronopus* (Buck's-horn Plantain) and *Stellaria pallida* (Lesser Chickweed).

The main speciality of the island is *Allium ampeloprasum* (Wild Leek), which is believed to be native, having been first recorded here in 1688. Although not yet in flower it was already conspicuous, especially around the Victorian barrack buildings near the lighthouse. Also in this area were *Ranunculus parviflorus* (Small-flowered Buttercup), *Medicago arabica* (Spotted Medick) and an established introduction, *Ornithogalum angustifolium* (Star-of-Bethlehem).

An unexpected pleasure was to find *Paeonia mascula* (Wild Peony) just coming into bloom. Although better known from the nearby island of Steep Holm, one plant was discovered here in 1982 and is now fenced to protect it from grazing. One of its progeny grows in the farmhouse garden and this was much photographed, a rare opportunity as it flowers for only a few days each year.

Both tours ended at the farmhouse, where mugs of tea were provided by the resident volunteers, and our guides were thanked. Members who were unable to attend this meeting may arrange their own visit by telephoning the Flat Holm Project on 01446 747661. Places are sometimes available on boat trips organised for other groups, the dates and times being determined by the state of the tide.

GILL BARTER

FRIDAY 8 MAY, PORTHKERRY PARK

About 20 members and friends gathered at this country park on the coast of the Vale of Glamorgan near Barry where the botanical riches can be found on the Lias Limestone cliffs and behind the pebble bar at the bottom of the cliffs.

West along the vegetated inland part of the pebble bar *Trifolium striatum* (Knotted Clover) was just coming into flower but its common associate here, *T. scabrum* (Rough Clover), could not be seen. In a damper area further along, where there is occasional inundation by the sea, *Alopecurus bulbosus* (Bulbous Foxtail) was demonstrated, the swollen stem bases being clearly visible.

Moving east, still behind the pebble bar, below the start of the cliffs, eyes were down in search of *Poa bulbosa* (Bulbous Meadow-grass) which was spotted by the sharp eyes of Mary Gilham and Franz Hopkins. On closer inspection several patches of this diminutive grass could be seen along the more trampled ground. All the plants here are the viviparous variety, *P. bulbosa* var. *vivipara*, the proliferating spikelets being well-formed already. Nearby *Medicago polymorpha* (Toothed Medick) was discovered which, although not recorded from this site before, the party agreed had all the appearances of being indigenous here.

Moving on to the pebble beach, binoculars at the ready, one or two *Sorbus domestica* (True Service-tree) were pointed out to people by the discoverer, Marc Hampton. Marc discovered the population in 1993. A better view was had looking down on them by ascending the 'Golden Stairs' along the clifftop. At the bottom of the stairs was a splendid show of *Lithospermum purpureocaeruleum* (Purple Gromwell) prompting one member to suggest they were planted for the occasion! (He knows who he is.)

JULIAN WOODMAN

SUNDAY MAY 10, VARIOUS SITES IN GLAMORGAN

This excursion was a pick 'n mix of sites that make Glamorgan special to the leader and many others. The three sites included: The Leys & East Aberthaw Coast Site of Special Scientific Interest (S.S.S.I.), Cefn Cribwr Meadows S.S.S.I. and Old Castle Down S.S.S.I.

About 45 people gathered in the car park of one of the finest pubs in Glamorgan, 'The Blue

'Anchor', in East Aberthaw, walking down to the coast under the railway and by the side of the looming fly ash tip of the power station. The party was jointly led by myself and Marc Hampton, the voluntary warden of The Leys, which is a Glamorgan Wildlife Trust Reserve. On reaching the old lime works the dry ground in front revealed with some close inspection *Trifolium ornithopodioides* (Bird's-foot Clover), *T. scabrum* (Rough Clover) and *Ranunculus parviflorus* (Small-flowered Buttercup).

Over the sea wall on to the beach behind an area of saltmarsh/lagoon and pebble bar, a few small patches of *Frankenia laevis* (Sea Heath) can quite regularly be seen here although not always in the same spots (Marc Hampton, pers. comm.). In the drift line below the low cliff a white flowering form of *Raphanus raphanistrum* subsp. *maritimus* (Sea Radish) was noted as possibly the first mainland record for this subspecies in Britain.

Moving further east below the low cliff the just emerged silvery foliage of *Sorbus domestica* (True Service-tree) could clearly be seen and one of the smaller suckers also had flowers. Towards the end of the beach, several patches of *Adiantum capillus-veneris* (Maidenhair Fern) were seen in wet tufaceous seepages low down on the cliffs.

After lunch the party moved off in a 'loose' convoy of cars to the second site, Cefn Cribwr Meadows S.S.S.I. which is about three miles to the N.W. of Bridgend. We kept in the core of the S.S.S.I. consisting of five adjoining fields of species-rich *Molinia caerulea* marshy grassland. *Scorzoneroides humilis* (Viper's-grass) is one of the specialities of these fields, a large population having been discovered in June 1996. This was the first recorded site for it in Wales (a second smaller population was discovered on the Gower Peninsula in 1997). Other species that were flowering and are characteristic of these fields include *Genista anglica* (Petty Whin), *Cirsium dissectum* (Meadow Thistle), *Valeriana dioica* (Marsh Valerian) and the cottony seeds of *Salix repens* (Creeping Willow).

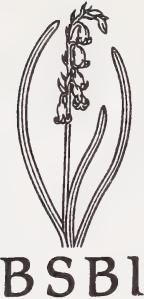
Next door to the S.S.S.I. there is an equally spectacular field where *Myrica gale* (Bog Myrtle), *Juncus subnodulosus* (Blunt-flowered Rush), *Pinguicula vulgaris* (Common Butterwort) and *Carex montana* (Soft-leaved Sedge) occur. The fronds of *Thelypteris palustris* (Marsh Fern) were just emerging in a very wet flushed corner of this field.

From Cefn Cribwr, those that were able to, moved on to the third site, Old Castle Down S.S.S.I., an area of calcareous grassland and heathland south of Bridgend. The calcareous grassland is found on the steep slopes of a dry valley, Pant St Brides, where *Carex montana* (Soft-leaved Sedge) was seen in abundance amongst a calcareous sward with *Helianthemum nummularium* (Common Rock-rose), *Thymus polytrichus* (Wild Thyme) and *Festuca ovina* (Sheep's Fescue).

Small areas of vegetation where species typical of more acid conditions grow side-by-side with species of more calcareous conditions were seen including: *Erica tetralix* (Cross-leaved Heath), *Molinia caerulea* (Purple Moor-grass), *Ulex gallii* (Western Gorse), *Calluna vulgaris* (Ling), *Stachys officinalis* (Betony), *Carex pulicaris* (Flea Sedge), *Helianthemum nummularium* (Common Rock-rose) and *Galium verum* (Lady's Bedstraw). More extensive areas of this type of vegetation occur further along the slope. Up on to the plateaux, the pale white/lilac flowers of *Viola lactea* (Pale Dog-violet) were seen along with probable hybrids between *Viola lactea* and *Viola riviniana* (Common Dog-violet).

There ended the day's excursion except for a select group (including the author!) who toasted the end of an enjoyable day in the Blue Anchor. My thanks to Gill Barter for helping with transportation and leading the Flat Holm trip, Arthur Chater for so courteously taking the role of chief recorder at East Aberthaw and Gwynn Ellis for organising people and ferrying on Friday. My thanks also to the owners for allowing us to visit the sites. 'Loose' convoy is a term that can be applied to most A.G.M. field meetings – now I know how a sheep dog feels!

JULIAN WOODMAN



BOTANICAL SOCIETY OF THE BRITISH ISLES (B.S.B.I.)

The B.S.B.I. was founded in 1836 and has a membership of 2,850. It is the major source of information on the status and distribution of British and Irish flowering plants and ferns. This information, which is gathered through a network of county recorders, is vital for the conservation of the plants and is the basis of the *Red data books* for vascular plants in Great Britain and Ireland. The Society arranges conferences and field meetings throughout the British Isles and, occasionally, abroad. It organises plant distribution surveys and publishes plant atlases and handbooks on difficult groups such as sedges and willows. It has a panel of referees available to members to name problem plants. Through its Conservation Committee it plays an active part in the protection of our threatened plants. It welcomes all botanists, professional and amateur alike, as members.

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Tables, figure legends & appendices should be typed on separate sheets and attached at the end of the typescript.

Figures should be drawn in black ink or be laser-printed and identified in pencil on the back with their number and the author's name. They should be no more than three times final size, bearing in mind they will normally be reduced to occupy the full width of a page. Scale-bars are essential on plant illustrations and maps. Lettering should be of high-quality and may be done in pencil and left to the printer. Black and white photographs can be accepted if they assist in the understanding of the article.

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Papers and Notes: Mr M. N. Sanford, c/o The Museum, High Street, Ipswich, Suffolk, IP1 3QH.

Books for Review: Mr D. A. Pearman, The Old Rectory, Frome St Quintin, Dorchester, Dorset DT2 0HF

Plant Records: the appropriate vice-county recorder, who should then send them to Dr C. D Preston, Biological Records Centre, Monks Wood, Abbots Ripton, Huntingdon, PE17 21S.

Obituaries: Mrs M. Briggs, 9 Arun Prospect, Pulborough, West Sussex, RH20 1AL.

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D. A. Pearman, B. S. Rushton, M. N. Sanford, D. A. Simpson

Botanical Society of the British Isles

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Accredited with the International Association for Plant Taxonomy for the purpose
of registration of new non-fungal plant names.

The cover illustration of *Euphorbia hyberna* L. (Irish Spurge) was drawn by
Rosemary Wise.

Biology, genetic variation and conservation of *Luronium natans* (L.) Raf. in Britain and Ireland

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ABSTRACT

Luronium natans (Floating Water-plantain) is a European endemic aquatic plant which is now rare and threatened across most of its extant range. Confusion with similar species has led to misunderstanding of its distribution and status in Britain and Ireland, but oligotrophic upland lakes now seem to hold the main populations. Isozyme studies show comparatively high levels of genetic variation among native populations in Wales, contrasting with the lack of variation reported in some closely-related aquatic species, but there is close similarity among samples of plants from canal populations on the Welsh borders. It has spread into this canal habitat relatively recently (post-1850), and the isozyme patterns found there indicate that the canal populations have originated from a native lake population connected to the canals by feeder streams. The greatest range of genetic variation now appears to remain in a few native "core" sites, and the survival of these populations is thus of particular importance. Conservation priorities are discussed in relation to the biology, distribution and metapopulation structure of the species in Britain and Ireland.

KEYWORDS: Floating Water-plantain, aquatic plants, isozyme variation, Wales, threatened species, oligotrophic lakes.

INTRODUCTION

Luronium natans (L.) Raf. (Alismataceae) is a stoloniferous aquatic perennial which grows in a range of habitats, and is phenotypically very plastic. The strikingly different forms that it can assume in different habitats nearly all resemble commoner aquatic species, with the result that it has often been overlooked or confused with these commoner plants (Ferguson, Briggs & Willby 1998). In shallow water *L. natans* produces stalked leaves with ovate or elliptical blades, up to about 4 × 1.4 cm, sometimes larger, which superficially resemble the floating leaves of some common *Potamogeton* species. When growing on exposed mud it produces similar but smaller ovate leaves with stiffer, shorter stalks, and then closely resembles *Baldellia ranunculoides*, even when it is in flower. In deeper water (0.7–2 m, perhaps up to 4 m in particularly clear lakes) it grows as "isoetoid" rosettes of linear-triangular leaves, about 0.5 cm wide at the base and 5–7 cm long, without any expanded lamina. These rosettes are practically identical to juvenile *Alisma plantago-aquatica*, and very similar when seen at a distance to those of *Isoetes* spp. and *Littorella uniflora*, both of which are often abundant in habitats that are suitable for *Luronium natans*, and may not be recorded in shore-based sampling. Finally, in flowing water it can produce long (50–60 cm), strap-like, flexible leaves about 0.5–0.7 cm wide, in dense masses, resembling the leaves of the species of *Sparganium* that grow in similar habitats. The forms (illustrated by Jones & Rich (1998)) appear to be phenotypically freely interchangeable, both in cultivation and in nature, with leaves of different forms being produced on one and the same rosette under appropriate conditions. Their common feature, found in otherwise similar aquatic species only in *Baldellia ranunculoides*, is the combination of slender stolons, 5 cm or more in length, with laminar leaves produced in

rosettes. The stoloniferous forms of *Baldellia ranunculoides* that most closely resemble *L. natans* can be distinguished in the field by the characteristic smell of coriander in their crushed foliage.

In Britain and Ireland *Luronium natans* is known from three main habitats. Its chief natural habitat is now in oligotrophic, moderately acidic lakes and pools, in upland areas but generally not at high altitudes (up to about 400 m). In these sites it can occasionally be detected by the presence in shallow water of flowering plants with floating leaves, but more often remains inconspicuous and unsuspected as submerged isoetoid rosettes, vegetative and growing at depths of 1–2·5 m. It appears to have been lost from similar, formerly oligotrophic lakes in the lowlands, for example the Shropshire meres and the larger pools and lakes in Anglesey (Ynys Môn) as a consequence of eutrophication, mainly during the early part of the century. A second characteristic habitat, which still survives in a few sites, is in shallow oligotrophic or mesotrophic ponds or pools on grazed heathland or commonland in low-lying western maritime areas. Scattered references to its former occurrence in such sites (e.g. Davies 1813) suggest that *L. natans* may have had a fairly wide distribution in ponds of this type in the past, but has drastically declined as they have been lost or altered by drainage, eutrophication, changes in agricultural practice or overgrowth. *L. natans* is now known to grow at only two such sites in western Britain, on Ramsey Island (Ynys Dewi) and Dowrog Common, both in south-western Wales. Heathland ponds of this type are or were often man-made, with their suitability as a habitat for *L. natans* maintained or enhanced by human or livestock activity, and at least some of the populations of *L. natans* in such sites can be seen as satellite populations utilising relatively transient and essentially artificial sites. Similar small and probably transient populations found in isolated farm ponds in Pembrokeshire, in scattered sites across the English midlands, and (perhaps introduced) in Norfolk (M. Wade pers. comm., Driscoll 1992) reflect this more opportunistic aspect of the ecology of *L. natans*, as does its third presently characteristic habitat, which is in abandoned or little-used canals. It has spread into this habitat fairly recently (since about 1850), colonising canals on the Welsh border and in north-central England, sometimes becoming locally abundant (Willby & Eaton 1993) but subsequently declining in at least some sites (Briggs 1988) as a consequence of eutrophication, overgrowth, increased boat traffic and other possible factors. It seems possible that the canal habitat effectively reproduces a formerly widespread but now very rare natural habitat of *L. natans*, in clear, oligotrophic or moderately mesotrophic, slow-flowing rivers. In Britain *L. natans* has been recorded from seven such river sites, but it is now known from only two, both in Wales. As with lowland pool and lake sites, suitable river habitats would almost certainly have been more common in the past, before widespread channel-straightening, eutrophication and sediment deposition took place, and river populations of *L. natans* have most probably declined as a result (Davies 1813; Lockton and Whild 1997). Whilst the present canal populations of *L. natans* clearly grow in an artificial habitat, their relationship to other populations of the species has been uncertain. The interconnection between and superficial similarity of canals to sluggish river channels suggests that canal populations might have had river populations as their source, although it is also possible that river populations are themselves satellites of "core" populations in upland Wales. A number of the current and former sites for *L. natans* in rivers occur downstream of lakes containing large, established populations.

Luronium natans is a European endemic species, with a distribution of the Suboceanic Temperate type (Preston & Hill 1997). Its range extends from north-western Spain and Ireland in the west to Lithuania, Bulgaria and Moldavia in the east. On much of the European continent it is now very rare and declining, with a scattered and disjunct distribution, and many surviving populations are reported to be under threat from drainage, eutrophication or acidification of their freshwater habitat (Roelofs 1983; Hanspach & Krausch 1987; Fritz 1989; Ferguson 1991; Rodriguez-Oubina & Ortiz 1991; Willby & Eaton 1993). As a result the species has been listed on the Berne Convention Appendix 1 (which requires signatory states to prohibit taking, and to take measures to conserve listed species), and the EC Habitats Directive Annexes IIb & IVb (which require designation of protected areas and special protection measures for them). Consequently, *L. natans* is now listed on Schedule 8 of the United Kingdom Wildlife and Countryside Act (revised 1992), which makes it an offence to pick, uproot, sell or destroy the species, and is included among the "Short List" species of the UK Biodiversity Action Plan, with a commitment to maintain and, if possible, enhance its present range.

In the British Isles its distribution has been rather poorly understood in the past, in part because of confusion with other commoner species, but it now seems clear that *L. natans* has a stronghold

in Wales, where it is fairly widespread in the uplands (Ellis 1983; Preston 1994). With the decline of heathland ponds, native or long-established lowland populations in adjacent English counties have dwindled greatly and may recently have become extinct in this habitat (S. Whild, pers. comm.). Past reports of the occurrence of *L. natans* in the mountainous Lake District of north-western England (Cumbria) were repeatedly copied and cited in County Floras and other publications (Turner & Dillwyn 1805; Smith 1828; Hooker 1831; Baker 1885; Hodgson 1898; Wilson 1938; Perring & Walters 1976; Halliday 1978; Willby & Eaton 1993), but investigation of these records, all dating from the nineteenth century, showed that they were questionable and in one case the result of a copyist's error (Kay & John 1995; Halliday 1997), and as such they were omitted from the maps published by Preston (1994) and Preston & Croft (1997). Subsequent re-investigation of likely habitats in Cumbria (G. Halliday, pers. comm.) has however shown that *L. natans* is locally abundant in at least two of the larger lakes, Derwentwater (Halliday 1997) and Bassenthwaite Lake, and it has also been found in a pool near Ullswater (G. Halliday, pers. comm.), so in this light it now seems probable that Greville's early record of the species from Derwentwater (Turner & Dillwyn 1805), which was first called into question by Hodgson (1898) was in fact correct.

Furthermore, there is now evidence that *L. natans* has been even more widely overlooked. Nineteenth-century records of its occurrence in south-western Scotland and western Ireland (e.g. Hooker 1831) had, in the absence of more recent records, come to be regarded as probable errors. However, Rich, Kay & Kirschner (1995) have recently found a new locality for the species in Ireland, and they have shown that several older records from other sites in Ireland are certainly or probably correct. It now seems likely that *L. natans*, although scarce, may be fairly widely distributed in western Ireland, at least from Killarney (where it was last seen in 1886) through Clare (1882) to Galway (1994). An equally interesting series of new records of *L. natans* has recently been reported from central and western Scotland; here, lake surveys have shown that it occurs at several sites in Argyll, although its status there is uncertain (N. Willby, pers. comm.). These records from Ireland and Scotland, and its rediscovery in the English Lake District, show that *L. natans* is considerably more widespread in western Britain and Ireland than had been thought, and suggest that it may be present but undetected in other sites.

The aims of the present study, which commenced in 1993, were to characterise the reproductive biology of *L. natans*, to assess its patterns of genetic variation using isozyme analysis, to interpret these findings in terms of its population and metapopulation structure, and to consider their implications for its conservation.

MATERIALS AND METHODS

Observations on reproductive biology were made both in the field and in cultivation. Plant samples for isozyme analysis were collected (under licence) by hand or grab sampling at intervals of at least 2 m in pond and stream populations and 5–20 m in lake populations. Grapnels do not attach well to *L. natans*, and simple diving equipment – a face-mask, snorkel and wet-suit – is the most effective means of sampling colonies below 1 m depth. One or more clones from most populations were grown on for further study, without difficulty, rooted in fine gravel in a 15 cm depth of rainwater in open-topped polythene containers 12–18 cm in diameter on a part-shaded open-air hardstanding. Isozyme analysis was carried out by horizontal starch gel electrophoresis, using about 0.5–1 cm² of fresh leaf material from each sample. The electrophoresis procedure was similar to that described by Shields, Orton & Stuber (1983) and Lack & Kay (1986). Staining was carried out using recipes following Shaw & Prasad (1970).

RESULTS

REPRODUCTIVE BIOLOGY

Luronium natans flowers during July and August, and appears to be adapted for both self-pollination and insect visitors. Plants growing in less than about 60 cm of water, or on exposed mud, produce bowl-shaped flowers which open to about 15 mm in diameter in sunny and calm weather, rising to or above the surface on long pedicels if the plant is submerged. In cultivation, the

TABLE 1. *LURONIUM NATANS* – SITES, SAMPLE SIZES, NUMBERS OF ISOZYME GENOTYPES AND NUMBERS OF VARIABLE LOCI FOUND

Population code, site name and grid reference	No. of samples collected	No. of isozyme genotypes found	No. of variable loci
WALES			
1. Llyn Cwellyn SH/565.548	1	1	0
2. Llyn-y-Dywarchen SH/560.534	4	2	1
3. Llyn Tegid SH/88.35	9	2	1
4. Llangollen Feeder Canal SJ/210.426	4	2	3
5. Montgomery Canal, Four Crosses SJ/258.191	4	2	1
6. Montgomery Canal, Nag's Head SO/194.990	2	2	1
7. Montgomery Canal, Fron SO/167.965	2	2	3
8. Llyn Hir SN/789.677	4	4	2
9. Llyn Teifi (all) SN/78.67	14	4	3
9A. Llyn Teifi A (South Bay) SN/785.675	6	4	2
9B. Llyn Teifi B (South Shore) SN/784.675	8	3	2
10. Llyn Egnant SN/792.675	9	3	2
11. Afon Teifi, Cors Caron SN/69.64	4	2	1
12. Afon Teifi above 'Flash' SN/675.620	3	3	2
13. Afon Teifi below 'Flash' SN/677.640	4	3	3
14. Llyn Eiddwen SN/606.670	6	1	0
15. Llyn Fanod SN/603.644	6	1	0
16. Ramsey Island, West Pond SM/702.235	10	1	0
IRELAND			
17. Invermore Lough (Connemara) L/899.390	1	1	0

flowers last for only a day, but regularly attract small flies. Their three delicate white petals have a conspicuous yellow base, and are unscented. Their nectar provision, if any, was not quantified, but they resemble the nectar-providing flowers of *Ranunculus* subgenus *Batrachium* (water crowfoots) which grow in similar habitats. In windy conditions, or when produced on plants growing at depths greater than about 60 cm, when the flowers fail to reach the surface, the petals do not open and self-pollination takes place cleistogamously within the closed flower. G. Halliday (pers. comm.) has observed the production of several long-stalked cleistogamous flowers from each of many ascending stoloniferous stems in plants growing in about 2 m of water in Derwentwater. There are normally six stamens per flower, and up to 13 carpels (an average number of 12.5 was found in samples from Ramsey Island (Ynys Dewi)), each containing a single ovule, and forming an achene when fertilized. The pollen grains are morphologically distinctive, bluntly octagonal in cross-section; the pollen fertility of a sample from Ramsey, assessed as acetocarmine stainability, was 83.97%, with about 12000 pollen grains per flower. The pollen:ovule ratio was 973, suggesting adaptation for at least partial outbreeding. No formal test of compatibility relationships was made, but the production of seeds by submerged and apparently cleistogamous flowers indicates self-compatibility. In suitable conditions, for example on the exposed mud of Llyn Teifi (Chater 1990) or in sheltered parts of Llyn Glaslyn (Catherine Duigan, pers. comm.), and in the Montgomery and Rochdale Canals (N. Willby, pers. comm.) flowering plants can produce conspicuous displays.

It seems probable that allogamy is possible only in plants that are growing in fairly shallow water where flowering shoots can extend to the surface, or on exposed mud, and that seed production is most abundant under these conditions. The small (1–2 mm) cylindrical achenes have no special adaptations for dispersal, and in water sink when released from the receptacle, although seedlings float (Ridley 1930) and it seems likely that the seeds can be dispersed by waterfowl. Seedling establishment is sometimes conspicuous (as, for instance, along the strand-line on Llyn Teifi, Cardiganshire), but the characteristically vigorous stoloniferous spread shown by *L. natans* suggests that reproduction within individual lakes, rivers or canal systems is likely to be predominantly clonal, by vegetative spread of stolons and detached rosettes. Rosettes and stolons might also occasionally become attached to the legs or necks of waterfowl, enabling vegetative

TABLE 2. *LURONIUM NATANS* – GENE FREQUENCIES

		Population																		
		Population																		
Locus and allele		1	2	3	4	5	6	7	8	9	9A	9B	10	11	12	13	14	15	16	17
PGI 1 A	B	0.333	0.167	0.333	0.240	0.333	0.167	0.167	0.167	0.167	0.333	0.333	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167
	C	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.167	0.111	0.333	0.333	0.333	0.333	0.333	0.333
	D	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.333	0.167	0.333	0.111	0.333	0.333	0.333	0.333	0.333
	E	0.167	0.333	0.333	0.333	0.333	0.333	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.111	0.333	0.333	0.333	0.333	0.333
	n	0.167	0.093	0.093	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.167
Number of genotypes		1	1	2	1	1	1	1	1	1	1	1	1	2	3	1	1	1	1	1
PGM 1 A	B	0.500	0.500	0.500	0.500	0.500	0.250	0.750	1.000	1.000	1.000	1.000	1.000	0.500	0.250	0.750	1.000	1.000	1.000	0.500
	C	1.000	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500
	D																			
Number of genotypes		1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	1	1
MDH A	B	0.250	0.667	0.278	0.750	0.667	0.250	0.250	0.250	0.250	0.333	0.333	0.167	0.250	0.250	0.500	0.500	0.333	0.500	1.000
	C	0.500	0.333	0.222	0.250	0.250	0.333	0.500	0.500	0.500	0.333	0.333	0.500	0.500	0.500	0.500	0.500	0.333	0.500	0.500
	D	0.500	0.250	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.333	0.333	0.500	0.500	0.500	0.500	0.500	0.333	0.500	0.500
	E	0.250	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.250	0.250	0.500	0.500	0.500	0.500	0.500	0.333	0.500	0.500
	n	0.250	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.500	0.333	0.333	0.500	0.500	0.500	0.500	0.500	0.333	0.500	0.500
Number of genotypes		1	2	2	2	2	2	3	2	3	3	3	2	1	1	3	1	1	1	1
SDH A	B	0.333	0.500	0.500	0.333	0.333	0.167	0.333	0.452	0.625	0.611	0.333	0.333	0.333	0.333	0.333	0.500	0.333	0.333	1.000
	C	0.333	0.500	0.352	0.444	0.417	0.440	0.190	0.292	0.111	0.333	0.333	0.111	0.333	0.333	0.333	0.333	0.500	0.333	0.333
	D	0.333	0.333	0.148	0.222	0.333	0.417	0.227	0.357	0.083	0.027	0.222	0.333	0.333	0.167	0.333	0.333	0.333	0.333	0.333
	E	0.333	0.333	0.148	0.222	0.333	0.417	0.227	0.357	0.083	0.027	0.222	0.333	0.333	0.167	0.333	0.333	0.333	0.333	0.333
	n	0.333	0.333	0.148	0.222	0.333	0.417	0.227	0.357	0.083	0.027	0.222	0.333	0.333	0.167	0.333	0.333	0.333	0.333	0.333
Number of genotypes		1	1	2	2	1	1	2	4	4	1	3	1	3	2	1	1	1	1	1

dispersal to occur between separate (although probably comparatively close) bodies of water. The results of our genetic analysis provide supporting evidence for the predominant rôle of vegetative spread within lakes, canals and river systems, and also for the occurrence of seed-mediated dispersal between water bodies. Within lake and river systems our genetic analysis also provides evidence of the occurrence of reproduction by seed and consequent recombination in some areas, but the frequency of successful sexual reproduction and of allogamy cannot be determined because of the small number of variable loci and the probable occurrence of fixed heterozygosity, as described in the next section.

GENETIC VARIATION

A chromosome number of $2n = 42$, probably hexaploid from a basic number of $x = 7$, has been reported for Swedish material of *Luronium natans* by Björkvist (1961), and a count of $2n = 38$, which we cannot trace, was reported for British material by Clapham, Tutin & Warburg (1962), suggesting that British material is also hexaploid. No counts on British or Irish material are documented in the Leicester Cytological Catalogue (R. Gornall, pers. comm.).

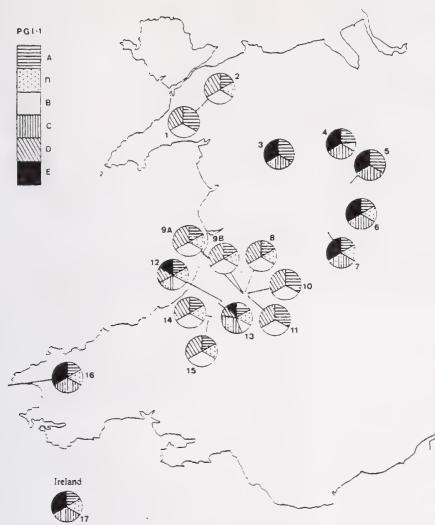
We obtained samples for isozyme studies of genetic variation from 16 populations or subpopulations in Wales, one of which was subdivided. A single sample was obtained from the newly-discovered population at Invermore Lough, Co. Galway (Connemara) in western Ireland. Details of the populations sampled are given in Table 1 and Figs. 1–4. Eleven loci in nine enzymic systems were assayed, of which only four were found to be variable, phosphoglucose isomerase 1 (PGI 1), phosphoglucomutase 1 (PGM 1), malate dehydrogenase (MDH) and shikimate dehydrogenase (SDH). Banding patterns were in agreement with the hexaploid chromosome counts reported for *L. natans*. Where all bands stained to the same intensity, it was assumed that there were equal numbers of copies of each allele. Where there were differences in staining intensities among the bands it was possible to estimate the number of copies of each allele that were present in an individual plant. Gene frequencies, together with the number of genotypes recorded at each site, are shown in Table 2. Two populations (Llyn Cwellyn and Invermore Lough) were represented by a single sample. Three of the 15 populations from which several samples were obtained (Llyn Eiddwen and Llyn Fanod, each with six widely-spaced samples, and Ramsey West Pond, with ten samples from a dense pond population) were monomorphic at all variable isozyme loci. Two or more genotypes, with a maximum of four, were found in each of the twelve remaining populations. While each genotype could represent a true-breeding inbred line, the strong vegetative spread and multiplication shown by the species suggest that apparent monomorphy, or paucity of genotypes within a population, is more likely to be the result of predominantly clonal reproduction. In a hexaploid, most isozymes will have three loci, so, in a survey of this type, it is not possible to distinguish true heterozygotes (individuals heterozygous at a single locus) from fixed heterozygotes (individuals which are homozygous for different alleles at corresponding loci in different genomes). Thus, although the observed frequency of heterozygosity was high, it was not possible either to confirm the occurrence of outcrossing and recombination, or to obtain an estimate of their frequency. The low ratios of numbers of genotypes found to numbers of variable loci (Table 2) and our examination of relative band intensities, which are normally proportional to the number of copies of each allele that are expressed (e.g. Lack & Kay 1986) suggested that the frequencies of sexual reproduction, and especially of recruitment of new recombinant genotypes within a population, were low, and possibly zero in some cases.

The distribution and frequencies of alleles at each scored locus are mapped in Figs. 1–4. The PG1 locus showed two major genotypes, one (found in Llyn Tegid, the Llangollen and Montgomery Canals, on Ramsey and in Ireland) with linked C and E alleles, and the other (from central and northern Wales) with linked B and D alleles. The Irish sample from Invermore Lough was the only one which showed monomorphy and homozygosity at two of the loci, but many of the central and northern Welsh populations were monomorphic for probable fixed heterozygosity at two or more loci.

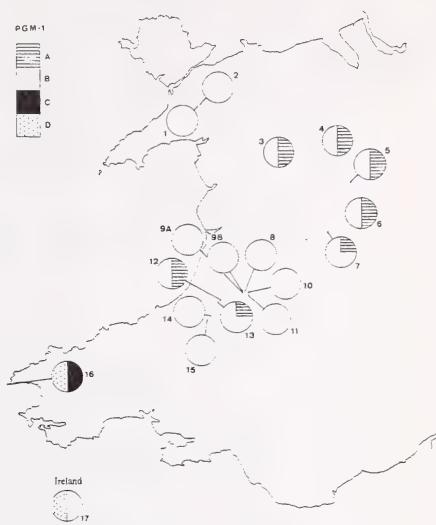
RELATIONSHIPS AMONG POPULATIONS

An unrooted phylogenetic tree of relationships among populations, based on the isozyme data and prepared using the CONML procedure of Felsenstein's PHYLIP package (Felsenstein 1993), is shown in Fig. 5, and Nei's (1972) measures of genetic distance between populations, also based on the four variable loci, are shown in Table 3. The distances between populations along the branches

1



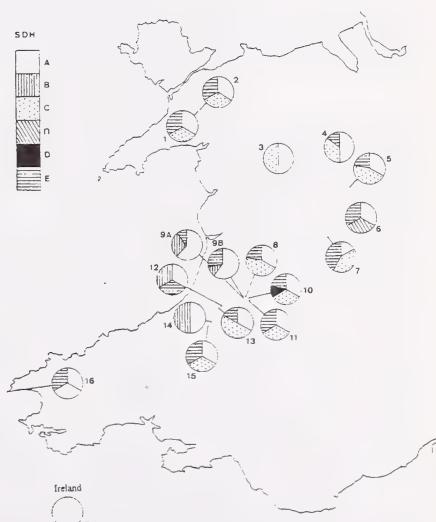
2



3



4



FIGURES 1–4. The distribution and frequency of alleles at four variable loci in 17 populations or sub-populations of *Luronium natans* in Wales and Ireland (inset). Sector size in each composite circular symbol is proportional to the frequency of the corresponding allele of each enzyme in the population sample from that site. PGI 1 is shown in Fig. 1 (top left), PGM 1 in Fig. 2 (top right), MDH in Fig. 3 (lower left) and SDH in Fig. 4 (lower right).

TABLE 3. *LURONIUM NATANS* - NEI'S (1972) MEASURE OF GENETIC DISTANCE AMONG POPULATIONS

Population	2	3	4	5	6	7	8	9A	9B	10	11	12	13	14	15	16	17
1 Llyn Cwellyn	0.043	0.337	0.458	0.317	0.417	0.196	0.050	0.130	0.106	0.019	0.093	0.459	0.119	0.185	0.013	0.743	0.569
2 Llyn-y-Dwarchen	0.460	0.388	0.458	0.532	0.259	0.006	0.086	0.062	0.045	0.079	0.532	0.151	0.141	0.030	0.851	0.724	
3 Llyn Tegid	0.143	0.026	0.170	0.135	0.422	0.514	0.505	0.378	0.569	0.367	0.106	0.562	0.363	0.451	0.301		
4 Llangollen Canal		0.169	0.269	0.241	0.376	0.432	0.376	0.475	0.556	0.404	0.215	0.466	0.611	0.467			
5 Montgomery Canal Four Crosses			0.112	0.074	0.444	0.587	0.520	0.388	0.588	0.297	0.115	0.618	0.343	0.343	0.332		
6 Montgomery Canal, Nag's Head				0.137	0.573	0.556	0.471	0.514	0.735	0.244	0.231	0.595	0.404	0.514	0.310		
7 Montgomery Canal, Fron					0.265	0.437	0.363	0.258	0.393	0.328	0.065	0.476	0.183	0.436	0.418		
8 Llyn Hir						0.097	0.084	0.045	0.085	0.575	0.134	0.147	0.037	0.857	0.730		
9A Afon Teifi A							0.027	0.119	0.169	0.464	0.260	0.026	0.117	1.023	0.532		
9B Afon Teifi B								0.113	0.167	0.413	0.255	0.059	0.093	0.981	0.470		
10 Llyn Egnant									0.052	0.454	0.142	0.178	0.033	0.850	0.658		
11 Cors Caron										0.546	0.247	0.254	0.109	1.043	0.985		
12 Afon Teifi A											0.393	0.422	0.446	0.889	0.490		
13 Afon Teifi B												0.322	0.106	0.473	0.436		
14 Llyn Eiddwen													0.172	1.120	0.556		
15 Llyn Fanod														0.730	0.556		
16 Ramseye (17 Connemara)															0.441		

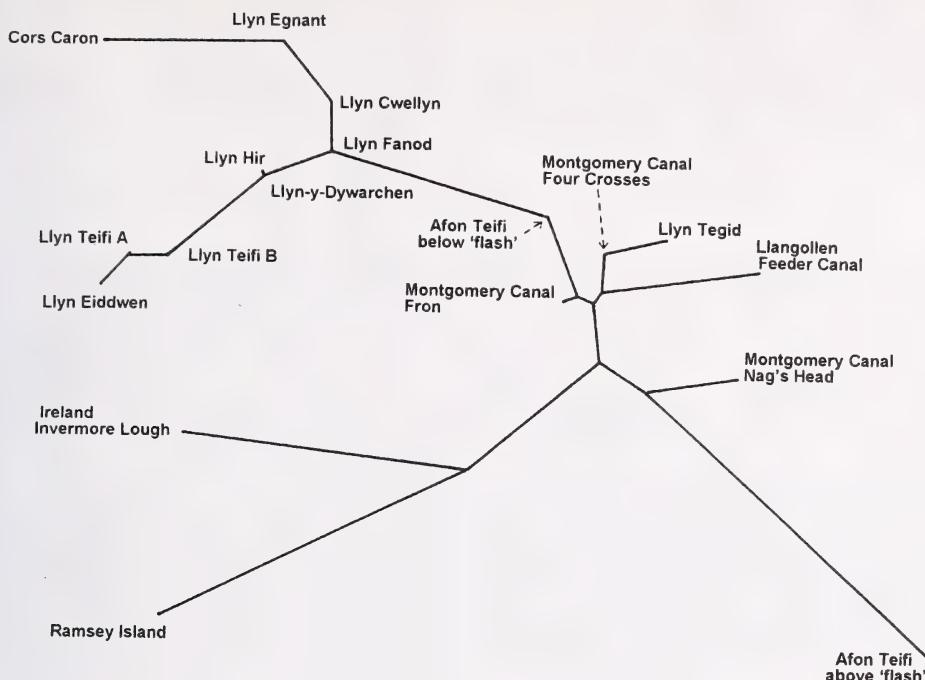


FIGURE 5. An unrooted phylogenetic tree, prepared using the CONML procedure from PHYLIP (Felsenstein 1993), showing inter-relationships between 17 populations or sub-populations of *Luronium natans*. Distances between populations, measured along the arms of the diagram, are proportional to calculated genetic divergence.

of the tree are proportional to calculated genetic divergence. While it must be remembered that this tree is based on only four variable loci, there is clear evidence of differentiation between geographic areas. The geographically isolated Ramsey and Connemara populations, which although well separated from one another are joined on a single branch of the tree, are also fairly widely separated from the other populations, suggesting that they might be representatives (or relicts) of one or more different western metapopulations. Ramsey Island, at the westernmost extremity of southern Wales, is actually closer to the Irish mainland (78 km) than to the nearest sampled populations of *L. natans* elsewhere in Wales (Llyn Fanod and Llyn Eiddwen, nearly 100 km to the north-west). Among the main group of Welsh populations, the populations from the Montgomery Canal and from Llyn Tegid (Bala Lake) and the Llangollen Feeder Canal form a relatively tight cluster in a central position on the tree, with the central and northern Welsh populations forming a much looser association. There is a surprisingly great genetic distance between the two subpopulations separated by the "Flash" on the Afon Teifi, perhaps as a result of downstream vegetative propagation of *L. natans* in the river current, from different older and effectively ancestral colonies upstream. The centre of genetic diversity of the species shown by the data within Wales lies in the upland pools and lakes around Llyn Teifi, which drain into the Afon Teifi.

Considering the pattern of genetic variability in more detail, there is some evidence of a cline of reducing genetic variability both northwards and westwards from the centre of distribution of the species in central Wales. The outermost populations have lower numbers of variable loci and lower numbers of genotypes than more central populations, although only a single individual could be found in the most northern population (Llyn Cwellyn) so there was no possibility of detecting variation in this population. However, each of the outlying populations in central and south-western

Wales (14–16) was represented by reasonable numbers of samples, and each population consisted of a single genotype, different in each case. At the PGI 1 and MDH loci, maximum variability was found in central Wales.

Because of the probable predominance of clonal reproduction in this species, it was not possible to carry out statistical correlation tests to quantify genetic erosion, but as it is likely that clones can survive for very long periods of time, potentially deleterious effects of genetic erosion would be masked for correspondingly long periods.

DISCUSSION

Our genetic analysis shows that substantial genetic variation exists among Welsh populations of *Luronium natans* as a whole, but within-population variation was usually limited. The lowest within-population variation was found in the very isolated Ramsey population (ten samples) and in the comparatively isolated but extensive Llyn Fanod and Llyn Eiddwen populations (six samples in each case) which each consisted of only a single genotype, different at each site. The greatest genetic variation and within-population diversity were found in Llyn Teifi and its surrounding lakes, which may form a particularly effective metapopulation group (that is, a cluster of sites for a species, all more or less self-contained, but linked genetically over time). Nevertheless, even here the number of genotypes that we found was small, suggesting that clonal reproduction predominates. Several genotypes are also present in the "canal" populations from the much younger (less than 200 years) habitat of the Montgomery and Llangollen Canals. However, these populations, especially the Four Crosses sample, are genetically close to the probably large and ancient Llyn Tegid lake population. As Llyn Tegid (Bala Lake) is connected to the Montgomery Canal via the Afon Dyfrdwy (River Dee) and the Llangollen Feeder Canal, it seems extremely likely that the canal populations, and their genetic variation, have been derived from the Llyn Tegid population, in agreement with the suggestions of Lousley (1970) and Willby & Eaton (1993) that the canal populations of the species in the Welsh Borders and the lowland industrial areas of central and north-western England had originated in upland Wales. Canal traffic and water flow, and the capacity of the species for rapid vegetative extension and multiplication, would have facilitated their subsequent, documented spread along the full extent of the Montgomery and Shropshire Union canal (Briggs 1988), ultimately to more than 125 km from Llyn Tegid, and perhaps also even further afield into the canals of central and north-western England.

The isozyme variability of *Luronium natans* contrasts with the extremely low or nil levels of isozyme polymorphism reported for other taxa in the same family (*Alisma* spp., Triest 1991, Triest & Roelandt 1991, and *Baldellia ranunculoides*, Triest & Vuille 1991) and emphasizes the importance of case studies of individual species and populations in conservation genetics and conservation practice, rather than generalizations and assumptions based on apparently similar situations. In *L. natans* each population or distinct metapopulation is likely to have its own genetic characteristics, and should thus be regarded as a separate unit in any plans for conservation.

The Welsh populations of *Luronium natans* (Figs 6 and 7) are probably one of its chief remaining strongholds within its world range, exhibiting the full spectrum of ecological diversity and, as we have shown, comparatively high levels of genetic variation. Their conservation and survival thus have particular importance. The declining or threatened status of *L. natans* across its world range, and the distribution, ecological status and importance of its native populations in Britain and Ireland, have not been fully appreciated in the past. In Britain, its colonization of abandoned canal systems led to the view that it was increasing (e.g. Rose 1983) and therefore had low conservation priority (Perring & Farrell 1983) although, in reality, expansion into canals probably did little more than to compensate for earlier losses from lowland pools and perhaps rivers. The observations of Briggs (1988), Willby & Eaton (1993) and Trueman *et al.* (1995) indicate that these canal populations are probably rather unstable and potentially transient. In addition to the deleterious effects of competition, eutrophication and succession, Murphy & Eaton's observations (1983) suggest that *L. natans* might in any case be eliminated from most of its existing canal sites if the canals were fully reopened for navigation by pleasure-boats.

This presents something of a dilemma for the Countryside Council for Wales, English Nature and British Waterways, which are the agencies responsible for the conservation of *Luronium natans*,

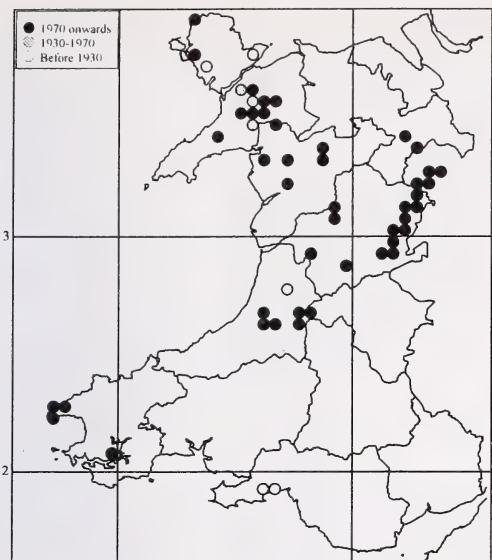


FIGURE 6. The distribution of *Luronium natans* in 5 km squares of the National Grid in Wales and the Welsh Borders. See Table 1 for details of individual populations; several 5 km squares contain more than one population. Map prepared using DMAP.



FIGURE 7. The distribution of sampled populations of *Luronium natans* in 5 km squares of the National Grid in Wales. See Tables 1 and 3 for more details; some 5 km squares contained more than one sampled population. Map prepared using DMAP.

but which also face strong pressure from recreational interests favouring re-opening or increased use of the canals for pleasure-boats. On the one hand, it can be argued that its spread into the canal habitat has reversed range decline for *L. natans* in lowland Britain, and that this habitat may now hold the largest population of the species anywhere in the world. On the other hand, this is a recent, highly artificial, and perhaps intrinsically transient distribution. British Waterways have attempted to conserve *L. natans* in a series of "off-line" canal reserves, and propose restoration of the Gwilsfield Arm of the Montgomery Canal for the same purpose, but site management and population maintenance have presented considerable difficulties (Briggs 1996) and the long-term persistence of *L. natans* in such sites will probably depend largely on an appropriate interventionist management regime.

The results of this study provide a new insight into this problem. They show that, despite the considerable abundance of *Luronium natans* in the Welsh canal system in which it occurs, there is comparatively little genetic difference between plants from different parts of the canal system. Indeed, they could probably all have been raised from a small proportion of the plants in Llyn Tegid and, given appropriate management, this could take place in a relatively short space of time. The whole series of Welsh canal populations could thus be seen as a subpopulation of the plants of one upland lake (Llyn Tegid). If correct, this interpretation indicates that the canal populations are of correspondingly less importance in terms of genetic conservation. The origins of the large population of *L. natans* centred on the canals of Manchester in north-western England, which we did not sample, are less clear, but we suspect that the same basic principles of low genetic diversity will apply, even if this population did not derive from the same source. In contrast, the long-established oligotrophic lake and river populations and metapopulations, and the surviving pond population on Ramsey, have been shown to have distinct genetic identities, markedly different from those in similar habitats elsewhere, and in a few cases even quite sharply different from closely adjacent sites.

Within the main series of native populations in Wales, the highest priority should be given to the conservation of the native populations or metapopulations that show the greatest genetic diversity and of those that are long-established but disjunct. Examples of populations that grow in unusual

TABLE 4. *LURONIUM NATANS* – CONSERVATION STATUS, DATES OF RECORDS AND HABITATS OF ALL KNOWN SITES IN WALES

Vice-county and site name	Grid reference	Status	First record	Latest record	Habitat	Status
ANGLESEY (52)						
Mynachdy Reservoir	SH/31.92		1983	1987	Modified heath pond	Probably extinct
Llyn Dinam	SH/31.77	SSSI	1813	1984	Lowland formerly oligotrophic lake	Probably extinct
Llyn Coron	SH/37.70	SSSI	1813	1895	Lowland formerly oligotrophic lake	Probably extinct
Llyn Bodgylched	SH/58.77	SSSI	1834	1834	Lowland formerly oligotrophic lake	Probably extinct
CAERNARFON (49)						
Llyn Glasfryn	SH/40.42	SSSI	1987	1987	Lowland formerly oligotrophic lake	Probably extinct
Llyn Nantlle	SH/51.53		1834	1992	Upland oligotrophic lake	Extant
<i>Llyn Cwellyn</i>	SH/56.54	SSSI	1895	1994	Upland oligotrophic lake	Extant
Afon Rhythallt	SH/54.63		1895	1967	Upland oligotrophic slow-moving river	Unknown
<i>Llyn-y-Dywarchen</i>	SH/56.53		1895	1994	Upland oligotrophic lake	Extant
Llyn-y-Gadair	SH/56.52		1964	1992	Upland oligotrophic lake	Extant
Llyn Padarn	SH/57.61	SSSI	1848	1997	Upland formerly oligotrophic lake	Extant
Afon y Bala	SH/585.601		1773	1985	Upland oligotrophic slow-moving river	Probably extinct
Llyn Peris	SH/59.59		1805	1905	Upland oligotrophic lake	Probably extinct
Llyn Idwal	SH/64.59	SSSI/NNR	1971	1971	Upland oligotrophic lake	Unknown
Llyn Cwmffynon	SH/64.56	SSSI	1992	1992	Upland oligotrophic lake	Extant
Llyn Llydaw	SH/62.54	SSSI/NNR	1971	1971	Upland oligotrophic lake	Unknown
Afon Glaslyn	SH/59.47	?	1950	1950	Lowland oligotrophic slow-moving river	Unknown
MERIONETH (48)						
Llyn Cwmorthin	SH/67.46		1961	1997	Upland oligotrophic lake	Extant
Llyn Eiddew Bach	SH/64.34	SSSI	1955	1955	Upland oligotrophic lake	Probably extinct
Llyn Cwmbrychan	SH/64.31	SSSI	1921	1997	Upland oligotrophic lake	Extant
Afon Eden	SH/70.30		1960	1997	Upland oligotrophic slow-moving river	Extant
Llyn Cynwch	SH/73.20		1888	1996	Upland oligotrophic lake	Extant
<i>Llyn Tegid</i>	SH/89.31	SSSI	1805	1996	Upland oligotrophic lake	Extant
DENBIGH (50) & FLINT (51)						
<i>Llangollen Canal</i>	SJ/296.397 - SJ/20.43		1862	1994	Lowland mesotrophic slow-moving canal	Extant

1. A 'site' is taken to mean a *continuous, still or slow-moving* water body; thus a canal population extending over 25 km or more is regarded as a single site, whilst two lakes linked by a fast-flowing stream would be listed separately. The names of the sites where one or more populations or subpopulations were sampled (see Table 3) are shown in italics.

2. 'Lowland' and 'upland' sites are defined by their *catchment altitudes*, so that Llyn Padarn at c. 100 m altitude is regarded as an 'upland' lake because of its primarily unenclosed catchment extending above 350m height, whilst Llyn Glasfryn at c. 130 m altitude remains wholly within a 'lowland' catchment.

TABLE 4. CONTINUED

Vice county and site name	Grid reference	Status	First record	Latest record	Habitat	Status
MONTGOMERY (47)						
<i>Montgomery Canal</i>	SO/12.94/- SJ/26.20	SSSI	1933	1997	Lowland mesotrophic slow-moving canal	Extant
Llyn Coch-hwyad	SH/92.11		1993	1997	Upland oligotrophic lake	Extant
Llyn Gwyddior	SH/93.07		1993	1997	Upland oligotrophic lake	Extant
Llyn Bugeilyn	SN/82.92	SSSI	1962	1995	Upland oligotrophic lake	Extant
Llyn Ebyr	SN/97.88	SSSI	1988	1988	Lowland mesotrophic lake	Unknown
CARDIGAN (46)						
Llyn-yr-Oerfa	SN/72.79		1893	1893	Upland oligotrophic lake	Probably extinct
<i>Llyn Eiddwen</i>	SN/60.67	NNR	1893	1994	Upland oligotrophic lake	Extant
<i>Llyn Fanod</i>	SN/60.64	SSSI	1893	1997	Upland oligotrophic lake	Extant
<i>Llyn Teifi</i>	SN/78.67	SSSI	1893	1997	Upland oligotrophic lake	Extant
<i>Llyn Hir</i>	SN/78.67	SSSI	1989	1997	Upland oligotrophic lake	Extant
<i>Llyn Egnant</i>	SN/79.67	SSSI	1893	1996	Upland oligotrophic lake	Extant
<i>Llyn-y-Gorlan</i>	SN/78.66	SSSI	1893	1996	Upland oligotrophic lake	Extant
<i>Llyn Gynon</i>	SN/79.64	SSSI	1893	1994	Upland oligotrophic lake	Extant
<i>Afon Teifi</i>	SN/67.62	SSSI/ NNR	1924	1997	Upland mesotrophic slow-moving river	Extant
RADNOR (43)						
Llyn Cerrig-llwydion isaf	SN/84.69	SSSI	1995	1997	Upland oligotrophic lake	Extant
Llyn Cerrig-llwydion uchaf	SN/84.69	SSSI/ NNR	1997	1997	Upland oligotrophic lake	Extant
GLAMORGAN (41)						
Singleton	SS/62.91		1840	1840	Lowland, site uncertain	Probably extinct
Crymlyn Bog	SS/69.94	SSSI/ NNR	1840	1840	Lowland oligotrophic fen	Probably extinct
PEMBROKE (45)						
Porthmelgan stream	SM/73.28	SSSI	1944	1944	Former heathland pond	Probably extinct
Dowrog Pool	SM/77.27	SSSI	1905	1997	Heathland pool	Extant
Penlan Farm reservoir	SM/74.25		1981	1982	Modified heathland pond	Unknown
<i>Ramsey Ponds</i>	SM/70.23	SSSI	1925	1997	Heathland pond	Extant
Houghton Farm reservoir	SM/98.07		1982	1982	Lowland eutrophic pond	Probably extinct

or particularly threatened habitats (rivers and heathland ponds) should also be conserved where possible. The lake and pool habitats are delicately balanced and face a variety of threats, including eutrophication, acidification by acid rain and run-off from extensive conifer plantations, reservoir construction, pollution and disturbance, especially by powered boats and other recreational uses. At the 48 sites where it has been recorded in Wales (Table 4), *L. natans* is certainly or probably still present (recorded in 1992 or later) in 28, of uncertain present status in six, and believed lost in 14 (five of these losses having taken place since 1980).

By far the most severe decline has been in lowland sites. Ten out of 17 recorded populations (59%) have been lost here, as opposed to only four of the 31 upland populations (11%). The true ratio is likely to be worse, since in lowland sites *Luronium natans* is comparatively easy to detect, and there were certainly more lowland sites for the species in the past, which were not recorded

individually (e.g. Davies 1813), whereas recent searches in upland lakes, where *L. natans* is often hard to detect, have yielded a number of rediscoveries and also some new sites.

The selection of sites and species for conservation has tended to rely on records of range and abundance (measured, all too often, in terms of 10 km square distribution). This study shows not only how changeable these data can be, but also what other levels of significance are being overlooked. In order to conserve the species as a whole we need to consider more than just its overall numbers and where it occurs: we need to see the relationships within and between these data – a population (if not a metapopulation) level of analysis. If, in this sense, the canal sites for *Luronium natans* do not quite have their former priority, they still have considerable ecological significance. One consequence of this study is to show the relationship between an apparently remote and isolated upland locality for the species and a newly-created artificial lowland site. The rapid expansion into the canal system demonstrates the possibility of recovery for this species in the lowlands, and the importance of low-nutrient (now mainly upland) refuge sites. A strategy for the conservation and recovery of *L. natans* needs to integrate maintenance of refugia with the restoration of natural lowland habitat. It is to be hoped that future population management will take account of both processes, within a framework of applied genetic research.

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Variation in the responses of infraspecific variants of wet grassland species to manipulated water levels

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ABSTRACT

The effects of water levels on the germination, growth and reproductive effort of three wet grassland taxa were studied using an experimental water table facility. In addition, effects on related taxa including ecotypes and cultivars were examined. There were significant differences in biomass allocation and reproductive effort between infraspecific variants of *Centaurea nigra* and *Lotus* spp. in response to water table level. Variants had higher root and shoot dry-weights, produced more inflorescences and, in some instances, showed greater seedling establishment in the low water table treatments. In addition, significant differences in seedling establishment between infraspecific variants of both *C. nigra* and *Lotus* spp. were apparent. These findings have implications for the success of grassland re-creation schemes, and the selection of seed for such projects, and suggest that detailed research is needed to provide accurate information regarding the contrasting water table requirements of wetland plants, both at the species and subspecies levels.

KEYWORDS: ecotypes, water regime requirements, wetland restoration.

INTRODUCTION

It is estimated that in the United Kingdom agriculturally improved grassland has increased by 90% in the past 50 years (H.M. Government 1995). Some of this increase has been at the expense of floristically diverse wet grassland communities which, in comparison, are of high conservation value. A possible technique for the re-creation of such habitats uses the sowing of seed to encourage the establishment of desirable plant species and communities (Wells, Cox & Frost 1989; Stockey & Hunt 1994). An objective of the present study was to assess whether commercially available seed is suitable for use in wet grassland re-creation projects.

Purchased seed may vary in its provenance and in the accuracy with which species are identified. In many cases the provenance of commercial seed may mean that it is ill-suited to wetter sites: either as it has been taken from plants growing under much drier conditions (and may therefore exhibit ecotypic variation), or it has been specifically bred, in order to increase vigour and agronomic yield, as a cultivar. Material may be accurately named at the species level, but there may be uncertainty as to the precise subspecies involved. This imprecision may be important where two or more subspecies have significantly different responses to environmental variation. A similar problem may arise where the taxonomy of a group is difficult, e.g. where only specialists are able to distinguish microspecies within a complex. For example, seed supplied as *Taraxacum officinale* may include numerous microspecies, some of which differ in their water table requirements.

Concern has also been expressed about the use of non-native genotypes of wildflower species in habitat restoration, and it has been postulated that genes from these non-native cultivars may dilute the gene pool of the native population (Cairns 1993; Akeroyd 1994). Non-native cultivars have often been specifically bred for rapid growth (Bullard & Crawford 1995), and may effectively out-compete and eliminate their native counterparts. If the restoration of wet grassland ecosystems is to be reliable and successful in the longer term, it is important to test the response of native and non-native genotypes to differing water regimes.

The experiment described within the present paper set out to examine the effects of water levels on the germination, growth and reproductive effort of native material of three species. These effects were compared with the observed responses to the same treatments of infraspecific variants of these species including cultivars, "ecotypes" and subspecies. The experiment was conducted using

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an experimental water table facility at the Institute of Terrestrial Ecology (ITE) Monks Wood, where allied experiments on a range of native flood meadow species (Walker *et al.* 1997) have been conducted as part of a wetlands research programme.

MATERIALS AND METHODS

SELECTION OF SPECIES

The selection of species was based on their occurrence within lowland wet grassland communities, and in particular their importance as constituents of seed mixtures prescribed for the restoration of such communities. Commercial seed of native provenance of *Lotus corniculatus* (Common Bird's-foot-trefoil), *Rhinanthus minor* (Yellow-rattle) and *Centaurea nigra* (Common Knapweed) were sown. Their performance was compared with hand-collected seed from native populations, a forage variety (commonly used as a fodder crop) and seed of closely related species more frequently associated with wet conditions. The variants selected are listed below, with their provenance and abbreviated codes used to annotate text, tables and figures:

1. *Lotus corniculatus* "commercial" (Lcc) – commercially available seed of English provenance;
2. *Lotus corniculatus* "forage" (Lcf) – commercial forage variety, unknown provenance;
3. *Lotus pedunculatus* (Lp) – seed hand collected from populations in Dorset;
4. *Rhinanthus minor* "commercial" (Rmc) – commercial seed, possibly of ssp. *minor*, which is more associated with drier, often calcareous, soils;
5. *Rhinanthus minor* ssp. *stenophyllus* (Rmw) – seed hand-collected from populations at Wicken Fen National Nature Reserve (NNR) in Cambridgeshire;
6. *Centaurea nigra* "commercial" (Cnc) – commercially available seed of English provenance;
7. *Centaurea nigra* "Wicken" (Cnw) – seed hand collected from Wicken Fen National Nature Reserve.

The seeds utilised in the study were less than a year old and placed in cold storage at 4°C prior to use.

EXPERIMENTAL DESIGN

The seeds were sown within circular plastic pots, 21 cm deep × 17 cm diameter, filled with approximately eight litres of soil-based compost. The soil had a silty-loam texture, broadly representative in physical characteristics of soils typically found on lowland alluvial grasslands, and was heat sterilised prior to use in order to reduce the number of weed species and pathogens present.

Each pot contained 10 seeds and was labelled to identify the species and seed source. Four replicate pots of each taxon were then placed within large fibreglass tanks, situated outdoors on a gravel bed, in which water levels could be maintained at a constant level. Sixteen fibreglass tanks were used in the study. The four treatments (water table levels) were as follows:

T0 – tanks with the water table at the same height as the soil surface within the pots

T50 – tanks with water table 50 mm below the soil surface within the pots

T100 – tanks with the water table 100 mm below the soil surface within the pots

T150 – tanks with the water table 150 mm below the soil surface within the pots

The four water level treatments were replicated within four blocks. Therefore, 16 pots per seed source were placed at each water level. The placement of pots within tanks, and tanks within blocks, was fully randomised in order to eliminate bias.

Evaporation losses and algal growth were reduced by placing white polypropylene granules on the surface of the water within the tanks.

MONITORING

GERMINATION AND SEEDLING DEMOGRAPHY

The numbers of seedlings in each pot were recorded every seven days from initial sowing in early December 1995 until the end of May 1996. Due to the large number of seedlings present (>5000) it was impractical to follow the fate of individual seedlings. Consequently successive cohorts of individuals were recorded within each pot. On four occasions germination could not be recorded when severe weather resulted in snow and ice covering the soil surface.

BIOMASS ALLOCATION

After approximately six months the seedlings were thinned to a single individual in each pot in order that plants could be grown on for destructive sampling without root competition. These individuals were then left to grow until October 1996, when they were harvested. After being oven dried at 80°C for 24 hours, both root and shoot dry-weights were obtained. It was not possible to obtain dry-weights for either of the *R. minor* variants as there were no surviving seedlings in October 1996.

REPRODUCTIVE EFFORT

At the final harvest the number of inflorescences present was also recorded. For the purposes of recording, the term "inflorescence" was taken to mean the capitulum in *C. nigra* and the cymose heads of the *Lotus* species. All species had seeded by the time of harvesting. Owing to seedling mortalities, it was not possible to gather inflorescence data for the *R. minor* variants.

STATISTICAL ANALYSIS

The preliminary statistical analysis, which was based on tank mean values, involved an examination of the effects of water table on the germination and survival of seeds of individual taxa (species and infraspecific variants). The effects of water table were broken down into constituent linear and quadratic components. It was considered important to make a preliminary analysis of how each taxon was responding to treatments, prior to "ecotypic" comparisons being made between infraspecific taxa of the same species.

For each taxon, the cumulative gains (i.e. germination) and losses (i.e. mortality) of seedlings within each of the four treatments were calculated for four different time periods; i) 49 days, ii) 98 days, iii) 154 days, and iv) 228 days after seed sowing. Over the four periods, a calculation was made of the mean number of seedling gains and losses per treatment for each taxon. Further analysis, using ANOVA, was carried out to examine whether individual taxa were exhibiting a significant response to treatment.

The second stage in the statistical analysis involved an examination of whether closely allied taxa showed any marked differences in their response to the four water level treatments. Using data for the cumulative gains and losses of seedlings, (49, 98, 154 and 228 days after the seeds were sown), species were analysed simultaneously using split-plot ANOVA. Comparisons of the germination and survival of seedlings were made between the following taxa: Cnc and Cnw; Lcc, Lcf and Lp; and Rmc and Rmw.

Further analysis of the variation in the responses of the infraspecific variants to water table depth was carried out using data on the establishment of seedlings, i.e. cumulative seedling germination minus cumulative seedling mortality. Possible differences in the establishment of taxa in the different treatments were examined using ANOVA.

By October 1996, the time of the final harvest, many of the seedlings had died and consequently it was not appropriate to analyse the root, shoot and inflorescence data using ANOVA. An alternative, and more conservative method used regression of the four water table means, weighted by the number of valid observations contributing to those means. The results were shown as an estimate of the slope of the variable on water table (\pm standard error) and an indication of significance.

TABLE 1. SIGNIFICANCE OF THE LINEAR EFFECT OF WATER TABLE DEPTH ON THE GERMINATION, MORTALITY AND ESTABLISHMENT OF RMC, RMW, CNC, CNW, LCC, LCF AND LP SEEDLINGS OVER A 228 DAY PERIOD.

Species	Seedling Germination				Seedling Mortality				Seedling Establishment
	(Days after seeds were sown)				(Days after seeds were sown)				
	49	98	154	228	49	98	154	228	228
Cnc	ns	ns	-	-	ns	ns	ns	ns	-
Cnw	ns	ns	ns	ns	ns	ns	ns	ns	--
Lcf	ns	ns	ns	ns	ns	ns	ns	ns	-
Lcc	ns	ns	ns	ns		ns	ns	+	-
Lp	ns	ns	(-)	(-)	ns	ns	++	++	---
Rmc	ns	ns	++	+	ns	ns	+	+++	ns
Rmw	ns	ns	ns	ns	ns	ns	ns	++	ns

Significantly higher rates of seedling germination, mortality and establishment in the highest water table levels are shown by: (+) = $p < 0.10$; + = $p < 0.05$; ++ = $p < 0.01$; +++ = $p < 0.001$. Significantly higher rates of seedling germination, mortality and establishment in the lowest water table levels are shown by: (-) = $p < 0.10$; - = $p < 0.05$; -- = $p < 0.01$; --- = $p < 0.001$. (ns = not significant).

RESULTS

EFFECTS OF WATER TABLE LEVELS UPON SEED GERMINATION, MORTALITY AND ESTABLISHMENT

Table 1 shows the significance of the linear effects of water table depth on the germination, mortality and establishment of Rmc, Rmw, Cnc, Cnw, Lcc, Lcf and Lp over a 228 day period.

Rhinanthus minor Wicken (Rmw) and *Rhinanthus minor* commercial (Rmc)

Seed of both taxa appeared to germinate more readily in the higher water table tanks. Germination was greatest 98–140 days after the seeds had been sown, after which time the rate of seedling mortality began to exceed germination, and hence net establishment of seedlings declined. After 228 days seedling establishment (Rmw and Rmc) had fallen to virtually zero in all four treatments.

Cumulative germination of Rmc was found to be significantly larger in the higher water table treatments at two intervals: 154 days ($p = 0.006$) and 228 days ($p = 0.010$) after sowing. Cumulative germination of Rmw was not found to vary significantly between treatments.

Cumulative seedling mortality after 228 days was, for both variants, significantly greater in the higher water table treatments. This offset the greater rate of germination in these tanks and consequently the overall establishment of Rmc and Rmw was not found to vary significantly between the different treatments.

When comparing cumulative germination and cumulative seedling mortality, a marginally significant difference ($p = 0.096$) between the response of the two *Rhinanthus* taxa was noted 98 days after the seeds were sown. The germination of Rmc seed was found to be slightly greater than that of seed collected from Wicken Fen. This result may be explained by the negligible germination of Rmw seeds in the first fourteen weeks after sowing. In the final two recording periods, in which germination of both Rmc and Rmw increased, the difference in the cumulative germination of commercial and Wicken material was not found to be significant.

Centaurea nigra commercial (Cnc) and *Centaurea nigra* Wicken (Cnw)

In contrast to the two *R. minor* variants, the seeds of Cnc and Cnw were found to have higher cumulative germination levels in the lower water table treatments. This higher germination in the lower water table tanks was found to be significant for Cnc but not the Wicken variant. Cumulative germination and mortality of Cnc, in all four treatments, is shown in Figure 1.

The final establishment of seedlings (i.e. cumulative germination minus cumulative mortality

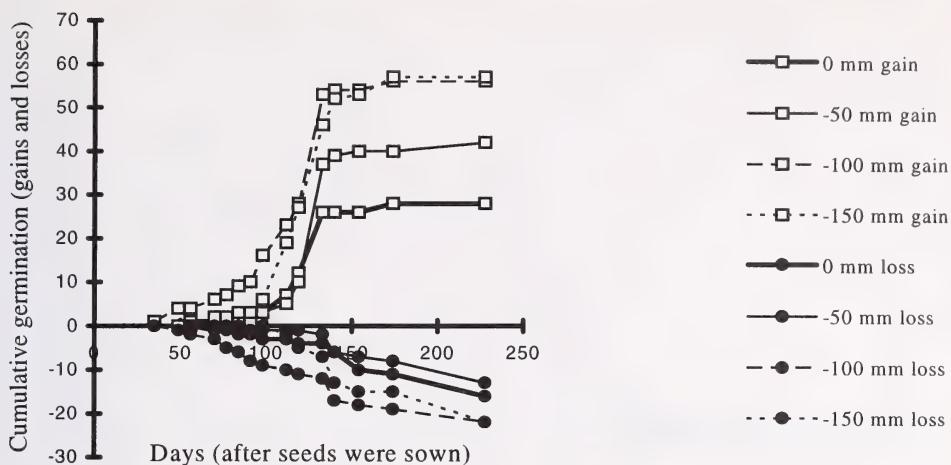


FIGURE 1. Cumulative germination and mortality of *Centaurea nigra* commercial seedlings at four water table levels over a 228 day period. 0 mm = water table at soil surface level, -150 mm = water table 150 mm below soil surface.

after 228 days) was significantly higher in the low water table treatments for both Cnc and Cnw (Fig. 2). However, a highly significant difference ($p = < 0.001$) was observed between the final establishment of Cnc and Cnw with a greater establishment of Wicken seedlings in three of the four treatments (Fig. 2).

Lotus corniculatus commercial (Lcc), *Lotus corniculatus* forage (Lcf) and *Lotus pedunculatus* (Lp) Over the 228 day recording period, the establishment of Lcc and Lcf seedlings was erratic due to variable rates of seedling germination and mortality. Both seed types had higher germination and establishment rates in the lower water table treatments, but this was not significant at the $p < 0.05$ level. Cumulative germination in all four treatments was considerably higher from seed of Lcc than from Lcf. The higher rate of Lcc germination was to some extent offset by seedling mortalities, which were higher than those experienced by Lcf. Net establishment of Lcf seedlings was, nevertheless, lower than that of Lcc in all four treatments.

As found with Lcc and Lcf, there was a tendency for higher germination rates of *L. pedunculatus* in the lower water table treatments. This, combined with greater seedling mortality in T0 (the high water table tanks), led to a significantly higher establishment of Lp in the low water table tanks ($p = < 0.001$).

Highly significant differences ($p = < 0.001$) in the final establishment of Lcc, Lcf and Lcp were observed 228 days after the seeds were sown. The final establishment of Lp was considerably higher than that of Lcf in all treatments, and also greater than that of Lcc in treatments T100 and T150 (Fig. 3).

EFFECTS OF WATER TABLE LEVELS UPON PLANT GROWTH AND REPRODUCTIVE EFFORT

Tables 2 and 3 show the mean root and shoot dry weights, and mean number of inflorescences for variants of *C. nigra* and *Lotus* spp. at the four different water table levels studied.

Centaurea nigra commercial (Cnc) and *Centaurea nigra* Wicken (Cnw)

Mean root dry-weights of both *C. nigra* variants were significantly higher in the lower water table treatments. In the highest water table treatments, both variants had a mean root dry-weight of approximately 3 g, compared to mean root dry-weight in the lowest water table treatment of c. 56 g for Cnw and c. 64 g for Cnc. Cnw had slightly higher mean root dry-weights than Cnc in T0, T50 and T100.

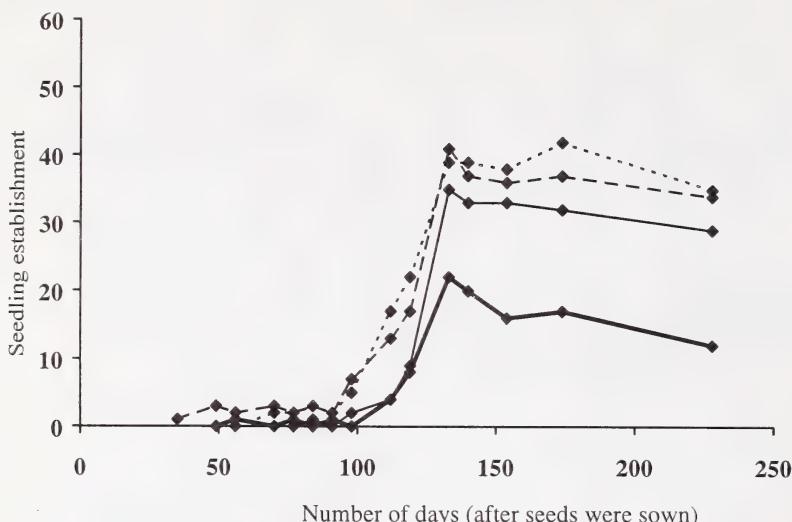
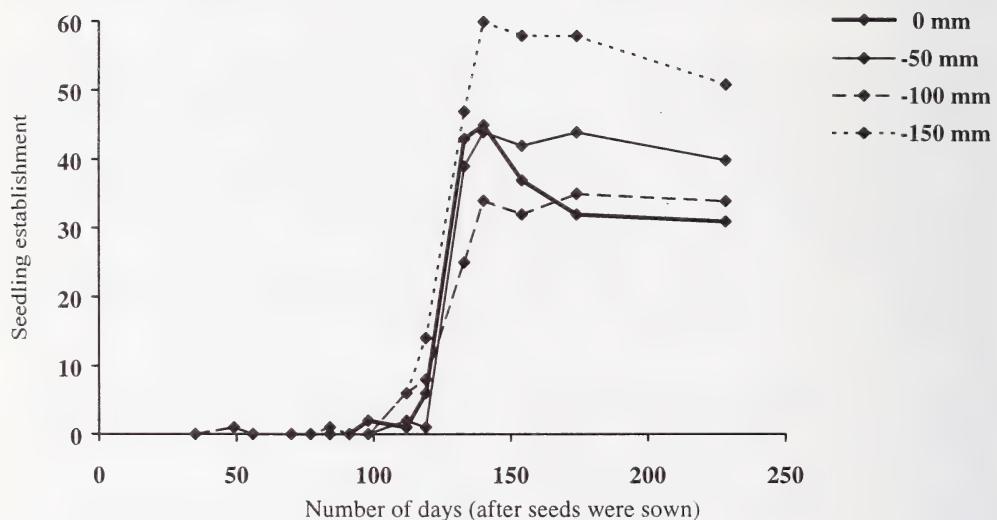
Centaurea nigra A*Centaurea nigra* B

FIGURE 2. Comparison of the establishment (germination minus mortality) of seedlings of *Centaurea nigra* commercial (A) and *Centaurea nigra* Wicken (B) at four water table levels over a 228 day period.

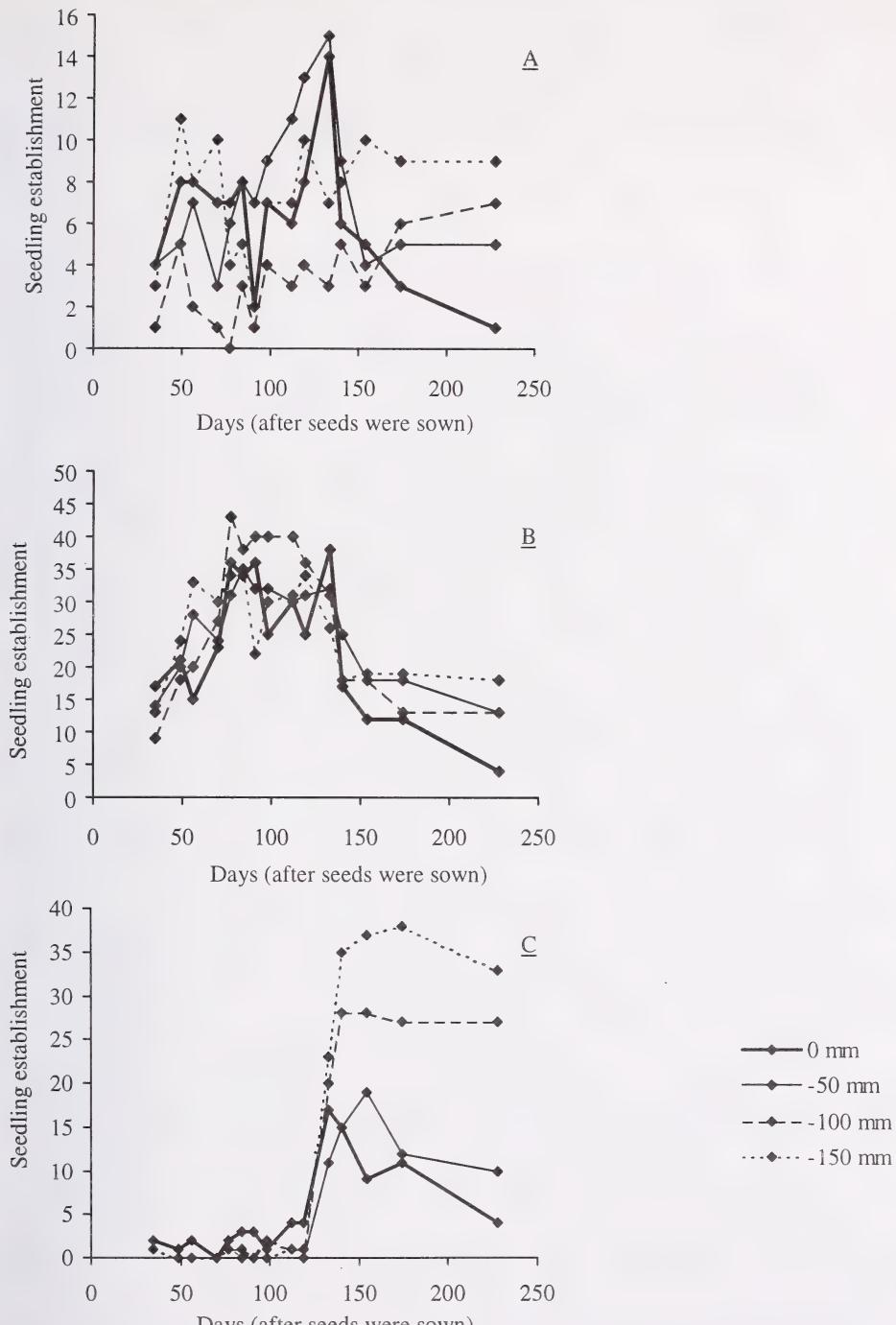


FIGURE 3. Comparison of the establishment (germination minus mortality) of seedlings of *Lotus corniculatus* forage (A), *Lotus corniculatus* commercial (B) and *Lotus pedunculatus* (C) at four water table levels over a 228 day period (note variations in scale).

TABLE 2. MEAN ROOT AND SHOOT DRY WEIGHTS, AND MEAN NUMBER OF INFLORESCENCES OF *CENTAUREA NIGRA* WICKEN (Cnw) AND *CENTAUREA NIGRA* COMMERCIAL (Cnc) SEEDLINGS AT FOUR DIFFERENT WATER LEVEL TREATMENTS (0, 50, 100 AND 150 MM BELOW THE SOIL SURFACE).

Treatment	Mean root dry weights (g)		Mean shoot dry weights (g)		Mean no. of inflorescences	
	Cnc	Cnw	Cnc	Cnw	Cnc	Cnw
T0	3.07	3.58	2.00	2.62	0.00	0.00
T50	4.98	7.21	3.53	3.80	0.33	0.37
T100	31.08	36.15	11.51	10.54	3.94	3.20
T150	64.29	56.48	15.49	13.54	6.71	5.00

TABLE 3. MEAN ROOT AND SHOOT DRY WEIGHTS, AND MEAN NUMBER OF INFLORESCENCES OF *LOTUS CORNICULATUS* FORAGE (Lcf), *LOTUS CORNICULATUS* COMMERCIAL (Lcc) AND *LOTUS PEDUNCULATUS* (Lp) AT FOUR DIFFERENT WATER LEVELS (0, 50, 100 AND 150 MM BELOW THE SOIL SURFACE).

Treatment	Mean root dry weights (g)			Mean shoot dry weights (g)			Mean no. of inflorescences		
	Lcf	Lcc	Lp	Lcf	Lcc	Lp	Lcf	Lcc	Lp
T0	0.00	1.19	0.65	0.00	1.83	0.70	0.00	14.00	0.00
T50	12.56	1.01	2.47	5.43	1.50	4.44	114.00	37.25	18.33
T100	26.76	7.42	14.87	9.32	6.77	12.85	76.33	63.50	29.44
T150	46.40	28.95	21.77	21.00	21.14	18.16	333.86	142.08	56.19

A similar trend was observed for mean shoot dry-weights, with marginally higher dry-weights from Wicken material in T0 and T50, and higher dry-weights of Cnc in T100 and T150. Again, both *C. nigra* variants had significantly higher shoot dry-weights in the lower water table treatments (Cnc p = 0.028, Cnw p = 0.034).

Neither Cnc nor Cnw flowered in the highest water table tanks. The mean number of inflorescences, of both variants, was significantly higher in the lowest water table tanks (Cnc p = 0.029, Cnw p = 0.032).

Lotus corniculatus commercial, *Lotus corniculatus* forage and *Lotus pedunculatus*

Mean root dry-weights of the three *Lotus* taxa were significantly higher in the lower water table treatments. The highest mean root dry-weight recorded was 46.40g for Lcf forage in T150. Mean shoot dry weights also increased significantly as water table level decreased, with this trend being particularly notable for Lp (p = 0.008).

Like the *C. nigra* variants, Lcc and Lp plants produced significantly more inflorescences in the lower water table treatments. Although not found to be significant, the number of Lcf inflorescences was also markedly higher in the lowest water table tanks than in the other three treatments. Indeed, in T150 Lcf produced substantially more inflorescences than the other two *Lotus* strains. Only Lcc flowered in T0, the highest water table treatment.

DISCUSSION

The effects of water stress upon plant physiology and germination have been well documented (e.g. Evans & Etherington 1990; Jackson 1990; Crawford 1996; Olsson *et al.* 1996). A rise in water levels can deprive plants of oxygen, may affect the production and transport of plant hormones and can increase the likelihood of microbial attack (Crawford 1996). Some species have developed adaptations, both morphological and physiological, to help them cope with water table changes (e.g. Voesenek, Blom & Pouwels 1989).

If a plant becomes adapted to suit the specific environmental conditions of its habitat, such that its requirements become markedly different from those of other populations within the same species, ecotypic differentiation has occurred. The ability to select plants that are suited to environmental stresses, such as flooding, drought or even soil contamination, has led to the creation of new plant and crop varieties through plant breeding (e.g. Elias & Chadwick 1979; Yaseen & Al-Omary 1994) and also has large potential for providing guidance when selecting natural species for habitat restoration schemes. For instance, as *L. corniculatus* is a highly variable species (Jones & Turkington 1986) it would seem appropriate to sow the seed of a wetland "ecotype" in sites with higher water table regimes.

RHINANTHUS spp.

Ter Borg (1985) studied the population biology of a number of hemi-parasitic Scrophulariaceae, and noted that *Rhinanthus* species often exhibit a wide infraspecific variation. *R. angustifolius*, for example, is thought to have at least eight different subspecies (Oberdorfer 1979). Taxonomic difficulties in *Rhinanthus* have contributed to the concept of seasonal dimorphism whereby species such as *R. minor* have been sub-divided into two taxa; aestival and autumnal, based upon the time of flowering and certain morphological characteristics. In some species of *Rhinanthus*, Soó (1970) has identified not only autumnal and aestival variants, but also montane, alpine and segetal variants (Karlsson 1974). Seasonal dimorphism, as a means of explaining variation in Rhinantheae, is now seen as an oversimplification with some of the apparent differences having been shown to have a genetic basis (Ter Borg 1985). Ecotypic variation may also have been overlooked when attempting to explain the apparent variations in the genus (Karlsson 1974). Grime, Hodgson & Hunt (1988) quote *R. minor* var. *stenophyllus* and *R. minor* var. *minor* as the two commonest *R. minor* ecotypes. *R. minor* var. *minor* is thought to prefer drier sites in southern England with *R. minor* var. *stenophyllus* being more suited to moist grasslands, particularly in the north.

In this study, *R. minor* appeared to germinate more readily in the higher water table tanks, though this trend was only statistically significant for the Rmc (after 154 and 228 days) and not Rmw. Owing to high rates of seedling mortality, no significant differences in the final establishment of Rmc or Rmw could be demonstrated. It is recommended that, for future research, sufficient numbers of plants are established to ensure full representation at each water table depth.

CENTAUREA NIGRA

The findings for *C. nigra* were both fuller and more interesting. Seed of both *Centaurea* variants had higher rates of germination in the lower water table treatments. However, unlike Cnw, the germination of commercial *C. nigra* seed was significantly higher in the low water table tanks, suggesting that germination of Wicken seed may be less dependent upon water table than seed which is commercially available. This supposition is supported by the seedling establishment data, which showed the final establishment of Wicken seedlings to be significantly greater than the establishment of commercial seedlings ($p<0.001$). These results imply that Cnw seeds are not only more suited to wetter sites than commercial seed, but also to drier sites as well. The germination of seed originating from Wicken Fen was not significantly affected across the range of water tables studied. Therefore, seed collected from Wicken Fen and similar sites may, in terms of germination and establishment, be more suited for use in wet grassland and other restoration schemes than seed which is commercially available at present.

Both *C. nigra* variants had significantly higher root and shoot dry-weights and number of inflorescences in the low water table tanks. In the T150 tanks, the commercial plants had slightly higher dry-weights, and produced more inflorescences, than the Wicken plants.

C. nigra is, according to Grime *et al.* (1988), a complex group in need of further taxonomic and ecological study. Although botanists have often identified the subspecies *nigra* and *nemoralis*, the distinction between the two is no longer believed to be consistent (Stace 1991). It is likely that the wide distribution of *C. nigra* is, in part, linked to its considerable genetic variation (Grime *et al.* 1988).

LOTUS spp.

Seed of the two *L. corniculatus* variants showed lower germination rates in the high water table tanks with significantly higher overall establishment of seedlings in the low water table treatments. These results contrast with the findings of Baker (1988), where waterlogging had no effect on the

germination of either *L. corniculatus* or *L. pedunculatus*. In the present study, the effect of water table on the establishment of *L. pedunculatus* seedlings was found to be highly significant ($p<0.001$), with highest establishment in the low water table treatments. This observation makes interesting comparison with the usually observed habitat preference for *Lotus* spp. where *L. corniculatus* is thought to be extremely tolerant of water deficit (Grime *et al.* 1988; Bullard & Crawford 1996) whilst *L. pedunculatus* tends to grow in damp areas with a higher water table. Nevertheless, the findings do support the hypothesis of Blumenthal, Aston & Pearson (1996) that "variation exists within *Lotus* species for ability to germinate over a range of moisture potentials", implying that the establishment of *Lotus* spp. in wet grassland restoration schemes may be markedly influenced by water table levels.

Highly significant differences between the establishment of the three *Lotus* taxa were revealed. The establishment of Lcf was lower than that of the Lcc and Lp in all four treatments. In the two lowest water table treatments, *L. pedunculatus* also had markedly higher seedling establishment than *L. corniculatus* commercial. These results suggest that, in terms of seedling establishment, seed of Lcf would be less reliable for restoration purposes than Lcc and Lp seed. Sites with relatively low water tables might also benefit if *L. pedunculatus* seed were sown, as it was found to establish better than the commercial seed in treatments T100 and T150.

The biomass data underlined the germination and seedling establishment findings, with all three *Lotus* species performing significantly better (with higher dry-weights) at the lower water table levels. Unsurprisingly, the mean root and shoot dry-weights of the forage variety were markedly higher than those of Lcc and Lp. When examining inflorescence data at the lowest water table treatment, Lcf produced almost six times as many inflorescences as Lp and twice as many inflorescences as Lcc. This highlights the need to consider a range of factors, and not just seedling germination and establishment, when making decisions on the suitability of seed for use within restoration mixtures. Introducing forage and commercial cultivars, which may grow quickly and produce many inflorescences, could put less vigorous native species at a competitive disadvantage.

Grant & Small (1996) have carried out a detailed examination of the ancestry of the *L. corniculatus* complex in which evidence regarding the geography, genetics, chemistry and morphology of the genus was reviewed. On the basis of this they have suggested that *L. corniculatus* may have arisen from a hybrid of *L. glaber* and *L. pedunculatus*. If *L. pedunculatus* is a direct parent of *L. corniculatus* this might partly account for the ability of *L. corniculatus* to germinate and establish in both damp and dry conditions. Following an examination of the response of 91 species to flooding, Justin & Armstrong (1987) classified *L. corniculatus* as a plant of intermediate habitats. Prior to this research, they had assumed it to be a species indicative of non-wetland environments. Such findings further underline the potential variability within this genus, which makes defining the precise water table requirements of any available strain of *L. corniculatus* difficult for restoration purposes. As the present study was based upon seed obtained from a small number of sources, only a small fraction of the genetic variation present within *Lotus* may have been examined.

The present study has shown that the germination and establishment of seeds and seedlings, both between and within species, can vary significantly depending on the source of the seed. Seed collected from "ecotypes", adapted to specific environmental conditions, may have significantly different hydrological requirements to those of seed collected from other populations. A recognition and understanding of the differing autecology of ecotypes, and other closely related species and varieties, is essential if wetland restoration schemes are to achieve their full potential. Seed obtained from commercial sources may, as demonstrated in the present study, perform poorly in comparison to seed obtained from other known populations. In addition, one is often uncertain as to the age of commercially supplied seed and the conditions in which it has been stored. A lack of accurate information regarding the identification (usually at the subspecies level) and precise origin of commercial seed is a further problem.

Further research is required to investigate the effects of different water table regimes on both intra- and inter-specific competition between a range of ecotypes and cultivars of common wild flower species. Such interactions may exert considerable influence on the outcome of secondary succession following the sowing of seed mixtures containing such ecotypes and cultivars. It is likely that competitive interactions will be significantly accentuated under higher water table conditions. Using an experimental water table facility, the effects of water levels on the

germination and survival of 23 wet grassland species have been studied (Walker *et al.* 1997). The first species to germinate were productive grasses, which suppressed the establishment of a number of herb species. This suggests that attempts to re-create wet grassland using seed may not always lead to the establishment of those species which germinate late and are subsequently out-competed. In such circumstances, plug plants may be a more effective means of introducing desirable species (Walker *et al.* 1997).

Crawford (1996) has reiterated the need for a holistic approach when studying how plants react to water table fluctuations. Plants may vary in their response to water stress at different stages in their life cycle (Evans & Etherington, 1990; Yaseen & Al-Omary 1994; Ollson *et al.*, 1996) and have to adapt to changing water levels whilst being in competition with other species (Walker *et al.* 1997). The present study was conducted under stable, non-competitive conditions and, as noted by White (1985), "there is doubt about the usefulness of studying the population dynamics of natural plant populations in isolation from their phytosociological environment".

CONCLUSIONS

It is estimated that between 1930 and 1984 semi-natural lowland grassland decreased by 97% in England and Wales (Fuller 1987; H.M. Government 1995). Re-creation of such communities and habitats needs to be underpinned by a scientific understanding of wetland species and ecosystems. This preliminary experiment has demonstrated that the autecological requirements of closely allied taxa and infraspecific variants should not be overlooked. The biomass and reproductive effort of variants of *Centaurea nigra* and *Lotus* spp. were found to be significantly affected by water table depth. Variants had higher root and shoot dry-weights, produced more inflorescences and, in some instances, showed greater seedling establishment in the low water table treatments. In addition, significant differences in seedling establishment between infraspecific variants of both *C. nigra* and *Lotus* spp. were apparent. It is probable that such differences also exist between "ecotypes" of other species and research is needed to further our understanding of the water table requirements of the main constituent species and subspecies of wet grassland vegetation (Mountford & Chapman 1993). Habitat re-creation will become more successful if species' requirements are matched to site conditions. At present, the suitability of commercially available seed for wet grassland re-creation schemes is largely unknown and requires further investigation.

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The distribution and habitat of *Potamogeton × suecicus* K. Richt. (*P. filiformis* Pers. × *P. pectinatus* L.) in the British Isles

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ABSTRACT

Recent studies of *Potamogeton × suecicus* K. Richt. (*P. filiformis* × *P. pectinatus*, Potamogetonaceae) have shown that the hybrid can be identified by morphological criteria and by isozyme analysis. The latter suggests that all plants studied are F₁ hybrids and does not provide any evidence for backcrossing to the parents. The hybrid is widespread in Britain in the area where both parents occur and also occurs in two rivers south of the current distribution of *P. filiformis*. In recent years it has been discovered at widely scattered localities in Ireland. The localities from which *P. × suecicus* has been recorded are listed, with records confirmed by isozyme analysis distinguished. In some rivers, streams and lakes it is the dominant macrophyte, growing in large, almost pure stands, whereas in other localities it is found as scattered plants in more open communities. The vegetation at the British sites is summarised from the results of 40 quadrats recorded at 21 sites. Sites where the hybrid may grow in the absence of one or even both parents are identified; they include rivers and shallow coastal lakes over sand. The history of the hybrid in Britain suggests that it is very easily over-looked; almost all records have been made in two periods (1940–1950, 1986–1998) when observers familiar with the plants were active on fieldwork. It is almost certainly still under-recorded in Scotland and Ireland.

KEYWORDS: Aquatic vegetation, hybridisation, isozyme analysis, orphaned hybrids.

INTRODUCTION

The detailed studies of the genus *Potamogeton* which J. E. Dandy and G. Taylor carried out between 1936 and 1976 did much to clarify the taxonomy and distribution of the British and Irish species and their hybrids. Indeed, it might be argued that Dandy & Taylor accomplished almost as much as one could hope to achieve using the traditional methods of herbarium taxonomy, leaving to their successors only the publication of a detailed account of the British and Irish taxa (which Dandy & Taylor never completed) and the tying up of the loose ends which are inevitably left at the end of any botanical career. However, the ever-increasing range of molecular techniques which have become available to plant taxonomists since the 1960s have allowed many aspects of the subject to advance beyond the restrictions hitherto imposed by traditional methods. This paper arises from a study of the distribution and ecology of the widespread and taxonomically difficult hybrid *Potamogeton × suecicus* which has combined traditional field and herbarium studies with the now well-established techniques of isozyme analysis.

Potamogeton × suecicus K. Richt. is the hybrid between the two species of *Potamogeton*

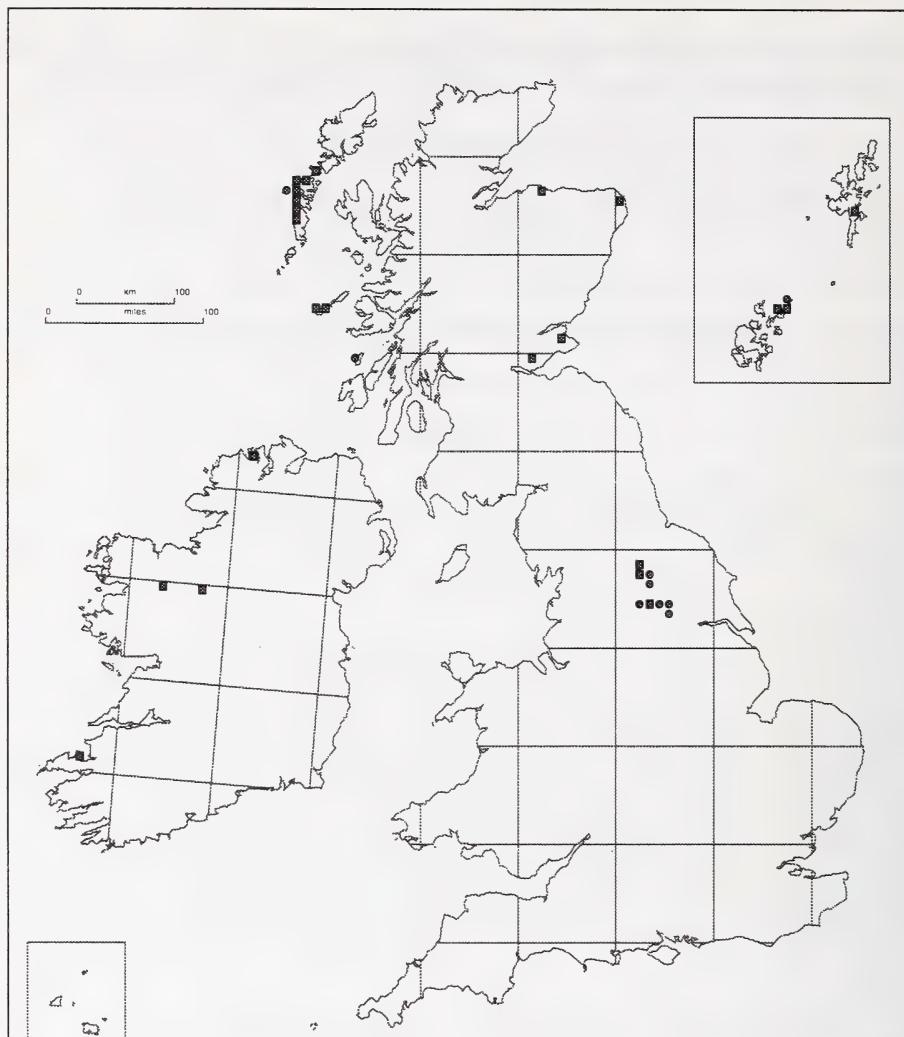


FIGURE 1. The distribution of *Potamogeton* × *suecicus* in the British Isles. Squares indicate 10-km grid squares where the hybrid has been seen from 1990 onwards; circles indicate squares where it was last seen before 1990.

Subgenus *Coleogeton* which occur in the British Isles, *P. filiformis* Pers. and *P. pectinatus* L. In general appearance it is closer to *P. pectinatus* than to *P. filiformis* but unlike *P. pectinatus* at least some of the leaf sheaths are tubular at the base. The stigmas may be borne on a distinct style (as in *P. pectinatus*) or be sessile (as in *P. filiformis*). Plants of *P. × suecicus* may flower freely from May to October but their pollen is sterile and they do not set fruit. Certain identification of the hybrid is not possible in the field, but under the binocular microscope the hybrid can be identified with some confidence using morphological characters alone. All three taxa are described and illustrated in Preston (1995) and an updated key, modified to take account of the presence of the similar hybrid *P. × bottnicus* Hagstr. in Britain, is provided by Preston *et al.* (1998).

The presence of *Potamogeton* × *suecicus* in the British Isles was first established by Dandy & Taylor (1940). They showed that earlier records of *P. × suecicus* in Britain were erroneous, but they

recognised the hybrid from a few herbarium specimens collected in Scotland in the 19th and early 20th centuries and from collections made in the Outer Hebrides by J. W. Campbell, W. A. Clark and A. J. Wilmott in 1938 and 1939. Further details of the Hebridean records, and additional records from the Hebrides and elsewhere, were published by Dandy & Taylor (1941, 1946), Clark (1943), Clark & Heslop Harrison (1940), Heslop Harrison (1941, 1949), Heslop Harrison & Clark (1941, 1942), Heslop Harrison & Heslop Harrison (1950) and Heslop Harrison *et al.* (1941, 1942). By 1950 *P. × suecicus* had been recorded in eight vice-counties, two (v.cc. 93 and 102) on the basis of old herbarium specimens and the rest (v.cc. 64, 65, 68, 81, 103 and 110) solely or in part on the basis of plants collected since 1940. Dandy & Taylor's (1946) records from the River Wharfe and River Ure in Yorkshire were supported by the anatomical studies of Bance (1946) and were especially significant. These rivers lie south of the known distribution of the rarer parent, *P. filiformis*, although subfossil fruits of *P. filiformis* have been found in Late Glacial deposits in southern England (Godwin 1975) and the species persisted in Anglesey until 1826 (Preston 1990).

Although many records of *P. × suecicus* were published between 1940 and 1950, there were very few additional discoveries during the next 35 years. The sites in the English rivers were often visited, and N. T. H. Holmes extended the distribution of the plant from the River Tweed into its tributary, the River Till (Holmes & Whitton 1975a, b). In Scotland M. McCallum Webster (1978) discovered the hybrid in Moray (v.c. 95) and U. K. Duncan (1969) rediscovered it at one of Heslop Harrison's localities on Tiree (v.c. 103). The hybrid was mapped by Perring & Sell (1968) and covered by Dandy's (1975) account of British and Irish *Potamogeton* hybrids.

Since 1985 there has been renewed interest in *P. × suecicus*. In 1986 C.D.P. began preparatory fieldwork for the B.S.B.I. handbook *Pondweeds of Great Britain and Ireland* (Preston 1995), and with N. F. Stewart refound *P. × suecicus* at several of the sites from which it had previously been recorded. In 1991 P.M.H. & R.J.G. began a detailed study of *P. × suecicus* and its parents, using isozyme analysis, in collaboration with C.D.P. (Hollingsworth *et al.* 1996a, b). As a direct or indirect result of this activity the hybrid has been rediscovered at most of its old localities, and several new sites discovered. These have included the first records from three vice-counties in Scotland, and the first records from Ireland. This paper draws together the recent records of the hybrid, documents the populations which have been identified on the basis of isozyme as well as morphological evidence, and describes the habitat of the hybrid in the British Isles.

Although recent work has confirmed the identity of many populations of *P. × suecicus*, it has also indicated that the material from the River Till and River Tweed differs in both morphological and isozyme characters from the other plants studied, and is apparently referable to the hybrid between *P. pectinatus* and *P. vaginatus* Turcz. (*P. × bottnicus* Hagstr.). As we have recently published a detailed account of these populations (Preston *et al.* 1998) they are not considered further in this paper.

DISTRIBUTION OF *P. × SUECICUS* IN THE BRITISH ISLES

The known sites for *P. × suecicus* are listed below, with the first record(s), any later records of particular interest and records made by us since 1986. The records are arranged by vice-county and site, with a site being taken as a single river or stream or as a lake together with its associated inflow and outflow streams and ditches. We have cited appropriate literature references or herbarium specimens to support all records; unpublished determinations by Dandy are cited from the "Dandy index", the card index of herbarium specimens compiled by Dandy and now at BM. Almost all records of *P. × suecicus* made since 1940 are supported by specimens determined by Dandy & Taylor or us; the main exceptions are literature references to sites in the Outer Hebrides in the works of J. W. Heslop Harrison and his colleagues, which we summarise after the accepted records for the vice-county. The records of *P. × suecicus* accepted below are mapped in Fig. 1.

The identity of some of the populations has been confirmed by isozyme analysis. Isozyme studies by Hollingsworth *et al.* (1996a, b) revealed consistent differences between the parent species in four enzyme systems, with *P. × suecicus* showing the additive inheritance which would be expected of the hybrid between them. Sites are marked with a double asterisk (**) if the isozyme results are described in detail by Hollingsworth *et al.* (1996a) or by a single asterisk (*) if the morphological identity is supported by unpublished results based on the diagnostic AAT and/or IDH enzyme systems.

MID-W. YORKS. (V.C. 64)

River Wharfe: near Pool, SE/2.4, 1868, *F. A. Lees* (Dandy & Taylor 1946); Linton Bridge, SE/3.4, 1880, *F. A. Lees* (Dandy & Taylor 1946); Wetherby, SE/4.4, 1881, *J. Jackson* (Dandy & Taylor 1946); Arthington, SE/2.4, undated but probably collected before 1890, *J. Abbot* (Dandy & Taylor 1946); Arthington, Leathley & Weeton, SE/2.4, Linton, Harewood & Netherby, SE/3.4, Wetherby, SE/4.4, Ozendyke, SE/5.3, and Ulleskelf, SE/5.4, 1940–1945, *G. Taylor* (Dandy & Taylor 1946); Harewood Bridge, SE/31.46, East Keswick, SE/34.46, Linton Bridge, SE/38.46, and Linton, SE/39.47, 1989–1996, *Mrs P. P. Abbott, P.M.H. & C.D.P.* (CGE, E, LTR, NMW**).

River Ure: Sharow, SE/3.7, 1875, *G. Nicholson* (Dandy index); Ripon, SE/3.7, 1881, *H. H. Slater* (Dandy & Taylor 1946); Littlethorpe, SE/3.6, Nunwick, SE/3.7, and Ripon, SE/3.7, 1940–1942, *G. Taylor* (Dandy & Taylor 1946); near Ripon, SE/3.7, 1950, *U. K. Duncan & C. M. Rob* (Dandy index).

Tributary of River Ure, Westwick, SE/3.6, 1943, *G. Taylor* (Dandy & Taylor 1946).

N.W. YORKS. (V.C. 65)

River Ure: West Tanfield, SE/2.7, Masham, SE/2.8, Langthorpe, SE/3.6 and Norton Conyers, SE/3.7, 1940–1945, *G. Taylor* (Dandy & Taylor 1946); West Tanfield, SE/26.78 and Masham, SE/22.81, 1988–1996, *P.M.H. & C.D.P.* (CGE, LTR, NMW, RNG**).

[CHEVIOT (V.C. 68) AND BERWICKS. (V.C. 81)]

Records from these vice-counties are based on material which we have identified as *P. × bottnicus* (Preston *et al.* 1998). Both *P. filiformis* and *P. pectinatus* are found in Coldingham Loch, v.c. 81, but we have been unable to find the hybrid there although the locality appears suitable.]

[MIDLTHIAN (V.C. 83)]

The record from Duddingston Loch published in *Watsonia* 15: 138 (1984) was retracted in *Watsonia* 17: 481 (1989) as it was based on a specimen which is indistinguishable from *P. pectinatus*.]

FIFE (V.C. 85)

Loch Fitty, NT/12.91, 1992–1994, *P.M.H. & C.D.P.* (BM, CGE, E, LTR**).

*Cameron Reservoir, NO/477.113, 1998, *J. M. Croft, R.J.G. & C.D.P.* (**BM, CGE, E, LTR**).

N. ABERDEEN (V.C. 93)

Canal, St Fergus, NK/0.5, 1876, *J. H. Walker* (Dandy & Taylor 1940); the canal is now disused and dry for most of its length and P.M.H., C.D.P. & D. Welch were unable to find any *Potamogeton* species except *P. natans* in the very shallow pools remaining near Inverugie, NK/09.48, in August 1994.

*Loch of Strathbeg, Starnakeppie, NK/083.585, 1994, *P.M.H., C.D.P. & D. Welch* (**CGE, E**).

MORAY (V.C. 95)

Innes Canal, Urquhart, NJ/2.6, 1946, *G. Taylor* (Dandy & Taylor 1946); not resound by C.D.P. & P.M.H., 1994.

River Lossie: Calcots, NJ/2.6, 1967 & 1972, *M. McCallum Webster* (Dandy index, cf McCallum Webster 1978); Bridge of Calcots, NJ/254.638, and Arthur's Bridge, NJ/253.672, 1994, *P.M.H. & C.D.P.* (CGE, E, LTR, NMW**).

Loch Spynie, NJ/2.6, 1972, *M. McCallum Webster* (Dandy index, cf McCallum Webster 1978); NJ/237.663, 1994, *P.M.H. & C.D.P.* (**CGE, E**).

S. EBUDES (V.C. 102)

Loch Fada, Colonsay, NR/3.9, 1908, *M. McNeill* (Dandy & Taylor 1940).

MID EBUDES (V.C. 103)

** Abhainn a'Bheidhe (the stream from Loch a'Phuill to Balephuil Bay), Tiree, NL/9.4, 1940, *W. A. Clark* (Dandy index; cf Heslop Harrison *et al.* 1941; Heslop Harrison 1949); 1968, *U. K. Duncan* (Dandy index; cf Duncan 1969); 1989–1997, *P.M.H., C.D.P. & N. F. Stewart* (**CGE, E, LTR**). Ditch N.W. of Loch a'Phuill, Tiree, NL/953.422, 1990, *D. A. Pearman*, det. C.D.P. (**CGE, E**). **Loch a'Phuill, Tiree, NL/9.4, 1993, *R. N. Evans & P.M.H.* (**LTR**).

An Fhaodhail, Tiree, NM/0.4, 1897, *S. M. Macvicar* (Dandy & Taylor 1940); in main stream, a large backwater (Poll Orisgal) and nearby pools, 1989–1997, *P.M.H.*, *C.D.P.* & *N. F. Stewart* (CGE**, **E**, **LTR**).

OUTER HEBRIDES (V.C. 110)

Loch nam Budh, Monach Island, NF/63.61, 1949, *F. H. Perring*, det. *C.D.P.* (**CGE**, cf Preston in press).

*Loch Stilligarry, S. Uist, NF/766.379, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **LTR**). *Inflow stream to Loch Stilligarry, S. Uist, NF/767.380, 1995, *P.M.H. & C.D.P.* (**CGE**).

West Loch Ollay, S. Uist, NF/738.324, 1994–1995, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**).

*Loch an Duin Bhig, S. Uist, NF/759.468 & 760.470, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**, **LTR**).

Loch na Liana Moire, Benbecula, NF/76.53, 1940, *W. A. Clark* (Dandy & Taylor 1941; cf Heslop Harrison 1941, 1949; Heslop Harrison & Clark 1941); 1987, *C.D.P.*, *N. F. Stewart et al.* (CGE**, cf Preston 1991); 1994–1995, *P.M.H. & C.D.P.* (**CGE**, **LTR**). *Ditch between Loch na Liana Moire and Loch Torcusay, Benbecula, NF/763530, 1995, *P.M.H. & C.D.P.* (**CGE**).

*Loch Torcusay, Benbecula, NF/761.532, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**).

Loch Fada, Benbecula, NF/773.518, 1994–1995, *P.M.H. & C.D.P.* (BM**, **CGE**, **LTR**).

Loch near Borve Castle [this may be Loch a'Chinn Uacraich], Benbecula, NF/7.5, 1940, *W. A. Clark* (Dandy & Taylor 1941; cf Heslop Harrison 1941, 1949; Heslop Harrison & Clark 1941).

Loch a'Chinn Uacraich, Benbecula, NF/767.510, 1994–1995, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**).

Lochan near Uachdar, Benbecula, NF/7.5 or 8.5, 1940, *W. A. Clark* (Dandy & Taylor 1941; cf Heslop Harrison 1941; Heslop Harrison & Clark 1941). The record from a lochan near Gramisdale, NF/8.5, cited by Heslop Harrison (1949) may refer to the same site.

*Loch na Paisg, Baleshare, NF/786.618, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**).

*Loch Mor, Baleshare, NF/789.621, 1995, *P.M.H. & C.D.P.* (**CGE**).

*Loch Sandary, N. Uist, NF/734.684, 1995, *P.M.H. & C.D.P.* (**CGE**, **E**, **LTR**).

Loch Grogary, N. Uist, NF/71.70 & 71.71, 1994–1995, *P.M.H. & C.D.P.* (CGE**, **E**, **LTR**).

*Loch Scarie, N. Uist, NF/716.704, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**, **LTR**).

*Loch a'Chaoilais, N. Uist, NF/897.780, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**).

*Loch Bhruist, Berneray, NF/9.8, 1938, *J. W. Campbell* & 1939, *A. J. Wilmott* (Dandy & Taylor 1940); NF/915.822 & 920.829, 1995, *P.M.H. & C.D.P.* (**CGE**, **E**, **LTR**). *Outflow stream at S. end of Loch Bhruist, Berneray, NF/914.820, 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**).

Little Loch Borve, Berneray, NF/91.81, 1939, *W. A. Clark* (Dandy & Taylor 1940; cf Clark & Heslop Harrison 1940; Heslop Harrison 1941, 1949); 1995, *P.M.H. & C.D.P.* (**BM**, **CGE**).

*Outflow stream S. of Little Loch Borve, Berneray, NF/911.814, 1995, *P.M.H. & C.D.P.* (**CGE**).

Specimens at **BM** and **CGE** collected by A. J. Wilmott from Loch na Doirlinn, Barra, in 1938 (380718La) may be *P. × suecicus* but are inadequate for certain identification (Preston in press). We have not traced voucher specimens to support the records of *P. × suecicus* from Loch Bornish, Loch Hallan and lochs near Stoneybridge, all on S. Uist (Heslop Harrison 1949; Heslop Harrison & Clark 1942; Heslop Harrison et al. 1942) and Loch Cistaval, S. Harris (Heslop Harrison & Heslop Harrison 1950).

ORKNEY (V.C. 111)

Loch of the Riv, Sanday, HY/68.46, 1994, *N. F. Stewart*, det. *C.D.P.* (**CGE**, **E**, cf Preston & Stewart 1995).

Loch of Langamay, Sanday, HY/74.44, 1963, *E. R. Bullard*, det. *C.D.P.* (**BM**, cf Preston in press); 1986, *E. Charter*, det. *C.D.P.* (**CGE**, **NCCE**, cf Preston & Stewart 1995); 1994, *N. F. Stewart*, det. *C.D.P.* (**CGE**, **E**, **LTR**, cf Preston & Stewart 1995).

Loch of Rummie, Sanday, HY/75.44, 1920, *H. H. Johnston*, det. *C.D.P.* (**E**, cf. Preston in press); 1994, *N. F. Stewart*, det. *C.D.P.* (**BM**, **CGE**, **E**, cf Preston & Stewart 1995).

Loch Gretchen, North Ronaldsay, HY/74.52, 1920, *H. H. Johnston*, det. *C.D.P.* (**E**, cf. Preston in press).

SHETLAND (V.C. 112)

*Loch of Clickimin, HU/4.4, 1980, *R. C. Palmer*, det. *C.D.P.* (**SLBI**, *herb. R.C.P.*, cf Preston in press); HU/46.41, 1996, *P.M.H. & C.D.P.* (**BM**, **CGE**, **E**).

S. KERRY (V.C. H1)

*Lough Gill, V/61.14, 1993, *N. F. & R. J. Stewart*; V/61.13 & 61.14, 1994, *R. Fitzgerald & C.D.P.* (**BM, CGE, DBN, LTR**).

ROSCOMMON (V.C. H25)

*Callow Lough, 1.5 km S. of Cuil Bridge, M/70.96, 1998, *A. B. Carter, D. C. F. Cotton, A. Hill, N. Raftery & C.D.P.* (**CGE, DBN**).

E. MAYO (V.C. H26)

Glore River, Kiltamagh, M/38.90, 1994, *C.D.P.* (**CGE, DBN**). Similar plants grew upstream at grid reference M/38.89 and M/40.89 but were not collected as in the field the plant was thought to be *P. pectinatus*.

W. DONEGAL (V.C. H35)

Rosapenna, C/11.38, 1989–1990, *C.D.P. & N. F. Stewart* (**BEL, BM, CGE, DBN, LTR**, cf Preston & Stewart 1994).

TABLE 1. SPECIES ASSOCIATED WITH *POTAMOGETON × SUECICUS* IN RIVERS, STREAMS AND LAKES

	Rivers	Streams	Lakes (1)	Lakes (2)
<i>Potamogeton × suecicus</i>	V (5–10)	V (5–10)	V (3–9)	V (4–10)
<i>Myriophyllum spicatum</i>	I (4)	III (1–7)	I (1–4)	III (1–7)
<i>Potamogeton crispus</i>	II (2–5)	I (6)	I (7)	I (1)
<i>Potamogeton perfoliatus</i>	I (4)		I (1)	II (1–2)
<i>Potamogeton natans</i>	II (3–6)	II (2–5)	III (1–5)	
<i>Lemna minor</i>	II (1–2)			I (2–3)
<i>Elodea canadensis</i>	I (6)			I (1–5)
<i>Fontinalis antipyretica</i>	I (4)			I (1)
<i>Eleocharis palustris</i>		III (1–3)	III (1–6)	II (1–4)
<i>Potamogeton filiformis</i>		II (2–3)	I (1–6)	II (6–8)
<i>Potamogeton friesii</i>		I (4)	II (1–2)	I (1–4)
<i>Hippuris vulgaris</i>		I (3)	I (2)	I (3–5)
<i>Potamogeton × nitens</i>		I (2)	I (1)	I (5–6)
<i>Ranunculus baudotii</i>		I (2)	I (6)	I (5)
<i>Equisetum fluviatile</i>		I (2)		II (1–3)
<i>Chara aspera</i>		II (5)	III (1–8)	
<i>Chara vulgaris</i>		III (1–3)	II (1–5)	
<i>Chara contraria</i>		II (6)	I (1–5)	
<i>Potamogeton pusillus</i>			I (3)	II (1–7)
<i>Littorella uniflora</i>			II (!–8)	I (2)
<i>Callitricha hermaphroditica</i>			I (1)	I (2–4)
<i>Potamogeton pectinatus</i>			I (3)	I (6)
<i>Agrostis stolonifera</i>		III (1)		
<i>Sparganium erectum</i>		II (1–5)		
<i>Persicaria amphibia</i>			II (4–7)	
<i>Chara hispida</i>			I (3–7)	
<i>Chara virgata</i>			I (1–3)	
<i>Phragmites australis</i>			I (2–3)	
<i>Baldellia ranunculoides</i>				I (2–5)
<i>Carex rostrata</i>				I (1–2)
<i>Lemna trisulca</i>				II (1–2)
<i>Potamogeton gramineus</i>				I (1–5)
<i>Zannichellia palustris</i>				I (2–4)

TABLE 1. CONTINUED

	Rivers	Streams	Lakes (1)	Lakes (2)	
No. quadrats	9	7	10	14	
No. vascular plants & bryophytes	mean (range)	2.3 (1-4)	5.0 (2-8)	4.7 (1-8)	4.9 (2-8)
No. charophytes	mean (range)	0	0.9 (1-2)	1.2 (1-4)	0
% bare ground	mean (range)	16 (0-45)	9 (0-15)	5 (0-15)	15 (0-50)
Water depth (cm)	mean (range)	41 (15-80)	18 (15-25)	20 (10-45)	38 (12-70)
Substrate type (% quadrats)					
rocks	40	0	0	0	
stones/gravel	30	0	0	5	
sand	20	50	70	30	
silt/mud	10	50	30	65	

The roman numerals indicate the percentage of quadrats in which the taxon was recorded in each habitat: I, 1–20%; II, 21–40%; III, 41–60%; IV, 61–80% and V, 81–100%. The figures in brackets indicate the range of Domin cover-abundance values recorded. The lake quadrats are subdivided into two groups based primarily on the presence or absence of charophytes. The following taxa were recorded in a single quadrat: *Callitrichia hamulata*, *Sparganium emersum* (rivers); *Caltha palustris*, *Mentha aquatica*, *Ranunculus trichophyllus*, *Rorippa × sterilis*, *Veronica anagallis-aquatica* (streams); *Myriophyllum alterniflorum*, *Potamogeton × billupsii* (lakes 1); *Potamogeton rutilus*, *P. × zizii* (lakes 2).

HABITAT OF *P. × SUECICUS* IN BRITAIN

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Between 1994 and 1997 we visited 21 of the 28 localities in which *P. × suecicus* has been recorded in Britain recently, and recorded its habitat in forty 4m² quadrats. At each site one or more quadrat was recorded in stand(s) of vegetation where the cover of the hybrid was greatest. We assessed the cover-abundance of vascular plants, bryophytes and charophytes in each quadrat and noted details of substrate and water depth. The quadrats covered the range of water bodies from which the hybrid has been reported, including the River Lossie (v.c. 95), River Wharfe (v.c. 64) and River Ure (v.c. 65), the streams Abhainn a' Bheidhe and An Fhaodhail on Tiree (v.c. 103) and the outflow of Little Loch Borve, Berneray (v.c. 110), the ditch between Loch Torcusay and Loch Liana Moire, Benbecula (v.c. 110), and 15 lakes in Fife (Loch Fitty), Moray (Loch Spynie) and the Outer Hebrides (on Benbecula, Berneray, N. Uist and S. Uist). The number of sites covered should ensure that the quadrat data characterise the range of vegetation in which the hybrid occurs, although stands in deep water may have been overlooked.

The vegetation in the quadrats is summarised in Table 1. The quadrats from rivers, streams and ditches, and lakes are separated. The quadrats from lakes are presented in two groups, split primarily on the presence or absence of charophytes in the quadrat.

In rivers *P. × suecicus* is often present as robust plants growing in large, dominant stands. Very large, dense stands of *P. × suecicus* include those in the River Wharfe near Harewood Bridge (SE/31.46), East Keswick (SE/36.45) and Linton Bridge (SE/38.46) and the River Lossie near Bridge of Calcots (NJ/25.63) and Arthur's Bridge (NJ/25.67). Large stands of *P. × suecicus* are less frequent in the River Ure but the hybrid may often be found in abundance by the bridge at West Tanfield (SE/26.78), where it was photographed on 6 August 1945 (Dandy & Taylor 1946) and has therefore survived for over 50 years. In rivers *P. × suecicus* is rooted in a substrate of rocks, stones,

gravel or (on stretches of the River Lossie) pure sand. Where the substrate is rocky, plants of *P. × suecicus* are often rooted under boulders, stones or the masonry of bridge supports. Although the water flow in the *P. × suecicus* rivers is relatively rapid, patches of *P. × suecicus* may be so large that they impede the flow of water when they reach the surface, allowing a few fronds of *Lemna minor* to settle amongst them. Large stands may flower freely: flowering *P. × suecicus* in the River Lossie in August 1994 bore 9–42 inflorescences in sample areas of 400 cm², equivalent to 225–1050 m². These totals include inflorescences at anthesis and others which were decaying; some were on the surface of the water and others buried amongst the submerged foliage. The river quadrats in Table 1 are species-poor. The vegetation in these quadrats is similar to that in which the related hybrid *P. × bottnicus* grows in the River Till and River Tweed (Hollingsworth *et al.* 1998). Although no *Ranunculus* species were recorded in the quadrats with *P. × suecicus*, *R. penicillatus* subsp. *pseudofluitans* and *R. × bachii* grow in the same stretches of the Wharfe as *P. × suecicus*.

The streams and ditches in which *P. × suecicus* was recorded in quadrats are shallow and flow slowly and gently over substrates of sand or silt. *P. × suecicus* may span the entire width of the narrow channel of both Abhainn a'Bheidhe and An Fhaodhail in Tiree. Heslop Harrison (1949) reported that *P. × suecicus* grew at Abhainn a'Bheidhe in "dense masses for considerable stretches of the stream", still an apt description of its abundance in 1997. The stream quadrats are more species-rich than those recorded in rivers, and in addition to submerged species they include emergents such as *Eleocharis palustris*, *Sparganium erectum* and a few shoots of the normally terrestrial *Agrostis stolonifera* which extend into the shallow water of An Fhaodhail. The vegetation is usually more or less closed and there is little bare ground.

In some lakes *P. × suecicus* may occur in large, dominant stands. The largest stands we have seen in lakes have been in the very shallow bay at the northern end of Loch Torcusay (NF/76.53) where the water is only 10 cm deep and is completely dominated over an area of many square metres by *P. × suecicus* and associated charophytes (*Chara contraria*, *C. hispida*, *C. virgata* and *C. vulgaris*), and in the north-west arm of Loch an Duin Bhig (NF/76.47) which is covered in *P. × suecicus*. Equally dense but smaller stands may be found in other lakes, such as Loch Fitty (NT/12.91) and Loch Sandary (NF/73.68). In other sites *P. × suecicus* may occur only as scattered plants in more open communities over stones and boulders, or amongst other macrophytes such as *Hippuris vulgaris*, *Littorella uniflora*, *Persicaria amphibia*, *Potamogeton filiformis*, *P. × nitens*, *P. pectinatus* or *Zannichellia palustris*.

The quadrats where *P. × suecicus* was recorded with charophytes (Table 1) tend to be in shallower water than those which lack charophytes, and are more often found with sand as a substrate than silt. *Eleocharis palustris*, *Potamogeton natans* and *Chara aspera* are the most frequent associates in these quadrats and *Persicaria amphibia* is confined to this group. Charophyte cover is often high and there is little bare ground. *Eleocharis palustris* is less frequent in the quadrats without charophytes and neither *Persicaria amphibia* nor *Potamogeton natans* are recorded. However, *Equisetum fluviatile* is present and *Myriophyllum spicatum* and *Potamogeton pusillus* are more frequent in these quadrats. *P. filiformis* and *P. pectinatus* occur with *P. × suecicus* in both groups of quadrats.

HABITAT OF *P. × SUECICUS* IN IRELAND

P. × suecicus grows in lakes at three of its four known Irish sites. Two of these lakes are similar to sites in Scotland where the hybrid occurs in charophyte-rich communities. In Donegal (v.c. H35) it is found in a shallow lake in the calcareous sand dunes at Rosapenna. This site, which is described by Preston & Stewart (1994), is fringed by *Eleocharis palustris*, *Littorella uniflora* and scattered *Persicaria amphibia*. In the open water charophytes are abundant and in addition to *P. × suecicus* the macrophytes include *Apium inundatum*, *Potamogeton natans* and *Ranunculus trichophyllum*. The second Irish site is a large coastal lake, Lough Gill (v.c. H1). Here *P. × suecicus* is locally frequent at the south-east edge of the lake, growing in shallow water 12–15 cm deep over a substrate of silt mixed with stones and sand. Associated species include *Potamogeton filiformis*, *P. pusillus*, *Chara contraria* and *C. curta*. By contrast, in Roscommon (v.c. H25) *P. × suecicus* has been found in water 30–50 cm deep over a stony substrate at the edge of Callow Lough, the southernmost lough in the Lough Gara complex. Here it grows as scattered plants or, in more sheltered bays, as somewhat larger patches, with few associated species.

TABLE 2. SITES WHERE *POTAMOGETON* × *SUECICUS* MAY GROW IN THE ABSENCE OF ONE OR BOTH PARENTS, *P. FILIFORMIS* (F) AND *P. PECTINATUS* (P)

Site	Parents present	Notes
River Wharfe, v.c. 64	P	South of current distribution of F
River Ure, v.c. 64, 65	P	South of current distribution of F
Canal, St Fergus, v.c. 93	F	Both taxa known only from specimens dated 1876
Loch of Strathbeg, v.c. 93	P	F recorded by Trail (1901a,b) but never confirmed
Innes Canal, Urquhart, v.c. 95	Neither	Hybrid known only from specimen dated 1946
River Lossie, v.c. 95	Neither	
Loch Spynie, v.c. 95	P	P collected regularly since 1831; F never found
Loch Fada, v.c. 102	P	F recorded by McNeill (1910, p. 78); no specimen seen and species has not been reported from the island again (Clarke & Clarke 1991)
Loch nam Budh, v.c. 110	Neither	Specimen determined as F by Dandy and reported as such by Perring & Randall (1972) is the hybrid
Loch an Duin Bhig, v.c. 110	P	F recorded by Royal Botanic Garden, Edinburgh (1983); no specimen seen
Loch Fada, v.c. 110	P	
Loch a'Chinn Uacraich, v.c. 110	P	F recorded by Royal Botanic Garden, Edinburgh (1983); no specimen seen
Loch Mor, v.c. 110	P	
Loch a'Chaoilais, v.c. 110	Neither	Small site thoroughly surveyed in 1995
Little Loch Borve, v.c. 110	F	
Loch of the Riv, v.c. 111	F	
Loch of Langamay, v.c. 111	F	Specimen collected in 1963 and determined by Dandy as P is the hybrid (Preston in press)
Loch of Rummie, v.c. 111	F	Specimen reported by Johnston (1922) as F but determined by Dandy & Taylor as P is the hybrid (Preston in press)
Glore River, v.c. H26	Neither	
Rosapenna, v.c. H35	F	F collected in 1939 by Praeger but absent when this small site was thoroughly surveyed in 1989 & 1990

The remaining Irish site, the Glore River (v.c. H26), is a relatively shallow stream flowing over a substrate of silt and stones. *P. × suecicus* is recorded in patches up to 3 metres long, growing in water 40–50 cm deep with *Apium nodiflorum*, *Elodea canadensis*, *Myriophyllum alterniflorum* and the rare hybrid *Potamogeton × lanceolatus*. This stream has no close parallel to any of the other known sites for *P. × suecicus* in Britain, and perhaps provides a habitat which is intermediate between the large rivers of northern England and Scotland and the slowly flowing streams of the Hebrides.

OCCURRENCE OF *P. × SUECICUS* IN RELATION TO ITS PARENTS

In discussing the relationship between the distribution of *P. × suecicus* and its parents, three questions arise. What is the probability of finding *P. × suecicus* at sites where both *Potamogeton filiformis* and *P. pectinatus* occur? Does the hybrid occur at sites where one or both parents are absent? And is there any differentiation between the habitat of the three taxa when two or three grow together?

It is not easy to assess the frequency of the hybrid at sites where both parents occur as there are few areas in which the hybrid has been searched for systematically. In the Outer Hebrides in 1995 we visited 17 lochs which appeared to be likely sites for the hybrid, comprising 3 where *P. ×*

suecicus had already been recorded before we began our studies and 14 from which one or both parents had been recorded or seemed likely to occur. *P. × suecicus* grew in 15 of these 17 sites, the exceptions being one loch where we were only able to detect the parents in the limited area we were able to search and one small loch near the sea where *P. pectinatus* was the only one of the three taxa present. This is clear evidence to support Heslop Harrison & Clark's (1941) view that on Benbecula the hybrid "seems to occur wherever the parent species clash". However, *P. × suecicus* may be exceptionally frequent in the Outer Hebrides. In Shetland, where *P. filiformis* is much more frequent than *P. pectinatus*, we have visited all seven sites from which Scott & Palmer (1987) cite confirmed records of *P. pectinatus*. Despite the fact that *P. filiformis* grows in six of these seven sites, we detected *P. × suecicus* in only one locality.

The sites where *P. × suecicus* appears to grow in the absence of one or both parents are summarised in Table 2. The identification of such sites is not always straightforward. At some sites there are field or literature records of one of the parents made by recorders who did not report the hybrid; if these records are not supported by herbarium material it is not possible to say whether they are correct. At other sites the absence of the parents may be due to inadequate survey. Nevertheless, there are several localities where the presence of *P. × suecicus* in the absence of one or both parents is well-established. Three of the sites are rivers: the River Lossie, where neither parent is found, and the Rivers Wharfe and Ure, where only *P. pectinatus* occurs. The recently discovered population in the Glore River may also fall into this category. *P. filiformis* does not usually occur in large rivers, and its absence from these sites may be explicable on ecological grounds. The Yorkshire rivers are also south of the current range of *P. filiformis*.

Another habitat where *P. × suecicus* occurs in the absence of one or both parents is in shallow coastal lakes over sand. At Loch a'Chaoais and Rosapenna the hybrid is currently present and locally abundant in the absence of both parents. Ecologically these sites have much in common; both sites are fringed by *Eleocharis palustris* swamp and *Persicaria amphibia*, *Potamogeton natans* and *Chara aspera* or the closely related *C. curta* grow in the water. There is reliable evidence for the former presence of one of the parents at Rosapenna, as R. L. Praeger collected fruiting material of *P. filiformis* there in 1939 (DBN). The Orkney sites for *P. × suecicus* are also shallow lakes over calcareous sand where the hybrid grows with *Chara aspera* and *C. curta*; it is accompanied here by *P. filiformis* but there is no reliable record of *P. pectinatus* from these sites.

The presence of "orphaned" *P. × suecicus* in larger lakes has still to be established with certainty but it is interesting that the hybrid grows in Loch Spynie, where many collectors from 1831 onwards have gathered *P. pectinatus* but where *P. filiformis* has not been recorded. The Loch of Strathbeg is also a possibility: *P. pectinatus* has been recorded since 1883 but the only record of *P. filiformis* (Trail 1901a, b) lacks a supporting specimen.

At large and complex sites where the hybrid and both parents are present, the taxa are often concentrated in different areas. At Loch a'Phuill *P. filiformis* grows on the shallow sandy flats around the edge and *P. pectinatus* in deeper water. *P. × suecicus* occurs in the loch but it is particularly abundant in the shallow and slowly flowing outflow stream (Abhainn a'Bheidhe) which runs from this loch through sand dunes to the sea. *P. filiformis* grows in this stream (though it is less abundant than the hybrid) but *P. pectinatus* does not. At An Fhaodhail, Tiree, the shallow river is dominated by *P. × suecicus*; *P. pectinatus* is represented by a few individuals scattered sporadically amongst the hybrid and *P. filiformis* grows in nearby pools (Hollingsworth *et al.* 1996a). At less complex sites the distinctions between the taxa are less obvious. *P. filiformis* tends to be a plant of shallow water and although it may grow with *P. pectinatus*, the latter attains maximum luxuriance in deeper, less turbulent water (van Wijk 1988). Unlike *P. filiformis*, which may be found in water only a few centimetres deep and in sites which dry out completely when water levels are low, *P. × suecicus* is not found in very shallow water. It does, however, grow in slightly deeper water well within the habitat range of *P. filiformis* and it is more frequently found with that species than with *P. pectinatus* (Table 1). It would, however, be even more easily overlooked in deeper water than it is when it grows in the shallows. At Loch Fitty *P. filiformis* tends to grow on coarse sand or gravel, *P. pectinatus* on fine silt and *P. × suecicus* gravel mixed with silt, although this may simply reflect differences in the water depth and exposure of the sites favoured by the three taxa.

In summary, the habitat of *P. × suecicus* in lakes is intermediate between that of its parents. It tends to be most abundant in water at the deeper end of the range characteristic of *P. filiformis*, but

it rarely extends into the still deeper water where *P. pectinatus* reaches maximum luxuriance. It may grow in the absence of both parents in shallow coastal lakes over sand. In rivers it grows in shallow, fairly rapidly flowing water over stones, gravel or sand, a habitat where neither parent is found. A more detailed insight into the habitat of the hybrid in relation to its parents might be obtained by more intensive studies at sites like Loch Fitty where all three taxa occur.

DISCUSSION

RECOGNITION AND RECORDING HISTORY

Plants of *P. × suecicus* can easily be confused with *P. pectinatus* as the resemblance to that species is obvious in the field whereas the influence of *P. filiformis* is often apparent only when plants are carefully examined under the binocular microscope. Many specimens of *P. × suecicus* have initially been identified (at least in the field) as *P. pectinatus*: these include those collected by G. Taylor from the River Wharfe in 1940, the first specimens collected from Shetland in 1980, plants gathered by C.D.P. & N. F. Stewart in Co. Donegal in 1989 and material collected by P.M.H. at Loch Fada and Loch a'Chinn Uacraich, Outer Hebrides, in 1994. *P. × suecicus* has also been overlooked (rather than mistaken for its parents) in Scotland and Ireland, perhaps because fruiting plants of *P. filiformis* and *P. pectinatus* may often be found without difficulty, so that botanists can record both species with certainty and therefore do not feel obliged to examine vegetative material. The ease with which *P. × suecicus* can escape detection is well illustrated in the Outer Hebrides. The hybrid is now known to be widespread in species-rich machair lochs which have attracted the attention of many individual botanists and ecologists and some survey teams in recent years (Preston 1991). Rare and critical taxa such as *Potamogeton* \times *billupsii*, *P. × nitens*, *P. rutilus* and *P. × sparganifolius* were collected between 1960 and 1985 from lochs in which *P. × suecicus* is now known to occur, but *P. × suecicus* itself was never recorded during this period.

The fact that *Potamogeton* \times *suecicus* tends to be recorded only by botanists who are familiar with its appearance, and is overlooked even by others who are specifically recording in aquatic habitats, explains the numerous records in the 1940s, when both Heslop Harrison's team from Newcastle and George Taylor were actively engaged in fieldwork, followed by the subsequent falling-off of new records. The hybrid is almost certainly still under-recorded. One would expect to find it elsewhere in eastern Scotland (e.g. in Angus) and at other sites in the west. There are many potential sites for the hybrid in the Outer Hebrides, for example, which we have not had an opportunity to visit. Four sites have been discovered in Ireland in the last decade and there are many more places in the north and west where it might occur.

We have improved our ability to recognise *P. × suecicus* only by collecting material in the field, examining it from a morphological or isozyme perspective and then returning to the field to reassess the populations in the light of these detailed studies. On our return from visits to N.E. Scotland, the Hebrides and Shetland C.D.P. has examined the morphology of our collections and P.M.H. has looked at the isozymes. We have then compared identifications which were reached without knowledge of the other person's view. We have always been in agreement, though sometimes the isozyme results have provided welcome confirmation of a tentative identification of fragmentary or aged material based on morphology, or *vice versa*. However, an identification based on morphology often requires flowering material, or a supply of vegetative material which is large enough to allow the dissection of numerous young leaf sheaths.

The hybrid is more likely to be detected by a thorough examination of populations in the field than by the collection of a few herbarium specimens for later examination or determination by others. Recognition of the hybrid using morphological criteria relies on proving the presence of characters derived from both parents, and it is helpful to demonstrate that the plant is sterile. Herbarium material often provides an inadequate representation of the habit of the plant and a very small number of leaf sheaths for dissection. Flowers may not be available, and even if a flowering plant lacks fruit there is usually no evidence to indicate whether this was typical of the population from which it was collected. Even J. E. Dandy and G. Taylor, the foremost authorities on the genus, identified material which we now believe to be *P. × suecicus* as one or other parent (Preston in press).

DOES *P. × suecicus* BACKCROSS WITH EITHER PARENT?

Heslop Harrison & Clark (1942), in commenting on the application of the name *P. × suecicus* to the hybrid plant from South Uist which "grows in the Stoneybridge lochs, as elsewhere, in forms displaying a great variation range" said that "in our opinion, it is wrong to include these in one ragbag under the name *P. suecicus* because they differ phenotypically and genetically. Clearly, F_1 hybrids, backcrosses and segregates of F_2 and later generations are concerned; a common name cannot be forced to cover plants ranging from "almost" *P. filiformis* to "almost" *P. pectinatus*. It would, at present, be better to label them *P. filiformis* \times *P. pectinatus*, and to leave them until further study and experiment have clarified the position." This description suggests that a complex hybrid swarm is present in the Hebrides. We know of no evidence to support this suggestion. The plants of *P. × suecicus* in those localities where we have studied them in detail show little variation. The hybrid does vary in morphology from population to population, and some of these variants are closer to *P. pectinatus* than others, but this pattern of variation is much more easily explained by phenotypic response to different habitat factors or by the presence in different sites of a first generation (F_1) hybrid of different genetic origin than it is by invoking the possibility of backcrossing with the parents. The isozyme studies of eleven populations reported by Hollingsworth *et al.* (1996a) confirm this pattern of variation: no variation was detected at six sites and only two isozyme phenotypes were detected at a further four. This suggests that there may have been only one or two clones present at ten of the localities (although isozyme data are based on a small proportion of the genome and provide an estimate of the *minimum* number of clones present). An Fhaodhail on Tiree, where six isozyme phenotypes were detected, was the only exception. All isozyme phenotypes, including those from An Fhaodhail, were consistent with the assumption that the plants were F_1 hybrids, and there was no evidence for the disruption of additive inheritance of species-specific markers which would be expected if backcrossing had taken place.

SIGNIFICANCE OF STERILE *POTAMOGETON* HYBRIDS

P. × suecicus is one of eight widespread *Potamogeton* hybrids in Britain and Ireland identified by Preston (1995) and mapped by Preston & Croft (1997). Like most of these hybrids, its distribution is neither completely independent of the parents nor completely determined by the sites where they currently occur. Despite the fact that *P. × suecicus* was not recognised in Britain until 1940, it is known to have been present in three sites for at least 100 years (River Wharfe, River Ure, An Fhaodhail) and in a further five for at least 50 years (Abhainn a'Bheidhe, Loch na Liana Moire, Loch Bhruist, Little Loch Borce and Loch of Rummie). In sites where at least one parent is absent the presence over this period is almost certainly caused by the persistence of particular clones; if both parents are present one cannot conclude that individual clones are long-lived as the hybrid may have arisen by repeated hybridisation. Another notable feature that *P. × suecicus* shares with many of the widespread hybrids is that at some sites it is a significant feature of the aquatic vegetation, and may even be present in dominant stands. The further study of the ecology of these sterile hybrids in relation to their fertile parents might throw considerable light on the reproductive biology, dispersal and ecology of aquatic plants.

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The past and present status of *Moneses uniflora* (L.) Gray (Pyrolaceae) in Scotland

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ABSTRACT

Moneses uniflora (L.) Gray (Pyrolaceae), One-flowered Wintergreen, is a nationally rare plant in Britain. It is now restricted to three vice-counties in Scotland. The history, decline and present status of the plant are described. Botanical collecting, deforestation and other land use changes are identified as causes of decline. Sensitive management and effective communication are vital for the survival of colonies in commercial forests.

KEYWORDS: Woodland, conservation, forestry.

INTRODUCTION

Moneses uniflora (L.) Gray (Pyrolaceae), One-flowered Wintergreen (hereafter *Moneses*) is a nationally rare plant in Britain. It is not protected under Schedule 8 of the *Wildlife and Countryside Act* (1981) but is classified as vulnerable in the *British red data book for vascular plants* (Perring & Farrell 1983). The species has been previously reported from at least 15 vice-counties with doubtful records from a further three, including the English vice-county of Westmorland (69) (not included in Fig. 1 which shows the distribution of the species). There has been a marked decline and it is presently recorded in twelve 10-km squares in three vice-counties (Table 1).

TABLE 1. PRESENT SITES AND POPULATION SIZES OF *MONESES UNIFLORA* IN SCOTLAND

Site	Vice-county	10-km square	Population sizes
Culbin Forest	95	NH/9.5	A
Culbin Forest	95	NH/9.6	A, B, C, C
Culbin Forest	95	NJ/0.6	A
Old Grantown Wood	95	NJ/0.2	A
Burgie Wood	95	NJ/1.5	B
Lethenhill	95	NJ/1.5	A
Glen Affric	96	NH/2.2	A, C
Strathfarrar	96	NH/2.3	A
Strathfarrar	96	NH/3.3	A
Glen Einich	96	NH/9.0	A
Rothiemurchus	96	NH/9.0	A
Loch Morlich	96	NH/9.0	A
Loch Loy	96	NH/9.5	A
Abernethy Forest	96	NJ/0.1	A
The Mound	107	NH/7.9	A
Balblair Wood	107	NH/8.9	D

Vice-counties: 95 Moray, 96 Easterness, 107 Sutherland East. Population sizes: A – 1–199 rosettes, B – 200–499 rosettes, C – 500–999 rosettes, D – >1000 rosettes.

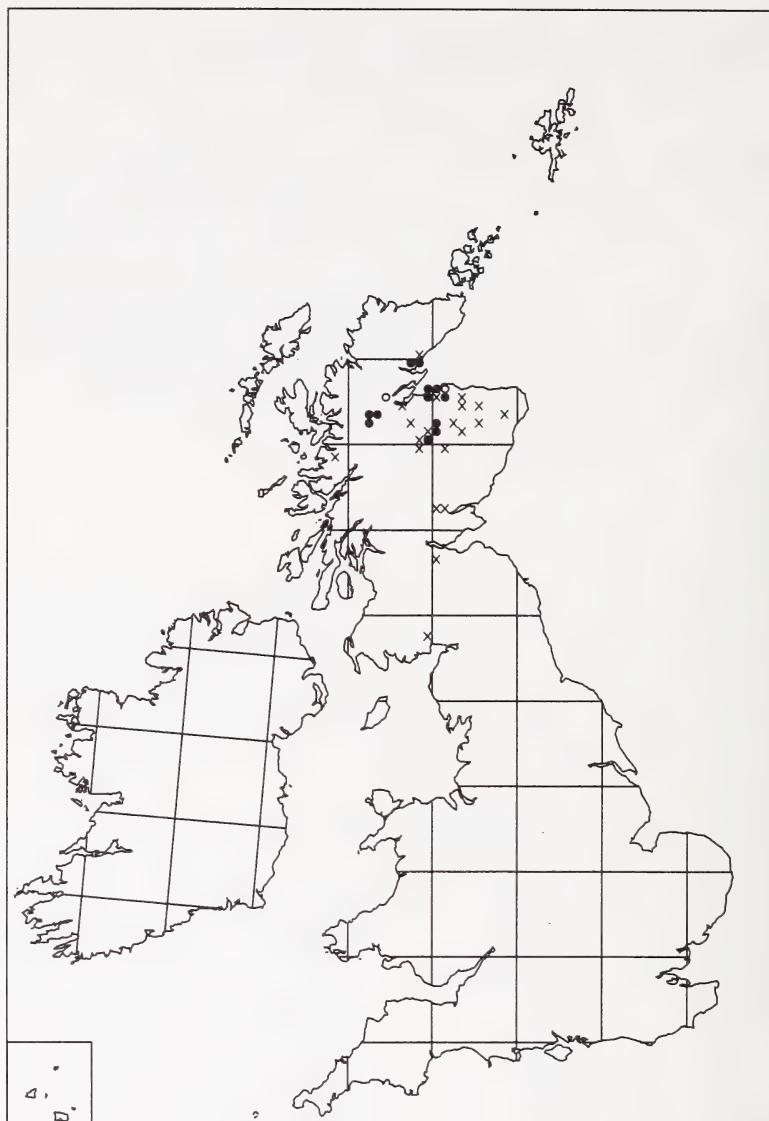


FIGURE 1. The distribution of *Moneses uniflora* in the British Isles. Symbols: ● – 1985 onwards, ○ – 1970–1984, × – pre-1970

Moneses is a member of the Circumpolar Boreal-montane element of the British flora and its occurrence in Britain represents the westernmost limit of its distribution in Europe (Preston & Hill 1997). The species ranges from central and northern Europe, south to the southern Adriatic and east to the Novosibirsk region in Russia. It also occurs in abundance in the eastern United States of America.

In central and northern Europe *Moneses* mainly grows in humid spruce woods but also occurs in drier forest dominated by Scots Pine (*Pinus sylvestris*). The field layer of these woods is dominated by dwarf ericaceous shrubs. In the Swiss Alps *Moneses* is a characteristic species of subalpine spruce woods with *Lycopodium annotinum*, *Liſteria cordata* and *Linnaea borealis* (Ellenberg

TABLE 2. VEGETATION OF MONESES UNIFLORA SITES IN SCOTLAND

Site	NVC Community (where identified) or other vegetation type
Lethenhill	M15b*
Balbar Wood	W18a*
Little Ferry	W18
The Mound	W18
Burgie Wood	W18a*
Culbin Forest	W18a*
Culbin Forest	Corsican Pine (<i>Pinus nigra</i> var. <i>maritima</i>)*
Glen Emich	W18b
Strathfarrar (both sites)	W18b
Rothiemurchus	W18b
Old Grantown Wood	W18c*
Abernethy	W18d
Glen Affric (both sites)	W18d

* = forest plantation.

Key to NVC communities (see Rodwell 1991a,b)

M15 *Scirpus cespitosus* – *Erica tetralix* wet heath; b = typical subcommunity.

W18 *Pinus sylvestris* – *Hylocomium splendens* woodland subcommunity, a = *Erica cinerea* – *Goodyera repens* subcommunity; b = *Vaccinium myrtillus* – *V. vitis-idaea* subcommunity; c = *Luzula pilosa* sub-community; d = *Sphagnum capillifolium* – *S. quinquefarium* subcommunity.

1988). On the German island of Rügen, *Moneses* occurs in moss-rich pinewoods on young wooded dunes (Meusel 1951), habitats similar to the Scottish coastal sites in Moray and East Sutherland. However, the plant communities of most of the Scottish sites (Table 2), are similar, both floristically and structurally, to the pine/birch forests of western Norway (Aune 1977). Across its total range *Moneses* occurs more abundantly in humid spruce forests rather than in drier pinewoods. At one locality near Elgin, *Moneses* has been found in a wet-heath (NVC M15b) (Table 2), but many plants did not appear healthy.

There are no fossil records of *Moneses* or any other Pyrolaceae in Britain or Ireland.

This paper reports the results of a field and literature survey carried out by the Scottish Rare Plant Project of Scottish populations of *Moneses*. Original sources were consulted to determine as precisely as possible the location of old records. Vice-county recorders, nature reserve wardens, staff of various conservation organisations, foresters, local botanists and others have been consulted in gaining up-to-date information on the status of different populations. Records were obtained from 24 herbaria. Unpublished and manuscript sources have been checked for additional records.

DISCOVERY OF MONESES UNIFLORA IN BRITAIN

Moneses was known only as a cultivated garden plant to herbalists in Britain in the sixteenth and seventeenth centuries (Gerard 1597; Parkinson 1640). Miller (1763) reported that *Moneses* grew "naturally in shady woods in the northern parts of Europe", but he did not know it was native in Britain. Philip Miller cultivated *Moneses* in 1748, making this the earliest record of the plant growing in Britain, albeit as an introduction (Murray 1799).

The first native record is of doubtful authenticity. There are two specimens in the herbarium of Sir J. E. Smith (LINN) labelled "From the western Isles of Harris and Bernera gathered in 1783 by Jas. Hoggan". These were sent to Smith in 1793 by R. Gotobed. There are no other records of *Moneses* from the Western Isles (Pankhurst & Mullin 1991).

James Brodie found *Moneses* in pinewoods near Brodie House, Forres, in 1792 (Clarke 1900); undated specimens collected by Brodie survive in E. The same year James Hoy, secretary and librarian to the Duke of Gordon at Gordon Castle, Fochabers, sent a specimen collected locally to the Linnean Society (Sowerby 1794).

SCOTTISH SITES OF *MONESES UNIFLORA*

WEST SUTHERLAND (V.C. 108)

A single collection by Collins from Scourie in 1905 (**LRS**) constitutes the northernmost record for *Moneses* in Britain (Fig. 1).

EAST SUTHERLAND (V.C. 107)

The largest and best known population in Britain is at Balblair Wood near Golspie; several thousand plants occur in a Scots Pine plantation covering about 40 ha. The first record was by Crawford in 1890 (Kenworthy 1976). Specimens labelled "Golspie" and "near Golspie" may be from this locality, but those labelled "Ferry Wood" and "Little Ferry" probably came from Ferry Wood which is separated from Balblair by a road. Certainly Anthony (E) made this distinction.

The present plantation of Scots Pine at Balblair is just over 75 years old and was established on the site of native pinewood which suffered windblow. The wood is owned by Sutherland Estates. Its conservation importance was recognised in 1970 when, in conjunction with Sutherland Estates, the Scottish Wildlife Trust established a wildlife reserve. Balblair Wood is also part of the Loch Fleet Site of Special Scientific Interest notified by The Nature Conservancy Council in 1975. A Nature Research Agreement has recently been secured by Scottish Natural Heritage with the intention to declare the area as a National Nature Reserve (F. Symonds, pers. comm., 1998).

Moneses was also collected from The Mound, 2.5 km north-west of Balblair, where it was first recorded by Foggit (Kenworthy 1976) and Crawford (E) in 1900. Druce noted that *Moneses* grew "in immense quantity in a larch wood near Golspie (a second locality)" (**OXF**). Druce's 1923 collection was the last known record from The Mound until Symonds rediscovered a small patch on the south side of The Mound within the Mound Alder Woods National Nature Reserve in 1997.

There are several collections (**ABD**, **BM**, **E**, **RNG**) dated 1939 from Cambusmore on the western shore of Loch Fleet. These are the only known records from this locality. There is also a single record from Dunrobin, north of Golspie (Watson 1837).

EAST ROSS-SHIRE (V.C. 106)

There are no extant sites in East Ross-shire. Records from the chief locality, variously known as "Knock Farril", "Coul Wood" or "The Cat's Back", near Strathpeffer, span the period 1830 to 1872. The most precise details are on a specimen dated 1835 (**ABD**) "In the Coul fir wood, about a mile [2 km] to the west of the Strathpeffer pump-room, ... in two or three large patches". Gordon (1867, ms letter to Dr J. Hutchinson, **ELN**) reported that "the firwood has been cut down, so I suppose the plants have perished for lack of shade". Hillhouse (1889) declared *Moneses* extinct at Knock Farril. However, *Moneses* was found at Strathpeffer in 1966 by Duncan (1980), but a programme of tree felling and replanting began there in 1968. Selby monitored the status of *Moneses* and made his last sighting about 1970. Brebner & Hulme (pers. comm., 1994) knew a few plants beside a track near Strathpeffer Youth Hostel during the mid-1970s, but these were unwittingly destroyed by widening and re-routing of the track.

A specimen collected by McRae dated 1905 (E) and labelled from the Black Isle may represent a second locality but is as likely a vague reference to Strathpeffer which is close to the Black Isle.

The plant has never been resound at Torr Achilty, south-west of Contin, where it was recorded in 1863 (Duncan 1980).

MID EBUDES (V.C. 103)

Moneses was listed from Torosay, east Mull, "according to Mr Middleton at Achnacroish" by Clerk (1845), but has not been included in any other plant lists for Mull.

MAIN ARGYLL (V.C. 98)

Marshall reported *Moneses* from Kilmory Estate near Lochgilphead, Argyll: "Sir John Campbell-Orde, Bart recently showed me this plant growing on his estate near Lochgilphead, and assured me it was not an introduction. This appears to be the first certain station for it in west Scotland" (Marshall 1896). No other record is known.

EASTERNESS (V.C. 96)

Moneses was collected by Ballie in 1890 (**BM**) "in a fir wood in rather boggy ground". In 1990 it was recorded from the margin of Loch Loy by North. Two small colonies, separated by a few

metres, are extant. The habitat is an open mixed Scots Pine and Downy Birch (*Betula pubescens*) wood.

There are extant populations in Strathfarrar and Glen Affric. *Moneses* was found in Strathfarrar by Miss Fraser Lovat in 1867 (Farquharson & Selkirk 1868). There was no other record from Strathfarrar until 1980 when Cameron discovered one of the extant colonies, east of Loch Beannacharan, at about 275 m altitude, in native pinewood. The flora is dominated by *Vaccinium myrtillus* and observations over the last ten years suggest an increase in density of this species, while the number of *Moneses* rosettes has declined. It may be necessary to reduce the competition from *V. myrtillus* to preserve this colony. The second population, on a trackside towards the eastern end of Strathfarrar, was discovered in 1992 by Mrs E. Lennard. The track is used at present for access to a hydroelectric installation, so this colony is also vulnerable.

In Glen Affric, *Moneses* was found in 1975 by Crawley (E), north-east of Loch Beinn a' Mheadhoin; this record is not included in McCallum Webster (1978). Despite recent searches, this colony has not been resound and may have been eliminated by tall heather (M. Barron, pers. comm., 1995). In 1988 and 1990 two populations were found on the margins of lochans on the south side of Glen Affric. Here the plants are growing just above summer water levels and are occasionally submerged in winter. One population comprises four small colonies distributed over some 200 m; the other is a single colony of a few rosettes. A further population in Glen Affric was found by Lennard on the lower slopes of Creag Dubh above Cougie (Lennard, pers. comm., 1993). A colony from a "field near the dam at Kingsmill, Inverness" found by Galloway before 1888 is no doubt lost and another from Strathdearn (McCallum Webster 1978) has not been recorded since.

Records from Abernethy are often imprecise but Traill (1910) and Davidson (ABC) recorded *Moneses* from Loch Mallachie on the southern margin of Abernethy forest. No recent records from this area are known. An extant population within Abernethy Forest was found by Horn in 1988 and consists of fewer than 100 rosettes scattered over an area of about 25 m². The vegetation is dominated by *Calluna vulgaris* and *Vaccinium myrtillus* with frequent *Carex nigra* and *C. panicea* in wet channels. A specimen labelled "Boat of Garten" (1919, (E)) may be from Abernethy Forest.

The forests of Rothiemurchus and Loch an Eilean have been known sites for *Moneses* since 1882 (Keith & Groves (FRS, BM)). MacMillan (1907) reported the plant "in some abundance in the woods at the south-west end of the Loch". Hillhouse (1889) noted that it was "disappearing from Rothiemurchen [sic] ... from the rapacity of collectors". Over 50 plants were gathered between 1882 and 1894, but at this site, at least, *Moneses* was not collected to extinction.

One small colony is extant in Rothiemurchus, in Glen Einich. About 20 rosettes occur at the base of a dead pine tree in atypically open, dry conditions. The associated vegetation is dominated by *Vaccinium myrtillus*, with *V. vitis-idaea* and common pleurocarpous mosses. The population occurs between two drainage channels which direct water away from the plants. This could account for lack of vigour in this colony.

Records from Loch Morlich and Glen More are first represented by a specimen collected by King and exhibited to the Natural History Society of Glasgow in 1885 by Boyd (Stirton 1887). Since then populations have been recorded intermittently. Two small colonies have been washed away by flash floods and another destroyed by Sitka Spruce plantation (D. Ross, pers. comm., 1990). In 1994 a population was found near Loch Morlich by Jones.

A colony at Kinraig, between Aviemore and Kingussie (McCallum Webster 1978) and one in Glen Feshie (Steven & Carlisle 1959), have not been confirmed by our survey.

MORAY (V.C. 95)

Moray is considered the headquarters for *Moneses* in Scotland. Although the extent of all colonies does not approach the size of the Balblair population, more populations have been recorded in Moray than in any other vice-county.

After Brodie's discovery in 1792 there are no further records from Brodie House other than a specimen in DBN dated 1798 (Nelson 1995). Several botanists reported the plant's disappearance at this site which was attributed to tree felling and gorse invasion (Bishop 1826; Brichan 1842; Ogilvie 1845). Therefore the original site was lost within about 30 years of its discovery.

The second record from Moray is in Gordon's *Collectanea for a Flora of Moray* (1839): "Discovered by John Lawson esq. about 20 years ago [1819] in the oakwood, near Aldroughty. It was afterwards lost sight of until 1836, when a few specimens were gathered by J. Shier, esq. and

pupils". One specimen is in ELN. This locality was recorded by Hooker (1830) as "Knock of Alva [Alves]". Other localities near Elgin are Loch Avain (Todd 1867, 1887 (**CGE**)) and Roseisle Forest, near Burghead, recorded by Cuthbertson in 1974 (McCallum Webster 1978). In 1908 the plant was found in Balnacoul Wood, west of Fochabers by Watson (Burgess 1935) but no specimen has been traced. This site is now a forestry plantation.

There are five extant localities for *Moneses* in Moray. Chief of these is the afforested sand dune system of Culbin Forest which occupies nearly 3000 ha of the southern coast of the Moray Firth between Nairn and Forres. Planting began on Culbin Sands in 1839 but was most extensive between 1922 and 1963 (McCallum Webster 1968). Without exact details it is not possible to ascertain whether records were from within Culbin Forest or whether they were from woodland outside its present boundary. Specimens labelled "Forres" dating from 1840 to 1871 could be from woodland existing prior to afforestation, but an 1869 collection from "Clunie Hill" (south-east of Forres) (Brown (**ABD, BM**)) is clearly a separate locality. No subsequent records of the latter site are known. Burgess discovered three stations in Dyke (0.8 km north of Brodick) in 1901 which may be within Culbin Forest and a specimen from "Snab Wood" collected by Patton in 1923 (**GL**) could also be from Culbin.

Miss Mary McCallum Webster knew Culbin Forest and the localities of *Moneses* better than any other botanist but was always vague regarding sites. Precise details were never handed on in her lifetime. Those fortunate enough to be shown a colony were led on a deliberately tortuous route along forest tracks which made relocation practically impossible! Consequently, it is not certain which sites discovered since the death of Miss McCallum Webster coincide with the ones she knew.

To date six colonies have been found in Culbin Forest by North, Farrell, White, Edelsten and Young. Population sizes range from less than 20 rosettes to several hundred, and habitats vary from very wet to dry (Table 1).

Records from Burgie date from 1870 with collections by Innes and Keith (**ABD, BM, FRS, K, OXF**). It was found again in 1910 by MacGregor (Burgess 1935) and in 1920 by McCallum Webster (**E**). A small colony was found under Scots Pine and Larch (*Larix decidua*) at the edge of Burgie Wood (now a large forest plantation) by Lusby in 1993. Immediately to the east of Burgie Wood at Lethenhill, Matthews found a small colony of *Moneses* among scattered Scots Pine and Juniper (*Juniperus communis*) in wet heath (Tables 1 & 2). This was the wettest site for *Moneses*; a number of rosettes displayed veinal chlorosis.

Records from Grantown-on-Spey (MacKechnie 1954, (**E**)) and Castle Grant (McCallum Webster 1978) probably refer to Old Grantown Wood where the plant is extant but in a precarious condition. Timber extraction has destroyed some colonies and grazing threatens others. *Moneses* is accompanied by abundant *Linnaea borealis*, *Goodyera repens* and *Ptilium crista-castrensis* at this site.

In the early 1950s Lennard recorded *Moneses* from "open heathy moorland but close to natural pinewood" (Lennard, pers. comm., 1993) about 3 km east of Nethy Bridge and south of Craigmore Wood but this has not been confirmed by our survey.

BANFFSHIRE (V.C. 94)

Moneses was collected between Dufftown and Drumuir in 1840 and 1890 (Anon (**E**)). Blizzard Bell (Greville 1841) and Dickie (1860) recorded the plant from Mortlach which could also be the same locality. It was found in Glen Livet by Keith in 1870 (**CMM**).

NORTH ABERDEEN (V.C. 93)

The earliest record for v.c. 93 is a collection from Haddo by Stewart in 1893 (**E**), but it has not been recorded subsequently from this site. Farther west, *Moneses* was collected in 1861 (Anon (**ABD**)) from a wood between Rhynie and Clatt. Since then, any habitat suitable for *Moneses* has been lost to agriculture.

Pirie (1906) recorded a small patch of *Moneses* from Bin Wood, 3 km north-west of Huntly, but recent searches have failed to refind the plant.

SOUTH ABERDEEN (V.C. 92)

Moneses has been recorded from possibly three localities. However, the collection from Braemar by White in 1877 (**ABD**) and the record from Ballochbuie Forest by Steven & Carlisle (1959) could

be the same locality. An undated specimen from "Burnwood, Kincardinshire" (Anon (ABD)), is probably from Burn of Wood near Kirkton of Glenbuchat.

ANGUS (V.C. 90)

Don recorded *Moneses* as "rare" in the Clova Mountains (Don 1813) but Gardiner (1848) questioned this locality. Don offered *Moneses* for sale from his Forfar nursery in 1813 but whether the source of Don's cultivated material was the Clova Mountains can only be guessed. This is the only known Angus record apart from a dubious specimen in OXF. This record is not included in Fig. 1.

EAST PERTH (V.C. 89)

Moneses was first reported from "near Perth ... in considerable abundance" by Bishop (1826) but less than a century later Barclay (1908) blamed collectors for the "greatly lessened quantity".

The plant was avidly collected from Scone between 1825 and 1833 (e.g. Gardiner 1848). Drummond-Hay holds the record for the largest number of specimens (25) on a single sheet. From this period 69 herbarium sheets and another 20 collections have been traced.

Sim (1859a) stated that *Moneses* "was found under the trees, among moss and grass, sparingly distributed over an area of about two acres [1 ha] ..." but revisited the site the next summer and "could only obtain a few rather stunted specimens" (Sim 1859b). However, the subsequent year he was more successful, advertising, "specimens of *Moneses grandiflora* ... will be supplied" (Sim 1860).

Several botanists including Hillhouse (1889), White (1898) and Barclay (1908) lamented the decline of *Moneses* at Scone and the last record traced from Scone is a specimen dated 1922 (PTH).

Records from Muirward Wood and New Scone are probably the same site and represent a second locality. Specimens were collected by Sadler in 1857 (E) (Balfour 1902) and the last record is Drummond-Hay's specimen of 1869 (PTH).

MID PERTH (V.C. 88)

Specimens collected from Methven by McNab in 1836 and Campbell in 1837 are in CGE and E respectively. However, Sadler and others failed to locate the plant there on an excursion in 1857 (Balfour 1902). A recent record for Craigvinean Forest in Strath Tay requires confirmation (Turl, pers. comm., 1998).

MIDLOTHIAN (V.C. 83)

Learmonth (1841) recorded *Moneses* from "Harburn Firwood", just south of West Calder. The rarer plants he listed have disappeared from this wood.

KIRKCUDBRIGHTSHIRE (V.C. 73)

This is the most southerly Scottish record. It was reported by Hillhouse (1889) as "Extirpated from Woodhead Hill, Traqueer [sic], Dumfriesshire". Woodhead Hill is within Mabie forest which is in the parish of Troqueer, south-west of Dumfries. No records of *Moneses* can be traced in the Floras of Dumfries or Kirkcudbrightshire.

WESTMORLAND (V.C. 69)

Borrer recorded *Moneses* from Bardsea, near Ulverston, where "he sought it unsuccessfully, notwithstanding 'a very particular direction' by Wright of Keswick" (Watson 1849). Baker (1885) doubted this record. The only English specimen is labelled "Westmorland" (det. Shillito 1820 (LIV)).

DISCUSSION

Moneses has been lost from at least 28 Scottish sites. More than half of these losses have been from north-eastern Scotland. There has apparently been not only a decrease in the abundance of the species but also a considerable contraction of its British range. As *Moneses* is easily overlooked, and appears to exist mostly in very small populations, it is possible that the plant is under-recorded, especially in the larger remnants of native pinewood. However, discoveries distant from well known areas for the plant are rare.

TABLE 3. HERBARIUM COLLECTIONS* OF *MONESES UNIFLORA* FROM SCOTLAND
(FROM 24 BRITISH HERBARIA)

Decade	Perthshire	Moray	East Sutherland	Easter Ross	Speyside	Grampian	Other	Total
1790s		3						3
1820s	1							1
1830s	31	1		31				63
1840s	30	1		3		1	1	36
1850s	9							9
1860s	14	2				1	1	18
1870s	3	26		1		2	2	34
1880s	1	2			4			7
1890s		4	9	1	18		2	34
							subtotal 1790–1899	205
1900s		1	9				1	11
1910s					2			2
1920s	1	2	6					9
1930s		1	9					10
1940s		1	1					2
1950s		2			3			5
1960s		1	5					6
1970s		1	1				1	3
1980s		2					1	3
							subtotal 1900–1989	51
Undated	8	2	2	1	2	1	0	16
Total	98	52	42	37	29	5	9	272

*A collection is defined as a plant or plants gathered from a named locality by one collector (where recorded) attached to a single herbarium sheet. Where two or more sheets with the same date, locality and collector have been distributed to different herbaria, these have been counted as separate collections.

Recently discovered populations have been spotted by chance, not by systematic searches of "lost" sites. *Moneses* is apparently able to persist for a considerable length of time in small, fragmentary populations, for example in Burgie Wood and The Mound. The small size of nearly all extant populations (Table 1) renders the plant vulnerable to habitat disturbance, a fact borne out by reports of *Moneses* disappearing from sites due to tree-felling or track-widening. Secrecy from those who should know about localities, rather than ensuring the plant's protection, is often more likely to result in its unwitting destruction, especially in managed plantations.

Although botanical collecting during the mid- to late-1800s (Table 3) was a major cause of decline of *Moneses* in Britain, this threat has now subsided. With the exception of traits that render *Moneses* sensitive to changes in its habitats, the main current threat is poor communication between conservationists, botanists and land managers.

Forestry practices have had both positive and negative effects on *Moneses* populations. Where modern plantations of exotic conifers have replaced old pinewoods, *Moneses* has been drastically reduced or lost, whilst some old Scots Pine plantations have either been colonised by *Moneses* or the plant has been introduced with stock. The latter may have been the origin of some populations on estates with large conifer plantings, for example Scone and Kilmory Estate, Lochgilphead.

Most of the British population of *Moneses* occurs on land which is managed for timber production. Therefore the future of the plant depends on sensitive management within areas of forests. In furthering this aim, considerable progress has been made in recent years by Scottish Natural Heritage (North Area) and Forest Enterprise maintaining regular and effective communication regarding the whereabouts of *Moneses* populations.

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Changes in the distribution and abundance of *Himantoglossum hircinum* (L.) Sprengel (Orchidaceae) over the last 100 years

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ABSTRACT

1. Species are likely to be most sensitive to climate change at the geographic limits of their distribution. The behaviour of such populations may therefore be a predictor of the response of the species to global change.
2. The northern limit of the Lizard Orchid, *Himantoglossum hircinum*, occurs in England, where 16 populations are currently known. British records over the past 100 years are particularly accurate for this species and it was one of the first for which changes in distribution were linked to an amelioration of climate (Good 1936).
3. Early records were checked to confirm the rise in population number in the early part of the century. Analysis of more recent data showed that this was followed by a sharp decline and numbers have only been rising again over the last decade. The range expanded with the earlier increase in population number, but did not contract as populations were lost.
4. Data collected between 1977 and 1998 in the largest population allowed flowering probability and seed production to be correlated with rainfall during the growing season. Analysis of the resulting model showed that both observed rises in population number followed periods during which the seasons for vegetative growth had been wet.
5. Populations have become both larger and more persistent due to an increased interest in conservation.
6. Changes in the abundance of *H. hircinum* are likely to depend on other factors, including patterns of human activity, as well as on climate change.

KEYWORDS: rainfall, life-cycle, range-limits, seed production, climate change.

INTRODUCTION

There is currently a great deal of research being undertaken to assess the effects of climate change on the distribution and abundance of individual species (e.g. Carey & Brown 1994; Sykes *et al.* 1996; Parmesan 1996). This research is based on the theory that ultimately the distribution of a species is limited by its physiological responses to climate. One of the earliest exponents of this theory was Ronald Good who in 1931 proposed his "Theory of Tolerance". He supported his theory with a paper on the distribution of the Lizard Orchid *Himantoglossum hircinum* (L.) Spreng. (Good 1936). In this paper he suggested that the increase in the distribution, and also the numbers of *H. hircinum* records, in the early part of this century were due to a climate change. Specifically, Good indicated that it had been "an amelioration of winter and spring temperatures and a slight increase in the preponderance of winter rain" that had made England similar to western France, which is at the heart of the species' range.

If Good was correct, we might expect that the distribution and abundance of *H. hircinum* in England would have increased further if the climate continued to be amenable. Furthermore, at least one climate scenario (Viner & Hulme 1994) suggests that England will become more like south-western France in the coming decades. Therefore, if *H. hircinum* does respond as Good suggested, we might expect the distribution and abundance of the species to increase (Carey & Brown 1994).

In this paper Good's theory is re-evaluated by re-analysing the early records of *H. hircinum* and also by adding records from the years 1934–1998.

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DATA AND METHODS

HISTORICAL DATA

The records used in this paper come from many sources. The Biological Records Centre (B.R.C.) at Monks Wood holds a historical database for species in Great Britain and has provided the majority of data. Within the B.R.C. file on *Himantoglossum hircinum* (L.) Sprengel is a large body of information collated by Mrs G. Crompton and L. Farrell to whom I am indebted. This information includes copies of correspondence between Good and various botanists within England and abroad as well as the notes he used to produce the 1936 paper. The record cards from the B.R.C. hold information on the date the species was seen, where it was seen and by whom. There are also sections for information on habitat and notes. The notes section often contains information on the number of flowers or plants seen.

Interpreting the records was not straightforward. It was not uncommon to have records from the same site in the same year given by different individuals who use different names for the location as well as different map references. Despite these inconsistencies it is almost always possible to determine which records are the same. I am fortunate that most of this work was done by others before me, by Good for the earlier records, and by G. Crompton and R. Fitzgerald for all records. I have added to their records by carefully re-reading the record cards, checking sources and correspondence on the species. The most modern records were supplied by M. Wigginton at the Joint Nature Conservation Committee and from personal observations.

The records suggest that two populations have arisen from garden escapes but there may be others. These two are included here. Several populations are due to "well-meaning naturalists" who transplanted whole plants to new sites and counties. The number of these "introductions" is impossible to estimate but any records that are known to have been due to introductions have been discounted from this analysis.

CONTINENTAL DISTRIBUTION

Himantoglossum hircinum is spread over much of southern Europe and a map of this distribution is published (Meusel *et al.* 1965) and also digitised on to an Atlas Flora Europaea grid (Carey *et al.* 1993). The species is especially common in the wine-growing regions of France where it is noted as a roadside weed growing on a wide range of neutral to basic substrates including broken concrete.

DEMOGRAPHIC CHARACTERISTICS

"How long do *Himantoglossum hircinum* seeds take to germinate?" and "how long does the protocorm which develops remain underground before a leaf is produced?" are questions that, as yet, are not fully resolved. A recent study (P. Carey & H. Scott unpublished data) following the methodology of Rasmussen and Whigham (1993), has shown that 0–10% of seeds had signs of mycorrhizal infection (the first stages of germination) in the first autumn and winter after they were produced in 1996 whereas 10–40% of seeds produced in 1997 became infected almost immediately. The difference between the two autumns was that 1996 was dry and 1997 was wet. At the time of writing no seedlings have been noted from either 1996 or 1997 seeds. There is anecdotal evidence to suggest that seedlings appeared three years after an isolated plant flowered for the only time (Good 1936). A matrix of plant states (Table 1), calculated from data collected from two permanent plots at the largest population in England from 1985–1994 (P. Carey & N. Stewart in prep.) indicates the proportion (0.59) of plants remaining at this "seedling" stage from year to year is very high. The low death rate of large and medium plants in the transition matrix (Table 1) also indicates that *H. hircinum* can be a long-lived plant. Some individuals first censused in 1987 are still alive and flowering today (L. Farrell, pers. comm., N. Stewart, pers. comm.). Many of these plants flower in successive years but, more importantly for this study, many do not. One individual plant in Sussex flowered in 1984, then again in 1995 and 1996, but never in between. It is also not unusual for plants to remain underground as tubers during any one year (N. Stewart, pers. comm.; L. Farrell, pers. comm. and pers. obs.).

In this paper the growing season is defined as September to August. The plant is typically wintergreen, emerging with the autumn rains anywhere from late August to April (G. Crompton, pers. comm., L. Farrell, pers. comm.; N. Stewart, pers. comm. & pers. obs.). Most plants are

TABLE 1: TRANSITION MATRIX FOR MOVING FROM ONE LIFE STAGE TO ANOTHER FOR *HIMANTOGLOSSUM HIRGINUM*. TRANSITIONS ARE TAKEN AS THE MEAN TRANSITION PROBABILITIES FROM NINE YEARS OF DATA FROM TWO PERMANENT 10 × 10 M PLOTS AT THE LARGEST POPULATION IN ENGLAND.

Plant size	seedling	small	year t+1		death
			medium	large	
year t					
seedling	0.59	0.18	0.01	0.00	0.22
small	0.15	0.50	0.28	0.01	0.06
medium	0.03	0.10	0.47	0.38	0.02
large	0.01	0.07	0.18	0.71	0.03

apparent by November and only very small plants (seedling category in Table 1) emerge after this. The plants flower from late June to late July. Data collected from three permanent plots within the largest population in England between 1977 and 1994 (Carey & Stewart in prep.) were compared with climate data from the nearest weather station at Manston which is approximately 8 km north of the population. These data showed that the probability of a large plant flowering (Y) in growing season t is related ($R^2 = 61.8$, $F = 25.29$, $p < 0.001$) to the precipitation (X) in the months September–April (the vegetative growth phase) in growing season t-1 (Equation 1). Therefore the flowering “initial” is likely to be determined by the size of the tuber set in the growing season before the growing season in which flowering takes place.

$$Y_t = 0.382 + 0.0019X_{t-1} \quad \text{Equation 1}$$

The production of seed pods was noted in the years 1988, 1989, 1991, 1992 and 1997. The number of pods produced per flowering spike (S) in growing season t was related ($R^2 = 90.00$, $F = 26.89$, $p = 0.014$) to the rainfall (X) in the growing season t (Equation 2).

$$S_t = -10.768 + 0.0343X_t \quad \text{Equation 2}$$

No relationship was found with temperature and flowering or seed pod production at this site.

The green leaves of this plant tend to brown either just before or during flowering. The plant then enters a brief dormant phase. Plants are maintained during the dormant phase by means of a tuber. If the plant is pollinated seeds take at least six weeks to ripen (L. Farrell, pers. comm.) and mature from late July to late August or even the beginning of September (pers. obs.). No relationships between climate and the seed ripening phase and dormant phase were found.

The seeds are approximately $130 \times 30 \times 30 \mu\text{m}$ and are assumed to fly long distances. However a large number of seeds remain lodged in many pods so that when the flowering stalk falls over the seeds drop near to the parent plant. This has led to swarms of seedlings around parent plants in the years 1987–1995 at the two largest populations (Carey & Stewart in prep; L. Farrell, pers. comm. and G. Crompton, pers. comm.).

DATASET

A dataset was assembled which includes date of record, national grid reference, number of vegetative plants seen, number of flowering plants seen, habitat, and reason for disappearance (if appropriate). This dataset allowed the persistence of populations to be calculated. For many populations a record was not made in each year but it was often possible to make the assumption that the population persisted. In the case of two records at Box Hill in Surrey which are 106 years apart I, like Good (1936), have assumed that these are independent and demonstrate the recolonisation of a suitable site. There have been two populations at Burnham-on-Sea in Somerset but these are separated by approximately 8 km and 60 years and I have assumed that these records are not the same population. Unlike Good I have been more ready to accept that separate records at the same site are the same population. This is based on the demographic information gathered from seven populations, which indicates that there can be a long interval between generations and also that plants can remain in a less conspicuous state for many years. Both of these reasons would allow for the absence of records from a particular site.

Records before 1895 are very widely spaced in time and make interpretation, especially of

figures, difficult. So for clarity in most of the Figures in this paper I have only analysed the period 1895–1998. Details of the earlier records are given by Good (1936).

Although many of the records are accurate to 1 km some are only accurate to 10 km and this, along with the need to keep the location of some sites secret, means that maps of the distribution of sites in England presented in this study are based on a 10 km grid.

If it takes three years for a seedling to appear (Good 1936), and another three years to become mature (P. Carey & N. Stewart in prep.) a time-lag of about six years would exist between the climatic conditions which lead to establishment and the date of first record for a population (although there may have been some delay between a plant first flowering and the first year in which it was seen).

In order to investigate the effect of climate on *H. hircinum* at the national level it was appropriate to use national weather statistics. Mean monthly rainfall data for England and Wales, supplied by P. Jones at the Climatic Research Unit at the University of East Anglia for the period 1895–1994, were available to compare with the records of *H. hircinum*. Equations 1 and 2 were applied to the rainfall data to give a probability of flowering and pod production for each growing season of the sequence. The product of these two equations gave a rough estimate (the standard error of this product based on the variance of Equations 1 and 2 was 0.54) of seed pod production per flowering plant in each year and, when multiplied by the number of populations recorded (assuming each population only had one flowering plant), an estimate of national seed pod production was obtained. The effect of severe droughts (more than 100 mm below the mean rainfall) on seeds was mimicked by reducing the seed pod production of year t, year t-1 and year t-2 in the model to zero. A six year time-lag was added to the date populations were recorded. Decadal smoothing was applied using LOWESS techniques (MINITAB 11) to both the data of the number of records and the estimate of seed production to mask some of the bias that is inevitable in the process of recording on a national scale.

RESULTS

Reassessment of the records has led to a few discrepancies between the data presented here and those in Good (1936). There are additional records of which Good was not aware and a number of records that Good considered as geographically separate which I consider were not. The population recorded in north-western England at Ingleborough Hill in 1810 (herb. G. B. Woodruff) seems the most unlikely of any that was not documented by Good and I ask the readers of this paper to look on it with scepticism.

The number of *Himantoglossum hircinum* populations in England varies dramatically with time (Fig. 1). There is a marked peak towards the end of the 1920s and early 1930s which is followed by a rapid decline and a remarkably constant number of populations from 1950–1990. Since 1990 there has been a rise in the number of populations.

There is a high turnover of populations with a high proportion of new records and a high proportion of populations disappearing from the records (Fig. 1) throughout the period 1895–1998.

Predictably, the mean age of populations declined as the number of populations increased (Fig. 2). Since 1940 the mean age of populations has increased steadily.

For 439 of the 750 records of *H. hircinum* it is possible to infer the number of flowering plants present in the population. This provides data from at least one year for 116 of the 201 populations. The total size of the population is known for 193 out of the 750 records which represents at least one year from 39 different populations. The mean size of *H. hircinum* populations has not increased over the last 100 years but since 1945 two populations have become much larger than any other recorded in England. One population on a golf links in Kent produced over 3000 flowers in 1991, although few of these produced any seed pods. This population was an order of magnitude larger than the other substantial population in Cambridgeshire, which was itself an order of magnitude larger than any other population.

The distribution of populations within England was mostly restricted to the south-eastern corner of England before 1910 with most of the populations being found around Dartford (Fig. 3a). During the next 30 years populations appeared in many of the counties of southern England (Fig. 3b). Despite the dramatic fall in the number of populations after 1940 the distribution of populations has not contracted (Fig. 3c) to the distribution that existed before 1910 (Fig. 3a).

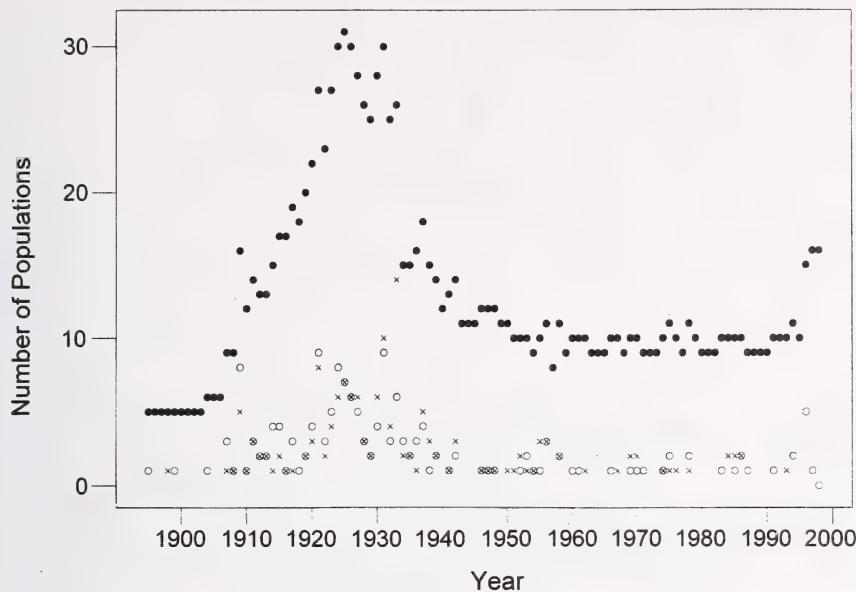


FIGURE 1: The number of populations of *Himantoglossum hircinum* present in England each year since 1895 (solid circles), the number of populations that are first records (open circles) and the number of populations with a last record in that year (crosses). For clarity, only years where there was at least one record of a new population are shown and also only years where there is at least one last record are shown.

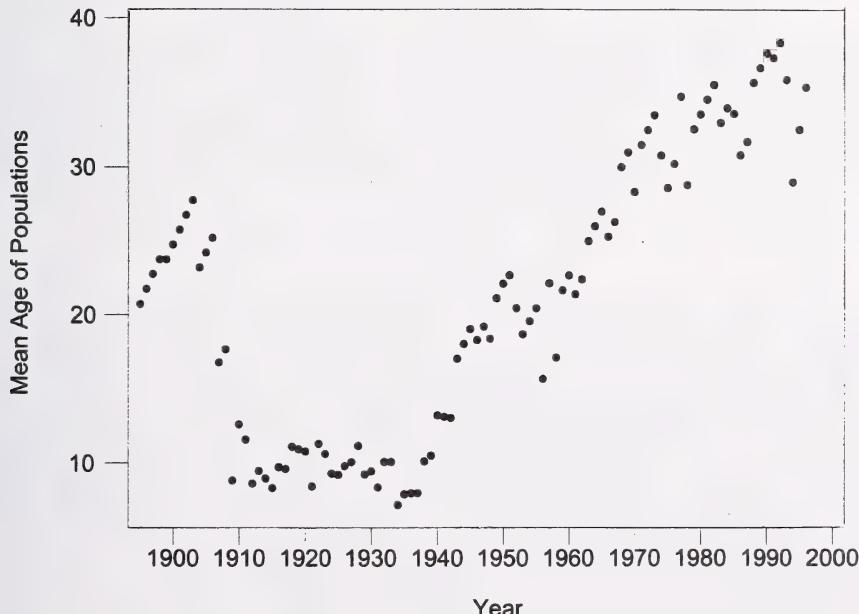


FIGURE 2: The mean age of populations of *Himantoglossum hircinum* in England from 1895 to the present.

a



b



c

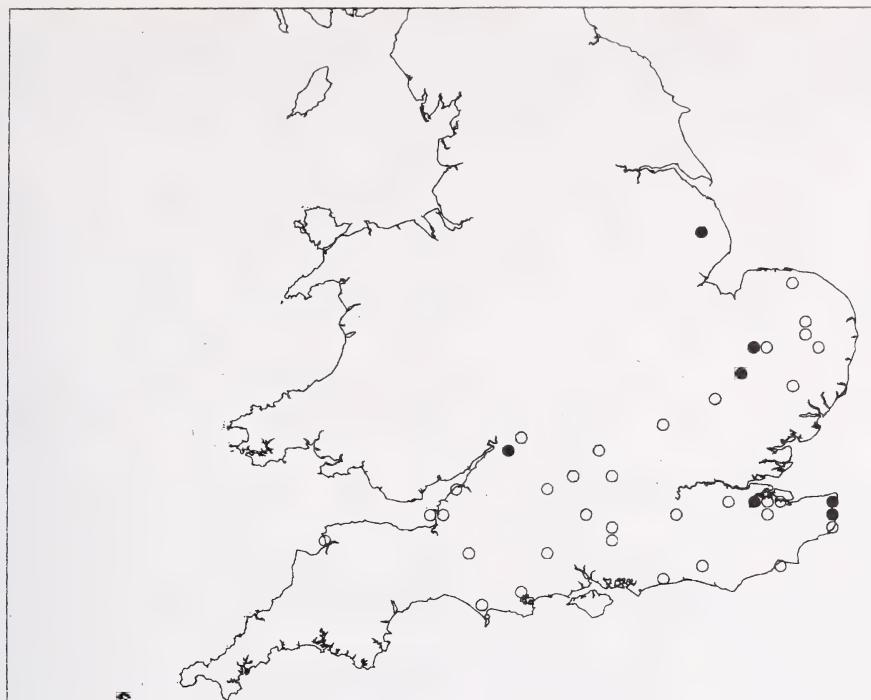


FIGURE 3: The distribution of *Himantoglossum hircinum* in England; a: all records from 1641–1910, b: 1911–1940, c: post 1940. Open circles denote one population, solid circles denote two populations, open triangles 3–5 populations. An open square represents the area around Dartford before 1910 which had 14 populations.

The results of applying the seed pod production index to the rainfall data from 1895–1995 suggested that there was probably a rise in the seed production of *H. hircinum* during the years of the First World War (1914–18) (Fig. 4). This was followed by a second peak around 1930. Subsequently, there was a period of low seed production until the 1970s. Since then there have been three peaks in the seed production index favouring seed production, each peak being higher than the last.

DISCUSSION

Evidently the abundance (Fig. 1) and distribution of *Himantoglossum hircinum* (Fig. 3) increased markedly in the early decades of this century. The reasons why there was such an increase are not easy to determine. The amelioration in the climate proposed by Good is partly supported by the seed production model (Fig. 4). A period of conditions favouring seed production and survival in the second and third decades of this century coincides with the rise in the number of populations and the recent period of high rainfall, and therefore suitable conditions, has lead to the rise in the number of populations from a stable 10 or 11 between 1950 to 1990 to 16 by 1998. What the model does not explain is the decline in the number of populations. There is no obvious climatic cause for the death of populations, although it is possible that temperature could be a factor. However, as temperature could not be related to the performance of *H. hircinum* at the site in southern England between 1977 and 1997 no model could be proposed from those data. The lack of a relationship with temperature at the population in Kent may be because temperature only becomes a limiting factor further north. More detailed analysis of plants growing at the very northern edge of the distribution would be required to gain this information. In the last two years (pers. obs.) mortality

has greatly exceeded the levels observed between 1987–94 (Table 1). The mortality of large plants followed the extreme droughts during the vegetative growth phase of the growing seasons 1995–96 and 1996–97. Severe drought could therefore explain the death of small populations. Detailed experiments (Woodward 1987, 1990) to determine the physiological limits of this species will be required, along with further analysis of long-term population data, to determine which climate factors are crucial in determining population survival.

There are several factors other than climate that might explain the rise and fall of *H. hircinum*. The first of these is land-use change. There was a large increase in the area of land set-aside to grassland in the south-east of England in the last decades of the 19th century after the passing of the "Corn Laws" of 1846 (Stamp 1948). Some of this land was ploughed again between 1914 and 1919. This land then went out of arable agricultural production until the start of the Second World War. After the Second World War much of the ploughed land remained in production. Large areas of remaining chalk grassland were lost to scrub as myxomatosis decimated rabbit numbers. The period in which *H. hircinum* showed its greatest expansion coincides with the era of least management of marginal farming lands in south-eastern England. Only 52% of the population records are detailed enough to list the habitat that the plants were growing in. Of those records that do list a habitat (Table 2) 50% of the populations lived in habitats that were along linear features or in pits and another 15% were found in managed grassland. These habitats were not affected by agricultural land-use. Only 14% of populations where habitat was listed were found on grassland that would be affected by the agricultural land-use change listed above (Table 2). All the populations where substrate was listed grew on calcareous soils or substrate, typically chalk, until 1996 when two populations growing on neutral soil were discovered and one growing on tarmac (Table 2). Either *H. hircinum* is becoming less constrained by substrate type, or the neutral soils and tarmac are overlaying calcareous substrate, or earlier records on neutral soils were not listed.

Populations were and still are found on earthworks, notably roadside verges and railway embankments (Table 2). It has been shown that south-facing slopes provide a microclimate that is analogous to flat areas many miles further south in latitude (Pigott 1968). This hypothesis would seem to be supported by the preference of *H. hircinum* for sloping embankments at the northern edge of its range. Unfortunately the theory fails at the large Cambridgeshire colony where most plants are found on the north-eastern facing slope of an earthwork where it is noticeably cooler than other parts of the site. I suggest that disturbance and/or a lack of a dense grass sward probably make earthworks a suitable habitat. The increase in building of roads and railways in the second half of the last century and the early years of this century would have led to a large increase in the available habitat for *H. hircinum* and could explain the increase in the number of populations. The subsequent decline of the species cannot be explained by a subsequent decline in the area of earthworks as road building has continued throughout this century and increased after the Second World War.

A change in "recorder effort" might explain the pattern shown in Fig. 1. It may be no coincidence that the number of populations recorded plummeted just after Good wrote his paper. The recording of plants in England went through a depression during the late 1930s and 1940s but has been relatively consistent and accurate since the end of the Second World War. Therefore, the decline in the number of populations was not necessarily as sudden as that shown in Fig. 1 but may have declined more steadily. The number of populations recorded from about 1948 onwards can be considered reliable.

The pattern of increase in the number (Fig. 1) and distribution (Fig. 3) of populations and the subsequent decline in number but not distribution is similar to patterns described for infectious diseases (Mollison 1986). In the case of *H. hircinum* perhaps there was an "outbreak" caused by an increase in the number of susceptible sites, and the decline was caused by a reduction in the number of susceptible sites. Factors limiting the population biology of diseases can at times be relaxed and allow an outbreak. Similarly the limiting factors on the success of *H. hircinum* may have relaxed at the end of the 19th century. Amenable climatic conditions could have promoted the "outbreak" with a period of less favourable conditions at the end of the 1930s and 1940s detrimentally affecting the population parameters that would have allowed persistence (Mollison 1986). The seed production model provides an explanation for the "outbreak" during the first three decades of this century and a reason why populations did not increase further between 1935 and 1975. The model also suggests that we may be at the beginning of another "outbreak". Further research is required to identify the climatic conditions that might explain the decline in the number of populations.

TABLE 2: THE SUBSTRATE AND LAND-USE ON WHICH *HIMANTOGLOSSUM HIRCINUM* HAS BEEN RECORDED. THE PERCENTAGE OF RECORDS FROM THOSE WHERE SUBSTRATE AND/OR HABITAT WERE LISTED IS GIVEN AS IS THE PERCENTAGE OF THE TOTAL OF 201 SITES. LAND-USE IS SEPARATED INTO MAN-MADE LINEAR FEATURES, PITS, MANAGED GRASSLAND AND "UNMANAGED" GRASSLAND.

	Percentage of listed sites	Percentage of total
SUBSTRATE		
chalk	67.2	19.4
dunes/links	10.3	3.0
limestone	3.4	1.0
coraline oolite	3.4	1.0
glacial sand	1.7	0.5
sand and stones	1.7	0.5
gravel/clay	1.7	0.5
gravel	1.7	0.5
chalky gravel	1.7	0.5
tarmac	1.7	0.5
neutral soil	3.4	1.0
(unlisted 71.1%)		
LAND-USE		
Linear features		
roadside verge	16.7	7.0
path/trackside	3.8	1.5
green lane	7.1	3.0
railway cutting/embankment	7.1	3.0
tarmac	1.2	0.5
wall	1.2	0.5
earthwork	4.8	2.0
Pits		
chalk pit	7.1	3.0
gravel pit	1.2	0.5
Managed grassland		
golf course	8.0	3.5
garden	3.8	1.5
parkland	2.4	1.0
churchyard	1.2	0.5
Unmanaged grassland		
edge of wood	8.0	3.5
edge of scrub/hedgerow	4.8	2.0
grassland	13.7	5.5
common	1.1	0.5
dune slacks	1.1	0.5
beach	1.2	0.5
riverbank	1.2	0.5
heath	1.2	0.5
pasture	1.2	0.5
uncultivated land	1.2	0.5
(unlisted 58.2%)		

The large and rapid increase of *H. hircinum* in England in the early part of this century could also have been due to an increase in the number of seeds arriving from France if the species became much more abundant in France. This theory may be testable but the abundance of *H. hircinum* in France before 1978 is unknown to the author. Changes in the weather of northern France are highly correlated with those of southern England and it is reasonable to assume that seed production in northern France is high in years when it is high in England. If France was the source of the seeds it could be instructive to think of a large core-population in that country with mostly satellite populations in England (Gotelli & Simberloff 1987). Satellite populations seldom reach an adequate size to maintain themselves without further input of individuals.

There is one other seed vector responsible for at least some populations. Many plants were collected, especially from France, and planted in gardens especially in the 19th century; to a lesser extent this is still occurring today. Potential escapes from these introduced plants, and introductions into the wild, make any proposed study of metapopulation dynamics awkward but not impossible. Of course, there were many more movements of people between France and England during the peak seed producing years 1913–1917 than is normal because of military activity. The adhesive properties of the seeds (pers. obs.) may have led to accidental transport of seeds from France during this period.

Populations die out for several reasons. Individuals can apparently be killed by drought. They can be dug-up or picked (Table 3), their habitat can be destroyed or there can be a slow change in the plant community e.g. a grassland may become covered in scrub. Of the 201 populations recorded the fate of 73 can at least partly be deduced from details in the record. Sixteen populations can be considered extant, 40 populations or large parts of populations were picked or dug-up by collectors, six populations died out because of disturbance to the habitat, e.g. ploughing, four were built upon, three became overgrown, two were mown and one was trampled and/or grazed by horses. Curiously, the earliest population recorded was lost in 1641 due to the road becoming wider (Pearsall & Hall 1933). This surely must be the first recorded damage caused to rare wildlife by road improvement.

The two largest populations in England may now be large enough to sustain themselves and act as core-populations unless the habitat in which they live is totally destroyed. As both populations are spread over an area greater than 500 m² it would have to be a considerable disturbance event to remove the habitat completely. As both of the sites are managed for the protection of the species, land-use change is also unlikely to cause their demise. In the last three years three new populations have been recorded several kilometres to the north-east of the largest population in Kent and are likely to have originated from seed being carried by the prevailing south-westerly winds from the largest population.

In addition to the three new sites listed above, seven other new populations have been recorded and these are widely scattered over southern England. It is difficult to predict such a distribution from wind dispersal alone as typically most seeds are only predicted to be dispersed up to a few hundred metres (Carey 1998). Three of these populations are on golf courses, one is on a road-side verge, two more populations are on chalk grassland and the last population is growing on broken

TABLE 3: NUMBER OF POPULATIONS PICKED OR DUG-UP IN ENGLAND.

Period	Number of populations	% of populations
pre 1901	14	37
1901–1910	1	5
1911–1920	3	8
1921–1930	8	11
1931–1940	11	19
1941–1950	1	6
1951–1960	1	5

The last population eradicated by this method was in 1952.

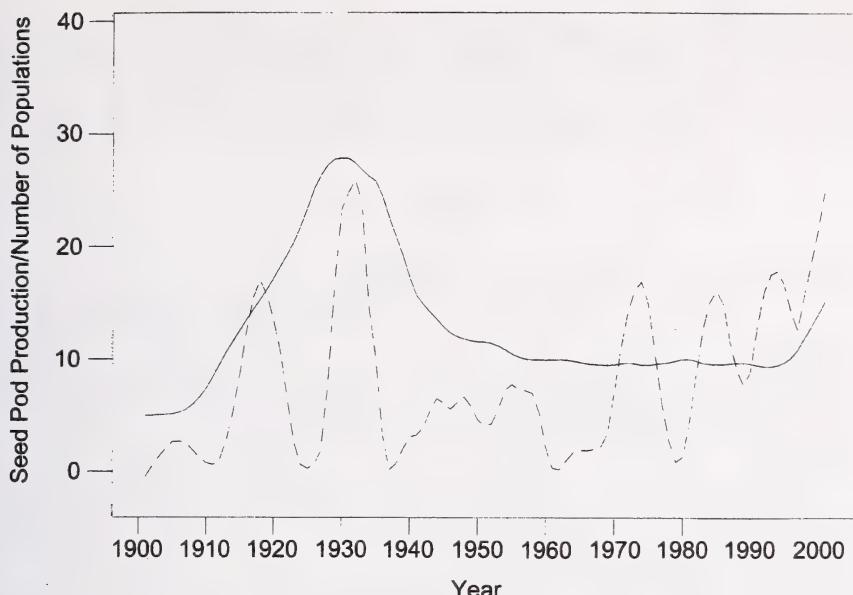


FIGURE 4: The number of populations of *Himantoglossum hircinum* (solid line) compared with the modelled annual seed pod production (advanced by six years) of *H. hircinum* in England (dashed line). Both lines have undergone decadal smoothing.

tarmac. Of the 16 extant populations six are on golf courses. This may indicate that golf courses (especially golf links) provide large areas of suitable habitat for *H. hircinum*. It is certainly possible that golfers provide a vector for the adhesive seeds that are subsequently deposited on other courses.

The protection of this species under law and a change in attitude to the collection of wild plants probably explains the increase in the persistence of populations since the Second World War (Fig. 2). The high percentage of populations picked or dug-up before 1901 (Table 3) is partly related to the fact that the records from this period largely come from herbaria and must have been picked to be placed in the herbaria. At least 19% of all the populations recorded in the 1930s were picked or dug-up (Table 3) which helps to explain why there was such a rapid decline in the number of populations in the late 1930s.

CONCLUSION

It seems that Good (1936) had good reason to believe that it was an amelioration in the climate that lead to the increase in the number of populations of *H. hircinum* in the early part of this century (Fig. 4) although the critical factor was increased rainfall and not temperature. The model created from demographic data collected in southern England showed that two successive wet growing seasons that were not followed by a severe drought were required to produce viable seeds. When the model was extrapolated to the rainfall data for England from 1895–1995, favourable conditions for establishment existed between 1910–1930 and post 1975. These conditions coincide with the peaks in the number of populations recorded in England.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Ronald Good. Writing it would not have been possible without the help of Mrs G. Crompton, R. Fitzgerald, L. Farrell and all the volunteer recorders of the Botanical Society of the British Isles. I would also like to thank many of my colleagues at Monks Wood, two anonymous referees and N. Stewart for suggestions to explain the pattern in Fig. 1. The work was carried out with partial funding from the N.E.R.C. TIGER IV 3a project T03088b6.

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Taxonomic separation of *Ulex minor* Roth. and *U. gallii* Planch.: morphometrics and chromosome counts

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ABSTRACT

Morphological separation of species in the genus *Ulex* (Fabaceae) is difficult because they and their hybrids seem to show overlaps in the ranges of all characters. Chromosome counts offer a method of accurately assigning plants to species, which can then be used to obtain definitive measures of character ranges. This study was carried out in order to address the issue of the identification of the two closely related species *Ulex gallii* Planch. and *Ulex minor* Roth., and to investigate hybridisation between the two species. Chromosome counts from 135 individuals growing at a site in Dorset gave results of $n = 16$ for 53 plants and $n = 32$ for 82 plants. These counts are those usually reported for *U. minor* and *U. gallii* respectively. There was no chromosomal evidence for any *U. gallii* \times *U. minor* hybrids.

Using chromosomal identification of species, measures of one vegetative and five floral characters were compared. All characters showed species differences, but all overlapped to a greater or lesser degree and could not be used individually to separate the species consistently. Use of a suite of characters gave more reliable separation of the species, but a small proportion of plants (1.5–2.5%) were misclassified. Use of the character ranges reported by Proctor (1965) gave less reliable identification, with 7% of plants misclassified.

Two possible barriers to hybridisation between the two species were investigated. The species show slightly asynchronous flowering, but this is probably insufficient to prevent cross-fertilisation. Both species had very similar insect pollinator assemblages, and it is concluded that interspecific pollen transfers between *U. gallii* and *U. minor* can and do occur.

KEYWORDS: *Ulex gallii* \times *U. minor*, discriminant analysis, gorse, phenology, pollinators.

INTRODUCTION

Ulex minor Roth. and *U. gallii* Planch. (Fabaceae) are very similar morphologically and difficult to separate (Gloaguen 1986; Proctor 1965). Following a study by Proctor (1965) they are usually distinguished by measures of particular characters such as lengths of standard, calyx or primary spine, or bush size. Studies which have measured large numbers of plants sampled over southern Britain (Proctor 1965), Brittany, France (Gloaguen 1986) and Dorset, England (Bullock *et al.* 1998) have demonstrated that the two species can be largely separated by morphometrics, but a substantial minority of plants of both species have character values which overlap with those of the other species. Therefore, the problem arises of whether it is possible to assign plants with intermediate characters to one or the other *Ulex* species with confidence.

Cytological methods provide an unambiguous way of separating the two species. *U. minor* is diploid ($2n = 32$) (Alvarez Martinez *et al.* 1988; Bullock *et al.* 1998; Castroviejo & Valdes-Bermejo 1990; Fernandez Prieto *et al.* 1993; Misson 1990; Misson & Gourret 1996) and *U. gallii* has been shown to be either tetraploid ($2n = 64$) (Bullock *et al.* 1998; Fernandez Prieto *et al.* 1993) or hexaploid ($2n = 96$) (Misson 1990; Misson & Gourret 1996). Although several studies have reported both tetraploid and hexaploid *U. gallii* (Alvarez Martinez *et al.* 1988; Castroviejo & Valdes-Bermejo 1983; Fernandez Prieto *et al.* 1993), it is sufficient for taxonomic separation that the two species have consistently different ploidy levels.

However, the link between chromosome number and morphology in these two *Ulex* species has never been made explicitly. The consistent ploidy differences between the species in the studies reported above would suggest that the authors have had few problems in distinguishing the species

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when sampling in the field. However, it is not clear whether difficult or intermediate specimens have been avoided in these studies. Bullock *et al.* (1998) went one stage further and carried out chromosome counts on specimens identified in the field using Proctor's characters. This paper takes the final step and provides numerical data on the correlation between chromosome number and the values of a range of morphological characters. The strategy is to use chromosome counts to assign plants definitively to one ploidy level and thus (by extension) to one species, and then to investigate whether one or (more probably) a combination of morphological characters serve to separate the species accurately and completely. This approach was used recently by Cubas & Pardo (1997) to investigate differences between *U. europaeus* subsp. *europaeus* and *U. europaeus* subsp. *lactobractaeus* in the Iberian peninsula. We also used this methodology to determine to what extent the widely-used character values reported by Proctor (1965) gave accurate identification of plants when tested against chromosome counts.

Taxonomic problems are complicated further by the possibility of hybridisation between the two *Ulex* species. Such hybrids were suggested by Corillion (1950) and Lambinon (1962), but these observations are not convincing as they are based on morphological observations. A survey carried out by Bullock *et al.* (1998) in a mixed population in Dorset found 84 plants with $2n = 32$ or $2n = 64$, but one plant had $2n = 48$ chromosomes. If this count, which had never been reported before, does indicate the existence of hybrids between *U. minor* and *U. gallii*, then such hybrids appear to be extremely uncommon. A secondary aim of the study reported here was to search for plants with this intermediate chromosome number and to characterize them morphologically.

U. gallii and *U. minor* are strictly insect-pollinated, allogamous plants. Little work has been carried out on the ecology of these species, so we used this opportunity to obtain information on their flowering phenology and insect pollinators. These data were used to carry out a preliminary investigation into the reasons behind the very low proportions of hybrids even in mixed populations (Bullock *et al.* 1998). Barriers to the hybridisation of two species can be due to geographical, ecological or phenological factors (Leebens-Mack 1998; Weiblen & Brehm 1996). There are many factors controlling the production of hybrid plants, such as pollen-stigma interactions, ovule abortion, viability of seed, or fitness of the hybrid offspring (Carney *et al.* 1996; Weiblen & Brehm 1996). However, here we look at just two: the identity of pollinators and the degree of synchrony in flower production.

To summarize, the following questions were addressed in this study:

1. Can *U. minor* and *U. gallii* always be distinguished accurately using morphometrics, when checked against chromosome counts?
2. Are there *U. gallii* \times *U. minor* hybrids, as detected using chromosome counts?
3. Are there any differences between *U. gallii* and *U. minor* in flowering phenology?
4. Are there differences in pollinator assemblages and/or pollinator behaviour which could act as a reproductive barrier between *U. gallii* and *U. minor*?

METHODS

The distributions of *U. gallii* and *U. minor* overlap in Dorset, England, but most heaths only contain one of these species of *Ulex* (J. M. Bullock unpublished data). The study site was Gore Heath (SY/924.900), where the two species are intermingled and grow in close proximity. This was ideal as it provided a situation where separation of the species was most difficult, where hybrids were most likely to occur, and where pollinator behaviour on both species could be observed. This is an area of mixed dry and humid heath, dominated by the two *Ulex* species, *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Ulex europaeus*, *Molinia caerulea*, *Agrostis curtisii* and *Agrostis capillaris*, with scattered *Pinus sylvestris* and *Betula pendula*.

In early July 1998, four 50 m transects were laid out in Gore Heath: two in areas where *U. minor* was more abundant than *U. gallii*, and the other two in areas where *U. gallii* was the predominant species. Along the transects, each bush of either *Ulex* species touching the transect line was marked – 135 plants in all. These plants were then sampled in different ways.

CHROMOSOME COUNTS

Chromosome counts were made using the same methods as Bullock *et al.* (1998). During mid- to late July flower buds of c. 2 mm length were collected from each plant and fixed in the field in Carnoy's fixative (3:1 glacial acetic acid:ethanol). The buds were refrigerated for at least 48 hours. The anthers were then dissected out on a microscope slide in a drop of aceto-carmine, and squashed under a coverslip. Gametophytic counts of stained chromosomes were made from pollen cells at metaphase 1 for at least two buds from each plant.

MORPHOMETRICS

One vegetative character and four floral characters were measured on each of the marked plants during mid-August 1998, but measures of the flower parts were not taken for seven individuals which were not in flower by that time. Measurements of the length of the longest primary spine on the flowering shoot were taken in the field: five measures were taken on different branches for each bush.

For the floral characters, five fully opened flowers were picked from each bush and kept chilled. Within 24 hours of collection each flower was measured for the length of the calyx, standard, keel and wings to the nearest 0.5 mm. The five measures taken for the five characters were used to calculate the mean of each character for each bush.

PHENOLOGY

Gloaguen (1986) described three phenological stages for *U. gallii* and *U. minor*. Stage 1, the closed flower bud. The size of the bud can be variable but only the sepals are visible. Stage 2, the more-or-less opened flower before fertilization. This is from the stage the flower begins to open showing the tip of the standard, to the fully opened flower. Stage 3, the flower after fertilisation. The flower withers and the petals burnish and fade. Once they have dropped, the pod becomes visible.

We monitored all three stages, but only stage 2, the receptive flower, is considered as this is the stage of relevance to hybridisation. Between 13 July and 10 November 1998, at intervals of an average of 11 days, the stage 2 flowers were counted on two branches for each of the 135 bushes. The amount of each branch sampled was restricted to the last 12 cm of the main branch and side branches within a 12 cm spread from the main branch. This was to keep the length of branch sampled roughly equivalent between bushes. The same branches were sampled at each census. As far as possible, the branches sampled were chosen in two different parts of each bush – for example one on the top and one on the lower part of the plant – in order to take into account the flowering heterogeneity within each individual.

POLLINATOR OBSERVATIONS

The pollination of *Ulex* spp. is described by Proctor *et al.* (1996). The flowers lack nectar, but are freely visited by bees. When a bee forces entry into a fresh flower, this causes the keel petals, which are held straight by the stamen tube and the style, to break apart. The uncovered stamens and style are brought sharply into contact with the underside of the insect, so dusting it with pollen. This is an explosive pollen-presentation mechanism. Once "exploded", the spent flower hangs limply open and is seldom visited again by insects.

Monitoring of flower visitations was carried out over eight 30 minute periods for both species of *Ulex*. During these periods, the number of individuals of each pollinator species visiting bushes of a single species (identified by chromosome counts) growing within a 2 × 2 m area was counted. Individuals were only counted if they showed pollination behaviour. All observations were made between 12 and 14 August and during the peak of insect activity between 11 a.m. and 5 p.m. The same number of observation periods for each of the two gorse species was carried out each day, so variation in weather conditions would not bias the comparison of the insect visitation rates between the *Ulex* species. A reference collection of insect visitors to the *Ulex* flowers was made and used to identify individuals in the field.

QUANTIFICATION OF OVERLAP

The overlap between *U. gallii* and *U. minor* in both flowering phenology and pollinator assemblage was calculated using the Proportional Similarity Index (Colwell & Futuyma 1971; Rozzi *et al.* 1997):

$$Ps = 1 - 0.5 \sum |P_{ij} - P_{ik}| \quad (1)$$

$P_{ij} = N_{ij} / Y_j$ and j and k represent the two species. For flowering periods, N_{ij} is the number of flowers for the species j on date i , and Y_j is the total number of flowers counted over all census dates for species j . For pollinator assemblages, N_{ij} is the number of flower visits made by insect species i on *Ulex* species j , and Y_j is the total number of flower visits by all pollinator species recorded on species j . The index Ps takes its maximum value of 1 when the proportional distributions of species j and species k among the categories (flowers among dates, or pollinators among insect species) are the same, and its minimum value of 0 when the two species share none of the categories.

RESULTS

CHROMOSOME COUNTS

Of the 135 plants sampled, 53 individuals had gametophytic counts of $n = 16$ and 82 individuals had counts of $n = 32$. No cytotypes with an intermediate number of chromosomes were observed. In the subsequent analyses of morphology, flowering phenology and pollinator assemblages, plants were classified according to their chromosome counts: plants with $n = 16$ chromosomes were assumed to be *U. minor*, and those with $n = 32$ chromosomes were assumed to be *U. gallii*.

MORPHOMETRICS

Four floral characters and one vegetative character were compared between the two (cytologically-identified) species, with the mean character value for each plant being taken as a sample. Proctor

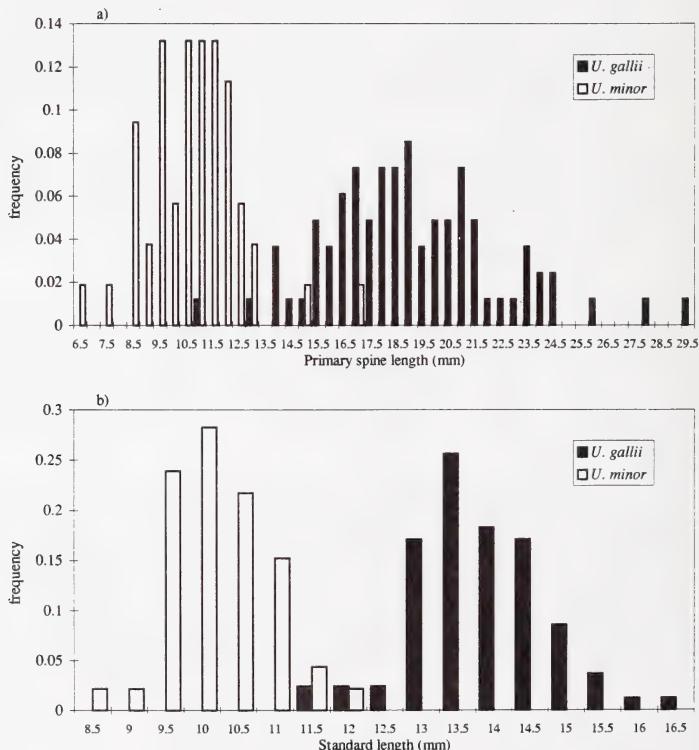


FIGURE 1. The frequency distributions of the floral and vegetative characters of the plants identified as *Ulex gallii* and *U. minor*.

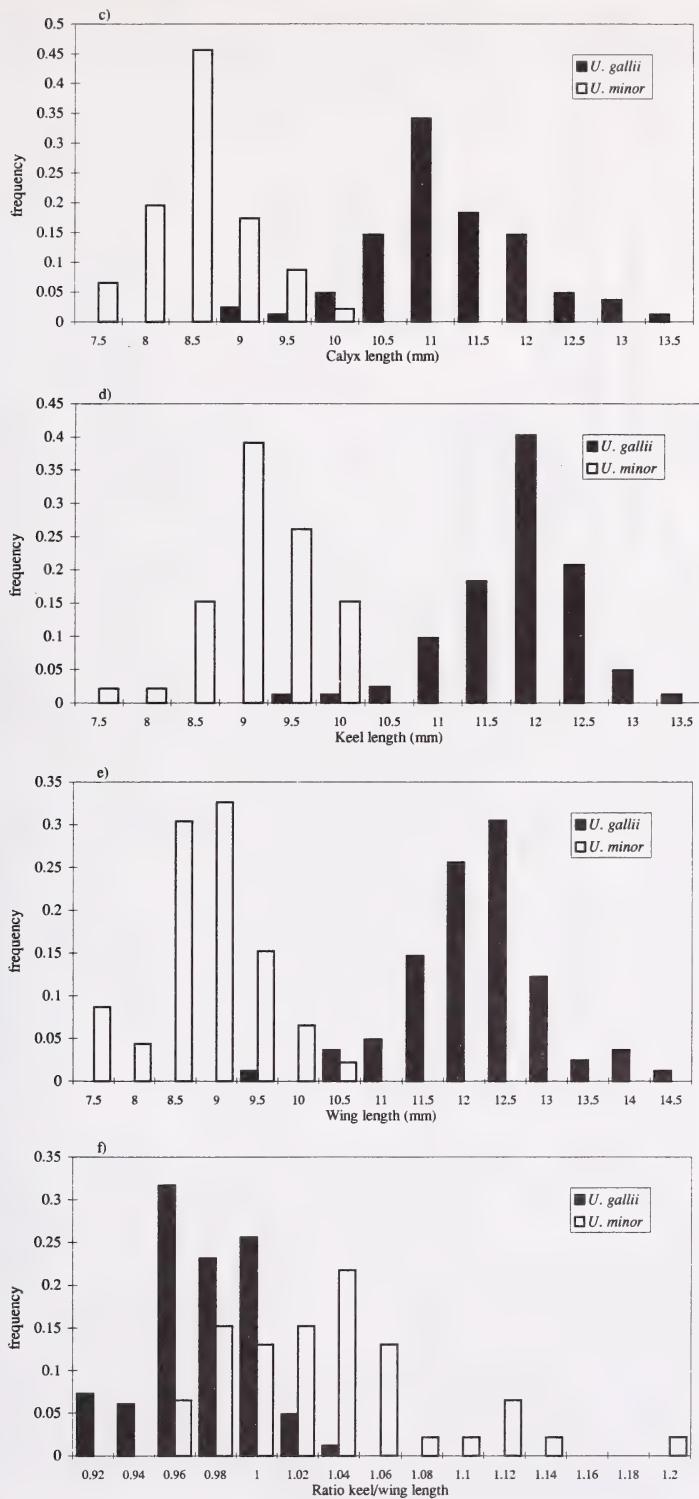


TABLE 1. THE DIFFERENCES BETWEEN *ULEX GALLII* AND *U. MINOR*
 (AS IDENTIFIED BY CHROMOSOME COUNTS) IN EACH CHARACTER
 WITH THE RESULTS OF T-TESTS.

	<i>Ulex gallii</i>	<i>Ulex minor</i>	<i>t</i>
	Mean ± se	Mean ± se	
Primary spine length (mm)	19.0 ± 0.36	10.7 ± 0.25	19.04
Standard length (mm)	13.8 ± 0.10	10.2 ± 0.10	24.49
Calyx length (mm)	11.2 ± 0.09	8.6 ± 0.07	22.23
Keel length (mm)	11.9 ± 0.08	9.1 ± 0.07	26.35
Wings length (mm)	12.2 ± 0.09	8.9 ± 0.08	25.09
Keel/wing ratio	0.98 ± 0.003	1.03 ± 0.007	7.48

Means are calculated using the *per bush* means as samples. The variances of the two species differed in each comparison, so t-tests were carried out using separate variance estimates. In this method, the degrees of freedom are modified using the sample standard deviations of the two species. All tests were significant at $P<0.0001$.

(1965) and Gloaguen (1986) reported that relative lengths of the wings and the keel can show some difference between *U. gallii* and *U. minor*. The ratio keel/wing length was included in the analyses, by calculating the ratio for each flower on a bush and taking the mean value per bush. Frequency histograms for primary spine, standard, calyx, keel and wing lengths of all plants sampled showed bimodal distributions (Fig. 1). These were formed by unimodal distributions of character values for each species (Fig. 1) and the peaks of each distribution appeared well separated between the species for each character. However, all distributions overlapped to a greater or lesser extent: 0.5 mm of overlap for standard and keel lengths, 1 mm of overlap for calyx and wing lengths, and 6.5 mm of overlap for primary spine lengths. The keel/wing ratio showed less of a species difference. Although the means were <1 for *U. gallii* and >1 for *U. minor*, as reported by Proctor (1965) and Gloaguen (1986), this character showed no clear bimodal distribution and substantial overlap (Fig. 1f). Despite these overlaps, t-tests showed significant differences between the two species in all six characters (Table 1).

The overlaps in individual character values between the species means that identification based on single characters will always have some degree of error. The question is therefore, can a suite of characters be used to separate the two species completely and consistently? Discriminant analysis (Seber 1984) on all six characters was carried out using PROC DISCRIM in SAS (1990). This gave a good, but not perfect, discriminant function: all *U. minor* plants were classified correctly, but three *U. gallii* plants were misclassified (a success rate of 96.3%). This is illustrated in Fig. 2, which gives the graphic representation of the separation of the species based on the canonical discriminant functions. Most *U. gallii* plants have a score <0, but three have a score characteristic of *U. minor* plants, >0.

Another way to address this question is to determine to what extent the measured ranges of each character can be used individually or in combination with other characters to separate the species. To do this we calculated which *U. minor* (or *U. gallii*) individuals had character values which fell within the ranges shown by the *U. gallii* (or *U. minor*) samples, for certain combinations of characters. The total of those individuals which would be classified as the wrong species using this method was used as a measure of the discriminating power of that character or group of characters. When carried out using the ranges measured by us at Gore Heath, no single character gave good discrimination between the species, but use of all characters together or all characters without spine length or keel/wing ratio accurately identified all but one of each species (Table 2). Proctor (1965) sampled plants from a large geographical spread of sites in Britain and his character values should be more representative of variation over Britain, so we repeated the analyses using Proctor's (1965) character ranges. This gave worse results. Individual characters, especially spine and standard lengths, gave high proportions of misclassification, and combined characters still misclassified 15% of *U. minor* plants and 2% of *U. gallii* plants (Table 2).

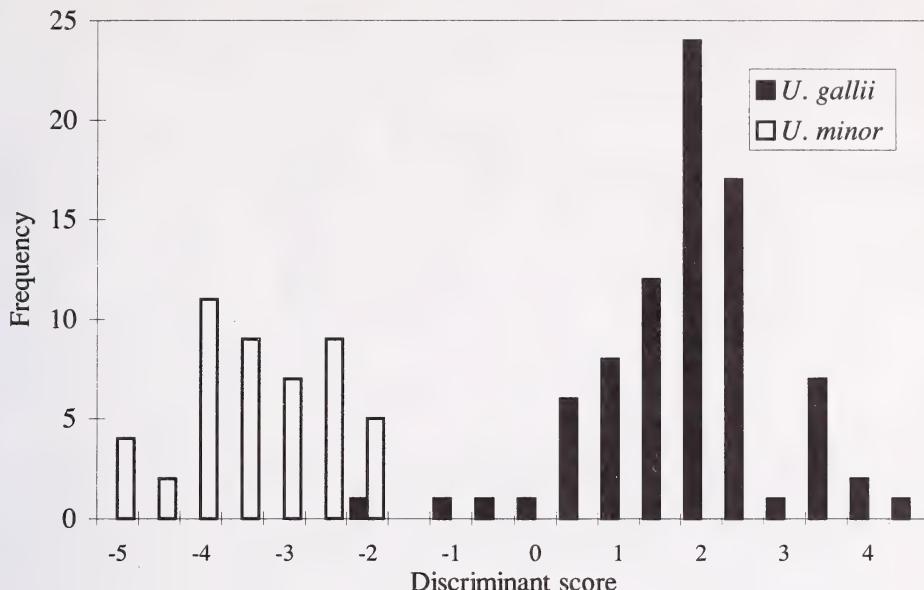


FIGURE 2. The distributions of the canonical discriminant scores for the 82 *U. gallii* plants and 46 *U. minor* plants, derived from the six measured characters. All *U. minor* scores are <0, and all *U. gallii* scores are >0 apart from three misclassified plants.

TABLE 2. THE RANGES OF CHARACTER VALUES FOR *ULEX MINOR* AND *U. GALLII* FROM THIS STUDY AND AS REPORTED BY PROCTOR (1965).

Characters used	<i>Ulex gallii</i>		<i>Ulex minor</i>	
Measures from this study	Range	Misclassified (%)	Range	Misclassified (%)
Primary spine length (mm)	11.1–29.5	24 (29)	6.5–17.1	22 (48)
Standard length (mm)	11.5–16.4	4 (5)	8.7–12.13	2 (4)
Calyx length (mm)	9.1–13.5	4 (5)	7.5–9.8	5 (11)
Keel length (mm)	9.25–13.3	1 (1)	7.7–10.0	19 (41)
Wing length (mm)	9.25–14.3	1 (1)	7.5–10.3	11 (24)
Keel/wing ratio	0.91–1.05	63 (77)	0.96–1.20	33 (72)
All		1 (1)		1 (2)
All except spine and ratio		1 (1)		1 (2)
Measures from Proctor (1965)				
Primary spine length (mm)	8–34	79 (96)	6–25	45 (98)
Standard length (mm)	10.5–18	5 (6)	6–12.5	16 (35)
Calyx length (mm)	8.5–14.5	15 (18)	5.5–10.5	30 (65)
Keel length (mm)	9–15.5	3 (4)	5.5–10.5	13 (28)
Wing length (mm)	9.5–15.5	5 (6)	5–11	9 (20)
All		2 (2)		7 (15)
All except spine		2 (2)		7 (15)

The ranges of one or more characters for a species were used to classify plants of the second species as overlapping with the first species (i.e. misclassified), or not overlapping. The numbers of misclassified plants in each species are given.

TABLE 3. INSECT SPECIES OBSERVED VISITING, AND PROBABLY POLLINATING, *ULEX MINOR* AND *U. GALLII* FLOWERS. TOTAL NUMBERS OF OBSERVATIONS ALONG WITH THEIR RELATIVE FREQUENCIES ARE LISTED FOR EACH SPECIES.

	Insect species	<i>Ulex gallii</i>		<i>Ulex minor</i>	
		number	frequency	number	frequency
Bumblebees	<i>Bombus terrestris/lucorum</i>	28	0.364	16	0.356
	<i>Bombus humilis</i>	5	0.065	4	0.089
Bees	<i>Andrena ovatula</i>	5	0.065	2	0.044
	<i>Apis mellifera</i>	2	0.026	0	0
Hover-flies	<i>Sphaerophoria scripta</i>	9	0.117	3	0.067
	<i>Syritta pipiens</i>	21	0.273	19	0.422
	<i>Eristalis</i> sp.	3	0.039	1	0.022
	<i>Episyphus</i> sp.	4	0.052	0	0

PHENOLOGY

The two species showed some differences in flowering phenology (Fig. 3). Phenology was examined in terms of the changes in mean number of flowers per plant (i.e. on the branches sampled) (Fig. 3a) and the proportion of plants in each census which reached their peak flower number at that census (Fig. 3b). The first *U. gallii* flowers were seen on 13 July, but *U. minor* started flowering later on 23 July. While the *U. gallii* population reached maxima in both the mean flower number and the proportion of plants at peak flower production on 18 August, these maxima were attained by the *U. minor* population on 9 September. Chi-square tests showed that the relative distribution of flower numbers between the censuses differed significantly between the species ($\chi^2 = 557$, $df = 10$, $P < 0.001$), and the average date of the peak in flower number per bush was later for *U. minor* (median = 28 August) than *U. gallii* (median = 18 August) (Mann Whitney $W = 4676$, $P < 0.001$). However, the species showed a large overlap in phenology as measured by the Proportional Similarity Index, $Ps = 0.78$.

POLLINATOR OBSERVATIONS

Five bee species were recorded visiting flowers (Table 3). Workers of the Buff-tailed and White-tailed Bumblebees *Bombus terrestris* and *B. lucorum* are difficult to separate with confidence, so we did not distinguish them in the field. Five hoverfly (Syrphidae, Diptera) species visited flowers (Table 2), but one, *Paragus* sp., was observed only once. Over the eight hours of observation, 77 insect visits were recorded for *U. gallii*, and 45 for *U. minor* (Table 3). *Bombus terrestris/lucorum* and *Syritta pipiens* were by far the most frequent insects seen visiting *Ulex* flowers, with *Bombus humilis*, *Andrena ovatula* and *Sphaerophoria scripta* also frequent. Fisher's Exact Test (used rather than a Chi-square test because of the small numbers of observations for several species) showed the pollinator communities of *U. gallii* and *U. minor* did not differ significantly ($P = 0.546$). This was illustrated by the high degree of overlap in the assemblages, as quantified by the Proportional Similarity Index, $Ps = 0.83$.

DISCUSSION

IDENTIFICATION OF ULEX SPECIES

In accordance with other workers in Europe, we have assumed plants with chromosome counts of $n = 32$ to be *U. gallii* and with $n = 16$ to be *U. minor* (Alvarez Martinez *et al.* 1988; Bullock *et al.* 1998; Castroviejo & Valdés-Bermejo 1983; Fernandez Prieto *et al.* 1993). Using chromosome counts as an absolute method for distinguishing the two species, we were able to assess accurately the degree to which the species show overlaps in morphology and other traits. Other studies have been hampered by the circularity which results from assessing morphological overlaps using plants which have been identified to species using morphology. We found that the species showed clear differences in the average values of all the measured characters, with all apart from the keel/wing

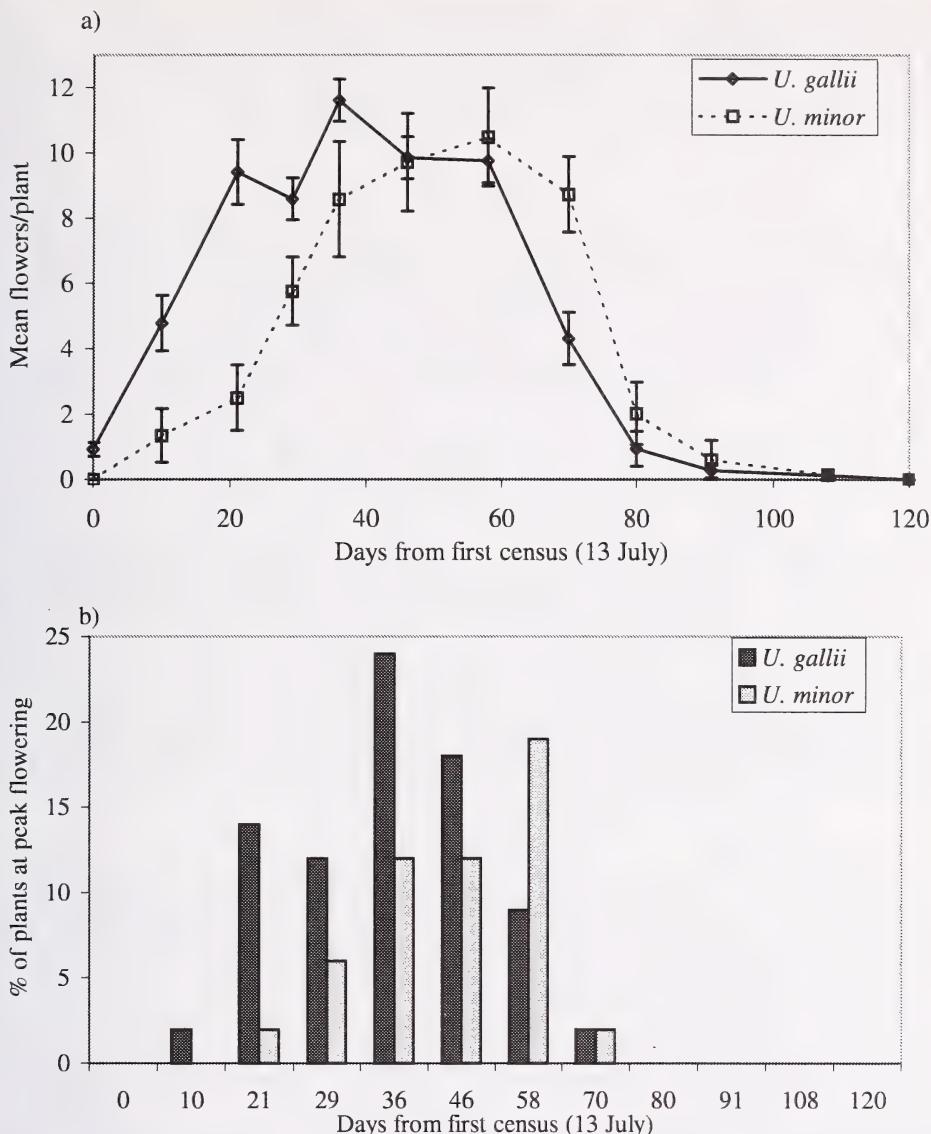


FIGURE 3. The flowering phenology of *Ulex minor* and *U. gallii*. a) Changes in the mean number of flowers per bush, with one standard error. b) The proportion of plants in the populations showing peaks in flower number at each census date.

ratio showing bimodal distributions (Note: Proctor 1965 did not find a bimodal distribution for spine length). However, all characters showed some degree of overlap, and use of one character alone would give a minimum of 5% (using standard length) and a maximum of 77% (using keel/wing ratio) of plants being misidentified. Using a suite of characters was more successful: discriminant analysis using all six characters gave only 2.3% misclassification. More useful to field botanists is defining what suite of characters should be measured to best identify species accurately. Using the ranges in character values measured in this study, we found that the use of standard, calyx, keel and wing lengths resulted in misidentification of only two of the 128 plants, 1.6%. The

keel/wing ratio is less useful for separating the two species. Proctor (1965) cast doubt on the idea that this ratio is always >1 for *U. minor* and <1 for *U. gallii*, although Gloaguen (1986) reiterated that this is a distinguishing feature. If this criterion is applied to the 128 plants sampled, 14 *U. minor* and 20 *U. gallii* plants are misclassified. Similarly, due to high plasticity, the length of the primary spine cannot be considered as a useful distinguishing character.

We achieved 98.4% accuracy in identification using the character ranges of the plants measured on Gore Heath in Dorset. The ranges given by Proctor (1965) were from plants sampled from Plymouth in the west to Woking in east-central England, and so these better represent the variation in characters in England (although identification was not supported by chromosome counts). These gave a much worse result: when all four floral characters were used 7% of plants were misclassified. It is clear, therefore, that morphological characters cannot be relied upon to give a completely accurate separation of *U. minor* and *U. gallii*. Although we had a very high success rate using the character ranges measured at our study site, it is more relevant to use Proctor's (1965) ranges when considering identification in Britain and Europe. Here, the 7% failure rate may sound small, but it translates to a large number of misidentifications if these character values are used extensively.

Our plants were sampled from a mixed heath in an area of range overlap. The ranges of these species are largely disjunct (Bullock *et al.* 1998; Gloaguen 1986; Proctor 1965). In Britain *U. minor* is virtually confined to the south-east of England, whereas *U. gallii* occurs mostly in the west and north-west of England, Wales and the extreme south-west of Scotland. The distributions can be divided coarsely by a line running from Dorset to the Humber estuary, roughly halfway up the east coast. Therefore, it might be tempting to use geographical location as a distinguishing character (e.g. Cuba & Pardo 1997). However, this is a dangerous strategy and may lead to misidentification of plants occurring outside their recognised range limits. In this way responses to climate change, or other factors which may change plant distributions, may go undetected. There are several cases where the *Ulex* species are found well outside any simply-described range limits. *U. gallii* is found in a few locations in south-eastern England, most notably in Kent in the extreme south-east and, in large numbers, on the East Anglian coast. *U. minor* has some records in north Wales and on the south-western Scottish border (current distribution maps are held by the Natural Environment Research Council Biological Records Centre). It would be useful to check these records with chromosome counts from these disjunct populations.

U. GALLII \times *U. MINOR* HYBRIDS

The chromosome counts performed on the 135 plants did not provide any evidence for the occurrence of *U. gallii* \times *U. minor* hybrids. These results – together with those of Bullock *et al.* (1998) who found a single putative hybrid ($n = 24$) out of 85 bushes sampled at Gore Heath – suggest that hybrids between *U. gallii* and *U. minor* are extremely uncommon. Therefore, the occurrence of hybridsation must be constrained in some way.

INTERSPECIFIC POLLEN TRANSFERS.

This study shows that the constraints on hybridisation are not flowering phenology or pollinator behaviour. It is an interesting and unexpected finding that *U. minor* had a significantly later start and peak in flower production than *U. gallii* (Fig. 3). Gloaguen (1986), working in Brittany, found that for *U. minor* flowering began in August, peaked in October (in terms of flower numbers) and finished in November. Flowering phenology differed between two *U. gallii* populations: flowering began in both during August, but one population peaked at the end of September and finished at the end of November, while the second peaked at the end of October and finished at the end of December. Therefore the species' differences we found may not be repeated in other sites. Despite differences in start dates and peaks, the flowering periods of the two species overlapped to a large degree ($Ps = 0.78$) and there was high intraspecific variation in the flowering period for both species (Fig. 3). Individuals of the two species bearing fully opened flowers simultaneously could be seen at any time during the flowering season.

The insect species seen visiting the flowers of the two species of *Ulex* were the same, and the relative abundance of the insect species showed no significant difference between *U. gallii* and *U. minor*. It seems that exactly the same pollinator assemblage was visiting both *Ulex* species and that the insects were not distinguishing between the species. Given their overlapping phenologies and pollinator assemblages and the large degree of physical intermingling between plants, pollen

transfer between *U. gallii* and *U. minor* probably occurs frequently. Indeed, over the eight hours of observation, there was one definite sighting of a *Bombus terrestris/lucorum* worker moving from *U. gallii* to *U. minor*. Therefore, other factors may act as barriers to hybridisation between the two species. Alternatively, if hybrid seed is formed, the lack of hybrid plants may be caused by very poor germination or establishment of hybrids. Neither hypothesis has been explored fully.

CONCLUSIONS

Given the taxonomic difficulties within the section *Neowilkommia* of the genus *Ulex*, there is a need to use chromosome counts to investigate further the morphological and ecological correlates of groupings such as *U. gallii*, *U. minor*, *U. europaeus*, and *U. europaeus* × *U. gallii*. It is insufficient to rely on morphology alone to distinguish species or hybrids definitively. Other authors have reported the use of traits other than the gross morphological characters used in this paper, such as pollen grain size (Misset *et al.* 1982), epidermal structure (Godeau 1977), stoma size (Cuba & Pardo 1997) or isoenzymes (Misset & Fontenelle 1992). However, chromosome counts provide a discontinuous measure allowing definitive separation of species and hybrids. Problems may arise in cases where *U. gallii* plants appear to show $2n = 96$ (e.g. Misset 1990; Misset & Gourret 1996), the same number as shown by *U. europaeus*. However, there is continuing controversy about such counts and there is a need to investigate ploidy levels in these species further.

This study was carried out on one heath in Dorset. To expand this work and test the conclusions over the full geographic distribution of both species, the next stage should be to repeat the study at a range of sites over Britain, France and the Iberian peninsula.

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Use of herbarium material for mapping the distribution of *Erophila* (Brassicaceae) taxa *sensu* Filfilan & Elkington in Britain and Ireland

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ABSTRACT

Specimens held in herbaria are a major botanical resource in Britain and Ireland but are currently being under-utilised by botanists in Britain and Ireland. The distribution of the taxa within the genus *Erophila* in Britain and Ireland has been selected as an example to illustrate the importance of herbarium specimens and one use for the collections.

KEYWORDS: *Erophila verna*, *Erophila majuscula*, *Erophila glabrescens*.

INTRODUCTION

Herbarium specimens are a major botanical resource which can be used for a range of purposes including taxonomic research, verification of identification, to provide geographical, historical and ecological information, and as an educational resource. The long history of collecting in Britain and Ireland means that a wealth of plant material is held in publicly accessible collections in Museums, Universities and other institutions around the British Isles.

Herbaria are currently being under-utilised by botanists in Britain and Ireland. For example, Rich & Sydes (1999) investigated two species included in the Scarce Plants Project and were able to trace 209 records in nine major herbaria additional to the 40 records in the Scarce Plants Database. The under-utilisation of herbaria may be a function of the increasing quality of books and illustrations allowing identification without comparison against a set of reference material, and the change in attitude to collecting related to concern for conservation of the plants. It may also simply be due to botanists, being unaware of the importance of existing collections or that they are accessible to the public. Limited public spending and increasing financial pressures have meant that it is becoming increasingly difficult to justify spending money on maintaining and enhancing

TABLE 1. NUMBER (AND %) OF RECORDS OF *EROPHILA* SPECIES FROM DIFFERENT PARTS OF THE BRITISH ISLES

Area	<i>E. majuscula</i>	<i>E. verna</i>	<i>E. glabrescens</i>
Southern England (v.cc. 1–32)	65 (50%)	656 (48.5%)	59 (22%)
Northern England (v.cc. 33, 34, 36–40, 53–70)	24 (18.5%)	320 (23.5%)	84 (31.5%)
Wales	11 (8.5%)	116 (8.5%)	21 (8%)
Scotland	17 (13%)	122 (9%)	61 (23%)
Ireland	13 (10%)	128 (9.5%)	39 (14.5%)
Channel Islands	0 (0%)	11 (0.8%)	2 (0.7%)

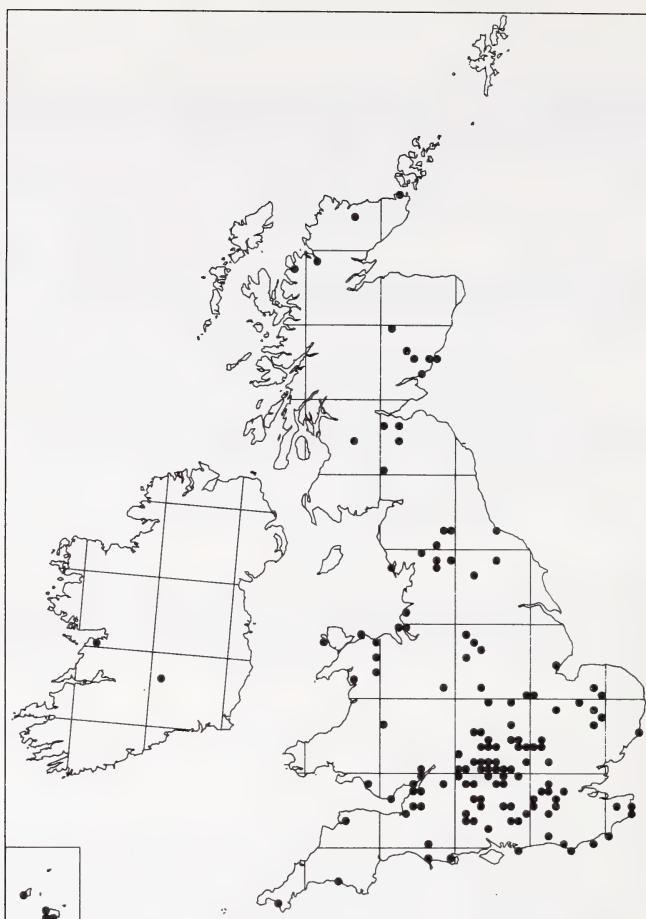


FIGURE 1. Distribution of all *Erophila* records held in the Fielding Druce herbarium, University of Oxford (OXF), showing the strong local representation.

herbaria which are not being used. Some financial controllers have even questioned the value of keeping herbaria at all.

The distribution of the taxa within the genus *Erophila* in Britain and Ireland has been selected as an example to show one role that herbarium collections can play in botanical research, as one of a range of issues being considered by the Herbarium Managers' Group of the UK Systematics Forum. The UK Systematics Forum was set up in 1994 to promote co-ordination and communication between the major UK collections-holding institutions and the wider systematics community, and a national strategy for systematic biology research has been drawn up in which zoological and botanical collections play a major role.

Filfilan (1984; summarised in Filfilan & Elkington 1988, 1998, and Elkington 1991) carried out a cytotoxicological study of *Erophila* populations in Britain, the results of which were correlated with those of Winge (1940). Three groups of cytotypes were distinguished at the specific level: *Erophila majuscula* Jordan, a densely hairy diploid, *E. verna* (L.) Chevallier *sensu stricto*, a medium polyploid, and *E. glabrescens* Jordan, a sparsely hairy to glabrous high polyploid. The distributions were summarised by vice-county in Filfilan & Elkington (1998), but no distribution maps were presented. Hectad (10 km × 10 km square) maps of these species are required for the B.S.B.I. *Atlas 2000* project, but relatively few records have been verified to species level. The opportunity was taken to draw together records for these species in selected major herbaria to show the wealth of information available.



Figure 2. Distribution of *Erophila majuscula* based primarily on herbarium records.

METHODS

Data on specimens were abstracted onto standard "pink cards" from material held in the following herbaria (abbreviations follow Kent & Allen 1984): **BEL** (74 sheets), **BM** (400 sheets, c. half the material), **DBN** (145 sheets, mostly named by Elkington & Filfilan), **E** (c. 200 sheets, partly named by Elkington & Filfilan), **K** (129 sheets, c. half the material), **LANC** (25 sheets, Cumbria material determined by T. T. Elkington only), **LIV** (155 sheets), **MANCH** (157 sheets), **NMW** (161 sheets, partly named by Elkington & Filfilan), **OXF** (189 sheets, many with up to 5 or 6 collections on each sheet), **RNG** (114 sheets) and **TCD** (32 sheets). Identifications by T. T. Elkington and/or S. A. Filfilan were accepted directly, with other material named by T. C. G. Rich. Grid references were allocated to the most appropriate hectad (10 km × 10 km square) following standard B.R.C. practice, though in some cases the original locations were not known with certainty (e.g. "near Manchester"; **LIV**). The handwriting on some sheets was difficult to read, and minor discrepancies were encountered between apparent duplicates. The labelling on some sheets is so poor (e.g. Druce's material in **OXF**) that some records were not included to avoid errors. Other records with illegible handwriting, or where the locality was ambiguous or could not be traced, have not been included on the maps.

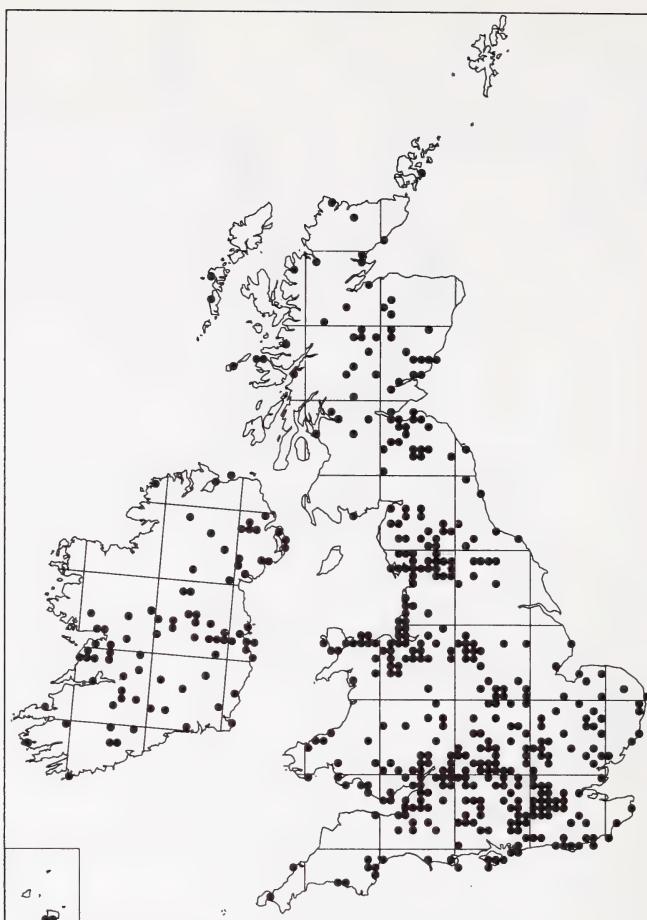


FIGURE 3. Distribution of *Erophila verna* sensu stricto based primarily on herbarium records.

A few additional records published in the literature and other records held by the Biological Records Centre (BRC), Monks Wood have been included, but no systematic search for other records has been carried out so that the maps very largely represent the data held in herbaria. The pink cards have been deposited at BRC, to which requests for details of the records should be addressed.

RESULTS

The exercise in collating records also provided an opportunity to test the taxonomy, which on the whole was found to work well. *E. majuscula* is a distinct species with a dense rosette (due to the short petiole), dense hairs and obovate fruits. In most cases identifications were checked by measuring seed sizes. *E. glabrescens* by comparison is sometimes difficult to separate from *E. verna*, and the dividing line between the two on sparsely hairy plants would appear to be somewhat arbitrary. The extent to which the petals are bifid does not appear to correlate well with hairiness and has not been used by TCGR. On mixed sheets, plants allocated to this species were almost always the smallest, and one wonders if hairiness is somewhat dependent on growth/habitat. A strict view of *E. glabrescens* has been taken to include only the most sparsely hairy plants. Most material was referable to the variable *E. verna* sensu stricto, of which a broad view has been taken.

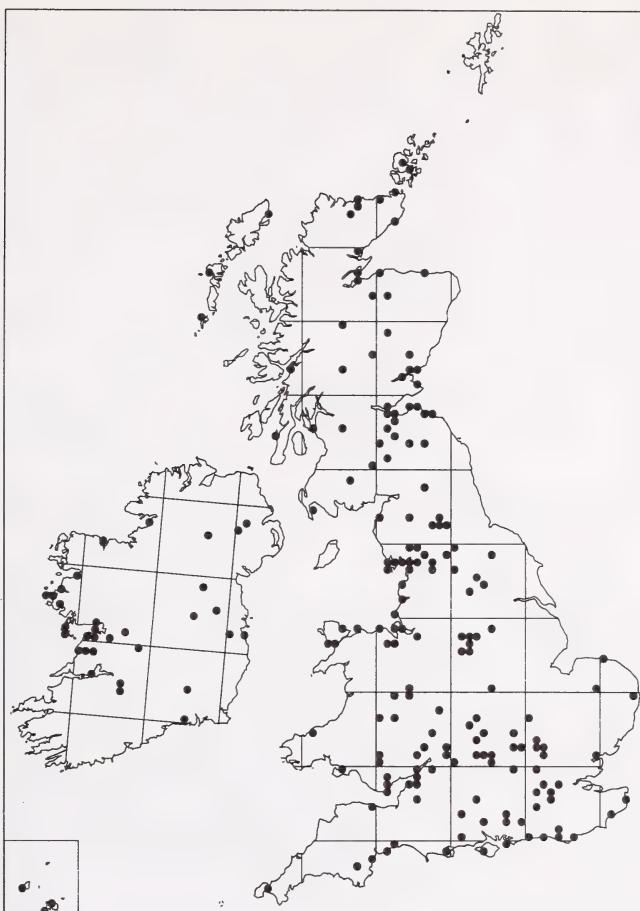


Figure 4. Distribution of *Erophila glabrescens* based primarily on herbarium records.

The correspondence between different herbaria and with specimens named by Filfilan and Elkington was found to be good, though it would not be too surprising if some duplicate collections in different herbaria have been given different names. It was not possible to name some immature or senescent material. Mixed collections do occur quite regularly, matching the situation in the field. Some *Erophila* names have been used historically in a different sense to how they are used by Filfilan & Elkington, and it is not possible to use old names, with the possible exception of material named as *E. virescens* Jordan by E. S. Marshall, which is usually *E. majuscula*.

The herbaria were found to have very strong representations of local material, with patchy representation of specimens from elsewhere. For example, Fig. 1 shows the distribution of all *Erophila* records held in OXF, which, as might be expected, shows a strong concentration from Oxfordshire.

The maps for the three species are shown in Figs 2–4. Records for *E. verna* s.s. var. *praecox* (Steven) Diklic were also abstracted from some, but not all, herbaria, and are shown in Fig. 5. The numbers of records from various parts of the British Isles are summarised in Table 1.

The numbers of distinct collections per decade (i.e. excluding duplicates) are summarised for all three species in Fig. 6. The changes with time reflect variation in collecting effort rather than changes in frequency of the plants (Rich 1997). There is a peak in collecting around the turn of the century when botanists such as E. S. Marshall and J. E. Little collected large quantities of material. Most post-1980 records are from Cumbria, Monmouthshire and Ireland.

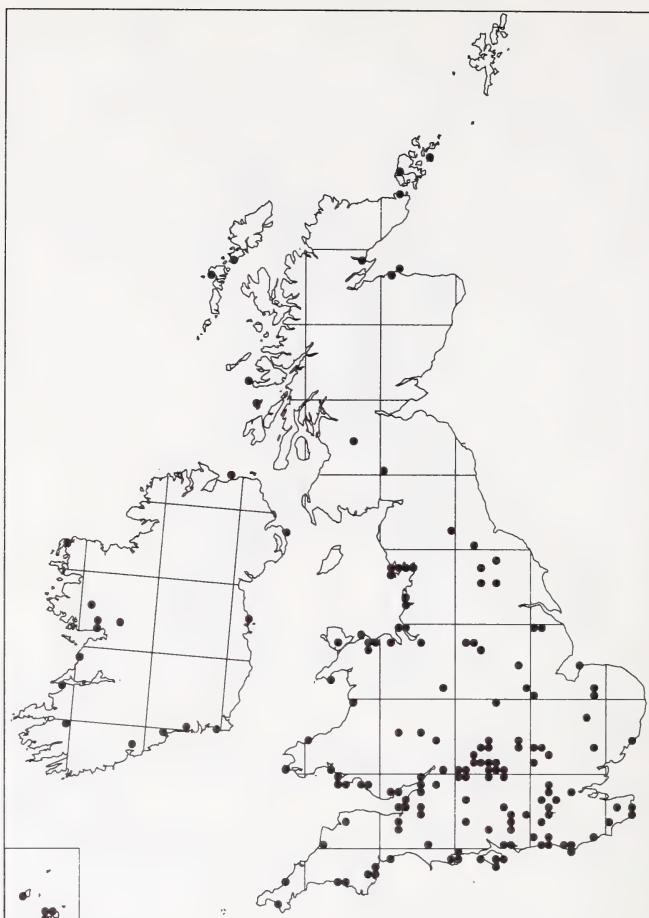


FIGURE 5. Distribution of *Erophila verna* var. *praecox* based on herbarium records.

DISCUSSION

The maps show how the large number of specimens held in UK and Irish collections can be used to provide valuable information on distribution. With any taxonomic revision there is an immediate requirement for information to bring the data up to a comparable standard with other taxa, and the collections provide an efficient means of doing this. Other taxa in the British Isles for which additional data are required for the *Atlas 2000* project include the *Juncus bufonius*, *Utricularia intermedia* and *Luzula multiflora* aggregates.

Whilst perhaps up to 20% of the *Erophila* material in different herbaria is duplicated (often material distributed through Botanical Exchange clubs), the majority is unique and often shows a strong local representation. For instance, there is much material from Edinburgh in **E**, from the Merseyside area in **LIV** and from Glamorgan in **NMW**. It is thus important to examine material from a range of herbaria to obtain a general overview of the distribution. However, a comparison of the summary map of all records (Fig. 7) with that from the *Atlas of the British flora* (Fig. 8) shows that some areas are still under-represented in herbaria compared to the frequency in the field, and caution is required in drawing firm conclusions about distribution or frequency based on herbarium material alone. Nonetheless, the information is invaluable for indicating which species may be present in an area and hence should be searched for.

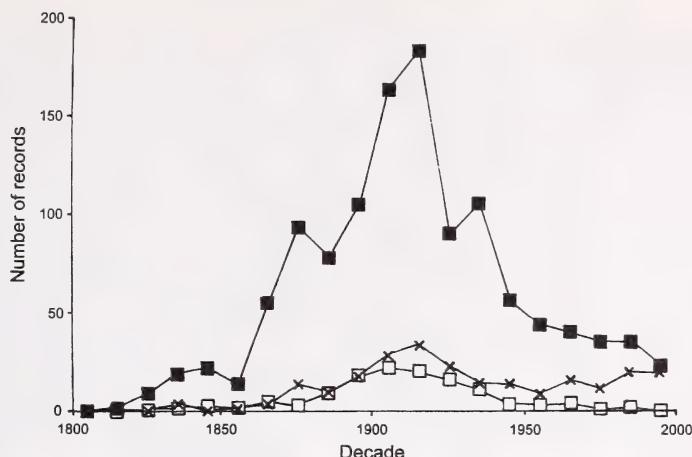


FIGURE 6. Number of records per decade for *Erophila majuscula* (□), *E. verna* (■) and *E. glabrescens* (×)

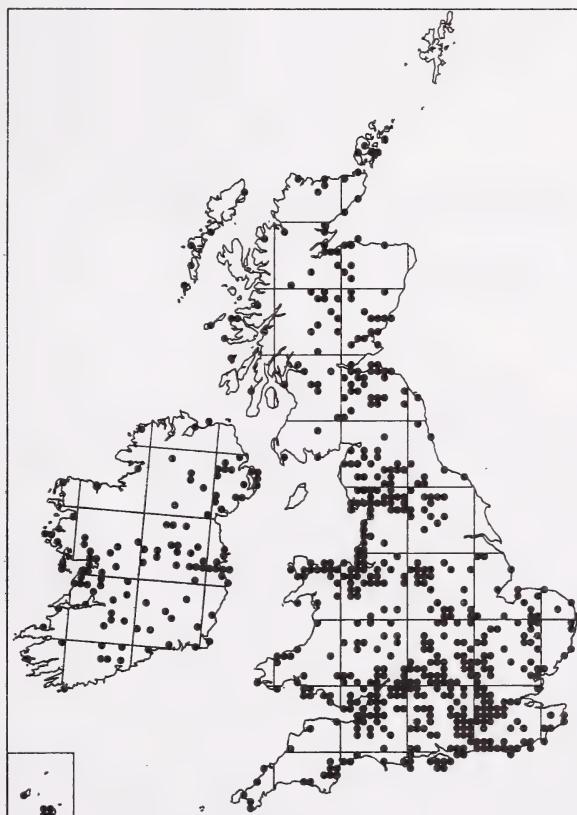


FIGURE 7. Distribution of *Erophila verna* sensu lato combined from Figs 1–5.

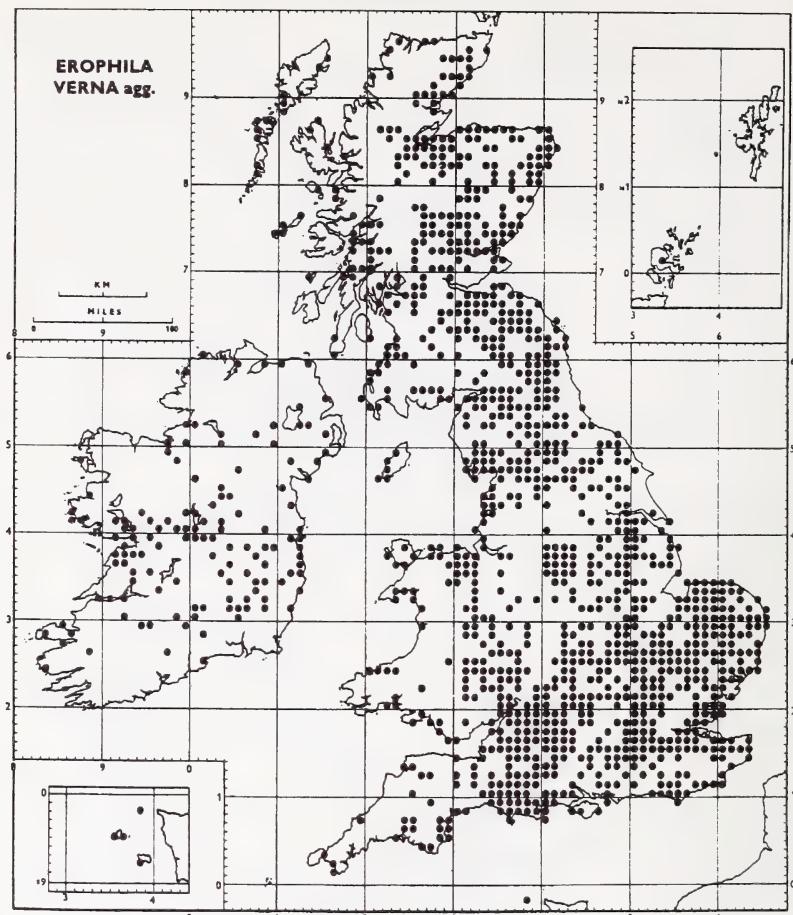


FIGURE 8. Distribution of *Erophila verna* sensu lato (Perring & Walters 1962).

The maps show that *E. majuscula* is the least common species, collected most frequently in southern Britain (Table 1) and becoming scattered or rare elsewhere. It is probably sufficiently uncommon to qualify as a Nationally Scarce species. *E. glabrescens* is not common but is widespread, and may be the commonest taxon in the north and west of both Britain and Ireland. *E. verna* s.s. is the commonest and most widespread species.

Examination of the herbarium material has also resulted in additional records for many Vice-counties to be found. The lists of Vice-counties for which we have seen specimens of each species are as follows (78 records new to the list of Vice-counties given in Filfilan & Elkington 1998 are given in **bold**):

E. majuscula: V.c. **1, 5, 6, 7, 9, 11, 12, 13, 14, 16, 17, 18, 20, 21, 22, 23, 26, 27, 28, 31, 32, 33, 34, 38, 40, 41, 49, 50, 51, 55, 57, 58, 59, 62, 64, 65, 68, 78, 80, 82, 83, 85, 90, 95, H9, H15, H17, H21, H22, H37, H38 and H40.**

E. verna: V.c. 1, 2, 3, **4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 62, 64, 65, 66, 67, 68, 69, 70, 72, 73, 76, 77, 78, 79, 80, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 94, 95, 96, 97, 98, 99, 100, 103, 105, 106, 107, 108, 109, 110, 111, H1, H2, H3, H4, H5, H6, H7, H8, H9, H10, H11, H12, H13, H15, H16, H17, H18, H19, H20, H21, H22, H23, H24, H25, H26, H30, H31, H33, H35, H36, H37, H38, H39 and H40.**

E. glabrescens: V.c. **1**, **3**, **5**, **6**, **8**, **9**, **10**, **11**, **12**, **13**, **14**, **15**, **16**, **17**, **19**, **20**, **21**, **23**, **24**, **26**, **27**, **28**, **29**, **30**, **31**, **33**, **34**, **35**, **36**, **37**, **38**, **40**, **41**, **42**, **43**, **44**, **46**, **47**, **49**, **51**, **52**, **54**, **55**, **56**, **57**, **58**, **59**, **60**, **62**, **63**, **64**, **65**, **66**, **69**, **70**, **72**, **73**, **74**, **76**, **77**, **78**, **79**, **80**, **81**, **82**, **83**, **85**, **88**, **89**, **90**, **94**, **95**, **96**, **98**, **100**, **101**, **106**, **107**, **108**, **109**, **110**, **111**, **H6**, **H8**, **H9**, **H11**, **H15**, **H16**, **H17**, **H20**, **H21**, **H23**, **H27**, **H28**, **H30**, **H34**, **H36**, **H38**, H39 and S.

Filfilan & Elkington (1998) suggested that the map of *E. verna* subsp. *spathulata* (Lang) Walters in Perring (1968) was applicable to their var. *praecox*. However, a number of the populations in the west with short fruits are *E. glabrescens* rather than *E. verna*; Perring's (1968) map is therefore not completely consistent with the modern treatment. The different distribution of this variety suggests that there may be some merit in retaining it as a taxon, though what the ecological basis for the difference in distribution is requires investigation (e.g. van Andel *et al.* 1986).

The importance of herbarium material to botanical research must be stressed to the B.S.B.I. membership. Whilst many herbaria only lend specimens to recognised institutions (e.g. local Museums), and some do not have the resources to post material, in most cases requests to visit or borrow material will be welcomed.

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The history and distribution of *Phyteuma spicatum* L. (Campanulaceae) in Britain

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ABSTRACT

Phyteuma spicatum L. (Campanulaceae) is a rare species in Britain occurring in low numbers in a small area of East Sussex (v.c. 14). Its history has been investigated, and herbarium records and Flora accounts examined, to determine whether it was formerly more widespread and abundant in Britain. It appears that *P. spicatum* has always been confined to East Sussex, but that it was more widespread within this vice-county in the past. Anecdotal information also suggests that it was more abundant at the end of the 19th century and during the early 20th century than it is at present.

KEYWORDS: Spiked rampion, rare plant, current distribution, historical distribution, England.

INTRODUCTION

Thirty species from the family Campanulaceae occur in Britain as natives, introductions or garden escapes (Stace 1997). Three of these species belong to the genus *Phyteuma*. *P. orbiculare* L. (Round-headed Rampion) is native and is found in chalk grasslands from Wiltshire to East Sussex. *P. scheuchzeri* All. (Oxford Rampion) is an introduced species which was formerly on walls and pavements in Oxford and is now naturalised in limestone cracks at Inchnadamph, W. Sutherland (Stace 1997). The third member of the genus, *P. spicatum* (Spiked Rampion), is confined to East Sussex (v.c. 14).

According to Damboldt (1976) there are two subspecies of *P. spicatum*. Subspecies *spicatum* has creamy-white flowers, whereas those of subsp. *coeruleum* are blue. Subspecies *spicatum* is the subspecies found in all the East Sussex sites, and is regarded by many as a native of Britain (Hall 1980; Clapham *et al.* 1987). Garden escapes are usually blue-flowered (Stace 1997). Whereas Bentham & Hooker (1954) place a question mark after "native" in their flora entry for *P. spicatum*, and Grigson (1958) fails to mention the species at all, Hall (1980), Clapham *et al.* (1987) and Stace (1997) all regard it as native. Its inclusion in the second and third editions of the *British Red Data Book of Vascular Plants* (Perring & Farrell 1983; Wigginton 1999), and its addition in 1992 to Schedule Eight, under Section 13 of the Wildlife and Countryside Act of 1981, support this view.

P. spicatum is found very locally on roadside verges, on steep roadside banks and in woodlands, on acid soils of the Ashdown Beds and Wealden Clay. The communities in which it is found on roadsides correspond to either the W25a *Rubus fruticosus* agg.–*Pteridium aquilinum* underscrub, *Hyacinthoides non-scripta* sub-community or, in more open areas, the *Arrhenatherum elatius* grassland, *Centaurea nigra* sub-community (MG1e), of the National Vegetation Classification. In wooded sites it is a component of *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* woodland (W10), particularly the *Anemone nemorosa* sub-community (W10b) (Rodwell 1991, 1992; Wheeler 1997). *P. spicatum* has also been recorded as a garden escape in Warwickshire, Staffordshire, Merionethshire, Derbyshire and Roxburghshire (Perring & Farrell 1983). Outside the British Isles, *P. spicatum* is endemic to Europe, occurring in many Central and Atlantic European countries. Ellenberg (1988) names *P. spicatum* as a component of the "noble broadleaved wood" (*Fagetaalia*), lime and oak-hornbeam woods, silver fir woods, woodland margins, and montane and sub-alpine

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meadows. Full details of the communities in which the species occurs, and of its ecology, are to be presented in a Biological Flora account (Wheeler & Hutchings, in prep.).

Willems (1980) has studied the size of continental populations of *P. spicatum* in the Leudal area of the Netherlands, a country where the species is rare. The number of plants he recorded declined between 1965 and 1980, culminating in population extinction. Detailed study of the demographic behaviour and changes in numbers of plants in three of the remaining British populations of *P. spicatum* will be presented in a future paper (Wheeler & Hutchings, in prep.). The present paper analyses the past distribution and abundance of *P. spicatum* in Britain to determine whether its current limited distribution and rarity has been typical throughout its history, or whether it has suffered a contraction in range and abundance. Evidence for such a contraction would suggest that development of a programme of active management is urgently needed to conserve the species.

METHODS

The current and historical distribution and abundance of *P. spicatum* in Britain were analysed using historical records, manuscripts, herbarium specimens and field observations. Records and specimens were examined from herbaria at **BM**, **BTN**, **CGE**, **LIV**, **K** and **NMW**. Records from other herbaria and site locations were supplied by English Nature, Sussex and Surrey Team. The B.S.B.I. vice-county Recorder was consulted for known locations, and the Joint Nature Conservation Committee and the Biological Records Centre at the Institute of Terrestrial Ecology, Abbots Ripton, supplied information on historical locations. In addition, known locations at which *P. spicatum* still occurs, and sites at which it has been recorded but at which its presence was unconfirmed between 1986 and 1996, were searched for the species. All records of *P. spicatum* are listed in the Appendix.

THE HISTORY OF *PHYTEUMA SPICATUM* IN THE BRITISH ISLES

The earliest account of *P. spicatum* in the British Isles is in Gerarde's 'Herball' (1597) under *Rapuntium maius*, an early name for the species. It was described as a garden plant, grown for its culinary and medical properties (the root was boiled and eaten in salads), rather than as a wild species. Gerarde stated that the plant was also known as *Rapunculum alopecuron* because of "the eare or spike that is full of flowers, which are like almost to tailes of foxes when they are bloomed". Gerarde's plant was blue-flowered, "sometimes white or sometimes purple", indicating that *P. spicatum* grown in gardens in Britain at that time was subsp. *coeruleum* R. Schulz (Damboldt 1976), which now grows wild in mainland Europe but only grows as a garden escape in Britain. Gerarde (1633) enlarged the list of names given to the species to include *Alopecuri comoso flore*, *Rapunculum sylvestre* and *Rapunculus sylvestris spicatus*. Parkinson (1640) also described the plant under the name *Rapunculus spicatus Alopecuroides*, or the "Long Foxtail Rampion". He stated that as well as being cultivated as a culinary plant, the species grew wild in "divers places of this land". This is the first record of *P. spicatum* as a wild species in Britain. Parkinson also commented on the origin of the name, stating that *Rapunculus* was a diminutive of *Rapum* (the turnip) and that the species was so-called because of the similarity in appearance and edibility between its root and the vegetable. Further names included *Rapum sylvestre majus*, *Rapunculum alopecuron*, *Rapunculus Alopecuroides longa spica* and *Rapunculus nemorosus primus*.

The first specific location given for *P. spicatum* as a wild plant is Knight's Farm, Mayfield, East Sussex in 1825. This record forms part of William Borrer's herbarium, now housed in **K**. Borrer's botanical knowledge of Sussex was unequalled in his day (Arnold 1907; Wolley-Dod 1937), lending credence to this record. A specimen from this first record, sent to the Linnean Society "was not considered an English plant" (Branwell 1872).

From 1825 onwards, there are many records and herbarium specimens of the species. The most extensive herbarium collection is in **BM**. Most specimens in other herbaria were duplicates of these. All the documented locations of *P. spicatum* growing wild were in East Sussex, and there is no evidence of the species as a wild plant in other counties – only as a garden plant or nearby escape. Most herbarium records provide information on the abundance and distribution of the species. Although some records are unspecific, referring only to a particular parish, the names of

particular farms or woods are frequently given. A note by W. A. Bromfield, made in 1835 (herbarium of W. B. Hemsley, Booth Museum, Brighton), is typical of the accuracy and form of these records; "...in the middle of a wood on Hole Farm in Buxted Parish, five or six miles from Uckfield; one of many stations about Mayfield and Waldron where this plant occurs, and which is certainly indigenous though so long overlooked by British botanists". Bromfield's view of *P. spicatum* as indigenous is supported by Jenner's (1845) observation on the species in woods at Warbleton where "No one who saw it there could doubt its being native".

In 1907, Arnold suggested that specimens of *P. spicatum* found in the wild were escapes from Warbleton or Michelham Priories. This theory originates from Michelham Priory itself. It was still in the apothecaries' garden at Michelham Priory in the late 1980s (FitzGerald 1987), and an exhibit in the Priory museum claimed that it was "brought to Michelham by the canons from its native France", although no evidence is given to support this claim.

The number and size of populations of *P. spicatum* in East Sussex appears to have been much larger in the past than at present. Throughout the 19th century, herbarium specimens were consistently accompanied by notes referring to its great abundance. In 1835, Bromfield "met this plant in plenty" (BTN) and Jenner's (1945) account of the species states that it "grows in the woods in such abundance ...". A later extract from a letter to W. B. Hemsley in 1875 (Herb. Borrer., K) describes "Abbots Wood which is quite carpeted with *Phyteuma spicatum*. We were there for two hours and which ever way we walked they were as common as dandelions". In 1996, Abbots Wood supported fewer than 30 plants.

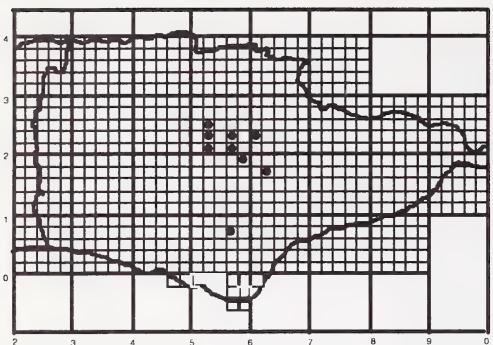
Several herbarium specimens from the early part of the 20th century also refer to *P. spicatum* as an abundant species. For example, Bray in 1919 (FitzGerald 1988) stated that "it came from Bramble Grove Wood ... There is a good bit of it." However later records suggest a decline. Druce (1932) described the species as rare, and other records around this time cease to describe the plant as occurring in large numbers. Wolley-Dod (1937) records it in Abbots Wood as "formerly abundant, now much less so". Later records are more specific about the location of the plant, referring to populations in small areas of the wood, rather than throughout. For example, Richards (1942 [in Herb. Babington, CGE]) records it as in a "Felled portion of Abbots Wood near Milton Hide".

DISTRIBUTION OF *PHYTEUMA SPICATUM* IN EAST SUSSEX FROM 1825 TO 1996

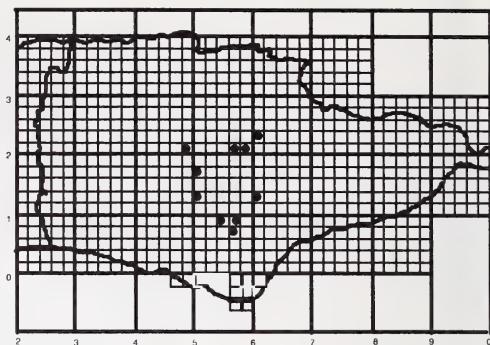
Figures 1a–e show the presence of *P. spicatum* within tetrads in East Sussex from 1825, the year of the first confirmed record of the species, to 1996. Between 1825 and 1875 (Fig. 1a) most records were from the Heathfield area. They do not support the suggestion that wild populations of *P. spicatum* originated from Michelham Priory (see above), since only one tetrad near the Priory (TQ/5.0T) has records of the species, whereas there are many tetrad records 10 km further north. The location of Warbleton Priory (TQ/6.1P) is closer to the early records and may be more credible as a possible source of *P. spicatum*, if the species is not native.

The distribution of *P. spicatum* appeared to spread between 1875 and 1925 (Fig. 1b), although few records remained in the tetrads in which the species had been previously recorded. This apparent increase in the geographical range of the species may be explained by the increase in regionally specific botanical documents during this period, allowing greater detail and accuracy in recording (Hemsley 1875; Arnold 1887, 1907), and by the increased number of amateur botanists collecting specimens for herbaria. The majority of herbarium specimens of *P. spicatum* originate from this period. The absence of records from many of the earlier locations cannot be explained. Their recurrence in later decades suggests a lack of recording in these locations, rather than that *P. spicatum* had become locally extinct.

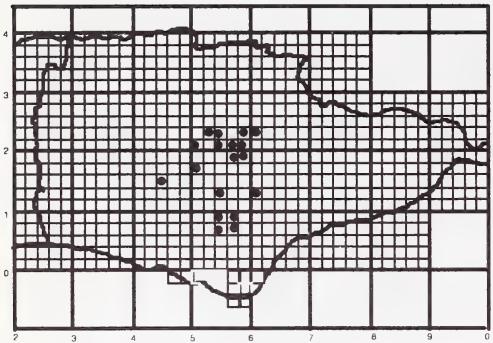
The records of *P. spicatum* reached their greatest abundance between 1926 and 1975 (Fig. 1c), but even during this period only 18 tetrads contained records. *P. spicatum* was still confined to a small area within a circle of radius 9 km, with two areas of concentration. These were the Heathfield/Cross-in-Hand area (TQ/5.2) and the woodland in and around Abbots Wood (TQ/5.0). From 1975 to 1989, the range of *P. spicatum* diminished (Fig. 1d), shrinking back to the two stronghold areas where it had formerly been concentrated. The outlying tetrad records shown in Figures 1b and c had been lost. By 1996 the strongholds for *P. spicatum* had declined in size (Fig. 1e),



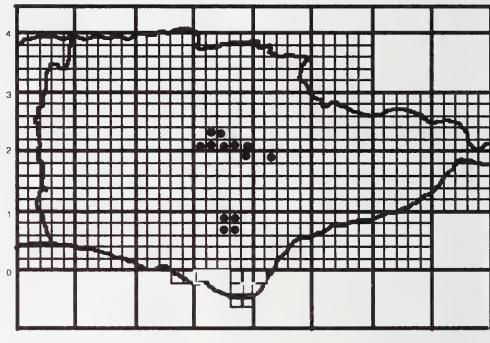
1a



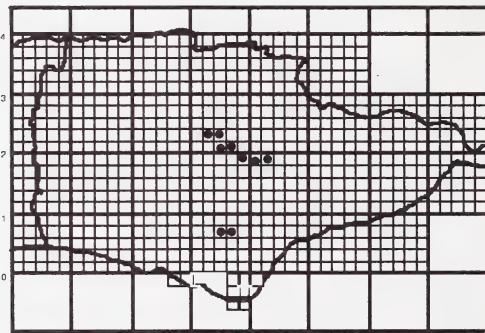
1b



1c



1d



1e

FIGURE 1a-e. The distribution of *P. spicatum* during the period 1825 to 1996, plotted from the historical and extant site records. (a) 1825–1875; (b) 1876–1925; (c) 1926–1975; (d) 1976–1989; (e) 1996–present. Distribution is shown as presence within 2 × 2 km square tetrads in v.c. 14, East Sussex. Those tetrads in which presence is marked as an approximate location only are an attempt by the author to place the earliest (1825 to 1875) historical records of *P. spicatum*. These early records are open to interpretation of location, due to the vagueness of descriptions.

TABLE 1. THE NUMBER OF *PHYTEUMA SPICATUM* PLANTS AT EACH EXTANT SITE DURING THREE RECENT CENSUSES, SHOWING THE PERCENTAGE CONTRIBUTION WHICH PLANTS AT EACH SITE MAKE TO THE TOTAL POPULATION IN BRITAIN.

Sites	1980/1		1986/7		1995/6	
	total number of plants	% of British population	total number of plants	% of British population	total number of plants	% of British population
Pound/Bridgeland Farm	2	<1	0	0	0	0
Brown's Lane	51	13	55	14	1	<1
Little England Farm	50	13	27	7	5	1
Malls Bank Farm	16	4	18	5	7	2
Tinkers Lane	198	50	175	44	285	83
Abbots Wood sites	77	19	30	8	23	7
Dower House	—	—	?	?	?	?
Maynards Green	—	—	78	20	14	4
New Sapperton Farm	—	—	12	30	?	?
Rushlake Green	—	—	—	—	4	1
St Dunstan's Farm	—	—	—	—	4	1
Total	397		395		343	

? Denotes no available information on population numbers during the survey period; — denotes no plants known at the site during the survey period.

leaving only nine tetrads containing records. The appearance of one new tetrad supporting a colony at TQ/5.0N (Abbots Wood) is misleading, since this record, which is adjacent to the older record of TQ/5.0T, is due to improvement in the accuracy of an earlier record. Both TQ/5.0N and T are a single record from one woodland which supports a handful of plants in a very small area crossing the tetrad boundary line (see Appendix records).

An analysis of the recent and current distribution of *P. spicatum* in Britain is given in Table 1, which shows, for three census dates, plant numbers, and the percentage of the total number of plants of *P. spicatum* contributed by populations at each extant site. The 1980/1 census was undertaken by the county recorder of the B.S.B.I. for the Sussex Botanical Recording Society, the 1986/7 census was commissioned by English Nature, and the 1995/6 census was carried out during this study. In 1987 there were eight sites with extant populations, supporting almost 400 plants (FitzGerald 1988). This was a similar number of plants to that recorded in 1980/1, but the distribution across sites had changed between the two dates. The census in 1996 confirmed the persistence of *P. spicatum* in seven of the tetrads occupied in 1987. The eighth had become inaccessible, so that the continued presence of *P. spicatum* here remained unconfirmed. *P. spicatum* was also discovered at two new sites. However, with the exception of one site, the numbers of plants at the sites where the species survived were much reduced since the 1987 census (Table 1), and the total number of plants had declined by 13% between 1987 and 1996. Although the spread of plants across the British sites was uneven at all three census dates referred to above, it has recently become more heavily concentrated on just one site, emphasizing the importance not only of conserving the population at this site but also of increasing the size of *P. spicatum* populations at the other remaining sites in which it survives. A catastrophic event or inappropriate management at the site of its largest population could now destroy over 83% of Britain's *P. spicatum* plants.

CONCLUSIONS

Historical records show that, although *P. spicatum* has never been widely distributed in the British Isles, it was formerly more widespread, and occurred in much larger numbers, than it does now. The low numbers of plants which now remain warrant its legal protection under Schedule Eight,

Section 13 of the Wildlife and Countryside Act (1981), and there can be little doubt that an effective plan for management of the sites where it still survives is now vital to safeguard the species against the risk of extinction in the British Isles.

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APPENDIX

A list of records discovered for *P. spicatum*, compiled from the sources described above is given. 10-km square and, where possible, standard B.S.B.I. tetrad reference (Ellis 1986), is given for each site. Only those records of *P. spicatum* growing wild are included and consequently all records are from v.c. 14. Only first and last (most recent) records are given, except where interim records provide valuable information, for example on plant numbers. The source of the record is given either as a publication reference or as a herbarium or report reference. Records courtesy of Paul Harmes, the B.S.B.I. Recorder for v.c. 14, are indicated by BSBI. Records courtesy of English Nature, Sussex and Surrey Team are indicated by EN. Records are arranged numerically by tetrad reference. The symbol < before a date indicates that the record is earlier than the date given, but that its exact date is not known. In such cases the date of the publication or document in which the record was located is supplied instead. The symbol * against a record indicates a currently extant (June 1996) population of *P. spicatum* at the site.

EAST SUSSEX, V.C. 14,

Firle (TQ/4.0), 1968, (BSBI); seems unlikely, no records prior to or after this one.

Near Glynde (TQ/4.0), (K). 1934, *Pickard* (**BM**); specimens of seedlings only in Herb. Musei Brittanica – seedling specimens difficult to confirm as *P. spicatum*; also G. C. Druce (Wolley-Dod 1937).

Ringmer/Isfield, Plashett Wood, along ride (TQ/4.1M), 1967, A. W. Jones; searched by David Lang and Paul Harmes in 1993, but no plants found.

Maresfield, a casual at (TQ/4.2), Rev. A. C. D. Ryder (Wolley-Dod 1937).

Uckfield, Hempstead Wood (TQ/4.2V), <1900, J. H. A. Jenner (Wolley-Dod 1937).

Uckfield (TQ/4.2), 1895, *Druce* (**K**).

Arlington, Park Wood Farm (TQ5.0P), E. Bray (Wolley-Dod 1937).

Near Hailsham (TQ/5.0), 1877, J. H. A. Jenner (**BM**); 1906, E. Bray (**K**); probably either Tilehurst, Bramble Grove or one of the Wilmington Forest woods.

Near Berwick (TQ/5.0), 1927, Miss Knox (BSBI); possibly a wood which has disappeared, or perhaps Plackett Coppice, in Wilmington Forest, the nearest known record.

Upper Dicker, Bramble Grove (TQ/5.0U), 1906, E. Bray (**BM**); "There is a good bit of it...", 1919, E. Bray in a letter to A. J. Wilmott (**BM**); Bramble Grove Wood searched by FitzGerald in 1987, no plants found, "uncoppiced for many years and very dark", EN.

Upper Dicker, Tilehurst Wood (TQ/5.0U), 1906, E. Bray (**BM**); 1919, E. Bray (**BM**); "access not gained", FitzGerald (1987).

Arlington, woodland (TQ/5.0I), 1885, J. H. A. Jenner (**LIV**); no exact location but could be referring to the nearby Wilmington Forest.

Copse near Michelham Priory, between Hailsham and Abbots Wood (TQ/5.0P or U?), 1933, J. E. Lousley (**RNG**); could perhaps be Bramble Grove or Milton Hide.

*Abbots Wood and Wilmington Forest (TQ/5.0N, T and U); there are numerous records for Wilmington Forest; most are Abbots Wood but many are Cane Heath, Nate Wood, Plackett Coppice, Milton Hide or Wilmington Wood – it is often impossible from the herbaria specimens to determine the precise location; first and last records for the Forest as a whole are given here; 1873, F. C. S. Roper (**BTN**) (also 1875 "dist. abundant"); felled portion of Abbots Wood near Milton Hide 1942, P. W. Richards (EN); "roadside show" along edge of Abbots Wood near Old Oak Inn, 1968, A. W. Jones; TQ/5.0N – ten plants on edge of woodland path in mixed deciduous area, TQ/5.0T – one plant on bank of main forest ride, TQ/5.0T – eleven plants in coniferous woodland edge by path, TQ/5.0T – two plants in overgrown dark woodland on bank of ditch, TQ/5.0T – five plants in a large clearing in the centre of Abbots Wood, and TQ/5.0N – one plant at the side of the road at the car park entrance, 1996, B. R. Wheeler.

Upper Dicker, Mill Wood, woodland ride (TQ/5.0P), 1954, D. Philcox (BSBI).

Nate Wood (part of Wilmington Forest) (TQ/5.0T), 1962, P. Cockburn (BSBI); woodland by stream, 23 plants in small patches, 1980, R. Minor, (BSBI).

Michelham Priory (TQ/5.0P, U) (Arnold 1907); "Originally perhaps an escape from Warbleton or Michelham Priories..." (Wolley-Dod 1937); "It is still grown in the apothecaries' garden", and an exhibit in the museum claims "it was brought to Michelham by the canons from its native France", 1986, R. FitzGerald (EN); the plant was not to be found in the apothecaries' garden in 1996 when a colleague of the authors visited, 1995.

Michelham Priory Wood (TQ/5.0U), 1924, *Foggitt* (CGE); most likely to be Bramble Grove or perhaps Mill Wood.

Laughton Woods, Laughton. (TQ/5.1B), <1900, J. H. A. Jenner, (Wolley-Dod 1937).

Bentley Wood, between Halland and East Hoathly, (TQ/5.1D), 1895, *E. H. Farr* (LIV); this record could refer to Bentley Wood at TQ/5.1D or at TQ/4.1Y; Druce's record for The Nursery, west of East Hoathly is for the same wood, Bentley Wood was named Nursery Wood on early 19th century maps; "NW part of wood, past S. of stream at about 51/506169, not very far east of public footpath.", C. A. Lister, pers. comm. to F. Rose, 1959, (EN); site searched by FitzGerald in 1987, no plants found, "very overgrown", (EN).

Wood near East Hoathly (TQ/5.1D, I, C or H?), 1896, *T. Hilton* (BM); this could be any of a number of woods in the area but may be Bentley Wood since it has confirmed records.

Bolt Wood, Chiddingly. (TQ/5.1L), 1930, *M. Abbott-Anderson* (LIV).

Waldrone (TQ/5.1P?), 1835 (Arnold 1907); "This is confined to a few square miles of the county and is not common there only a few hundred plants probably", 1892, *Farr* (NMW).

Little London (TQ/5.1U), H. S. Burder (Wolley-Dod 1937).

Heathfield, woods at Stillyans (TQ/5.1Z), 1869, *Dr Hogg* (BM); Stillyans is the farm just below the wood in which the following records also occur;

*Maynards Green (TQ/5.1Z); "Copse E. of Maynards Green", 1956 K. E. Bull (BSBI); "Plentiful in narrow bit projecting from main wood", 1957, K. E. Bull to F. Rose (EN), and "There were not so many plants as usual, perhaps a dozen to 20 scattered flowering plants", 1959, K. E. Bull to F. Rose (EN); "Both patches N of the stream (two plants and 69 plants) in tree-fall clearings, plants S (seven plants) of the stream in deep shade and more scattered", 1986, N. Stewart and R. FitzGerald (EN); Approximately 20 plants still to N of stream in main wood but Bull's patch in the copse was not found, nor those S. of the stream, 1996, B. R. Wheeler, 1996.

Maynards Green to Springdale Farm (TQ/5.1Z), 1965, *R. A. Boniface* (NMW); "This area is private gardens and coppices. Access not gained. Stream looks overgrown and dark", 1987, FitzGerald (EN).

New Sapperton Farm, Vines Cross/Maynards Green, twelve plants, (TQ/5.1Z), 1986, N. Stewart (BSBI); site not searched since, so possibly extant.

Sapperton Manor Farm, Vines Cross/Maynards Green, stream bank (TQ/5.1Z), 1968, P. C. Hall (BSBI); this area has not been searched since.

Knight's Farm / Hadlow Down, on the estate of the late Mr Day, at Hudlow (Mayfield).near the hedge of a hop-garden (TQ/5.2), Rev. R. Price, (Branwell 1872; Arnold 1907); on Hadlow Down, nr Mayfield and Knight's Farm, Mayfield, nr Cross-in-Hand, 1826, herb. *Borrer* (K); Hadlow Down, 1824, Rev. R. Price (herb. *Borrer*) (BM); Knight's Farm, Mayfield, a mile from Cross-in-Hand, 1829, (Wolley-Dod 1937); Wolley-Dod says "these two are the same station, and though formerly in Mayfield Parish, it is fully four miles from that village"; "The plant was growing in the wood and lane near the field, formerly a hop-garden, last July, A. E. Branwell (Branwell 1872).

Mayfield (TQ/5.2), 1887, *Rimington* (CGE); "Between Mayfield and Broadoak", T. Atkinson, (Wolley-Dod 1937).

Heathfield, on the old iron-foundries (TQ/5.2), E. Head in Wolley-Dod's notebook, (BTN); also in Notes on herb. *Borrer*. (BTN).

Heathfield, streambanks south of (TQ/5.1/TQ/5.2) (Wolley-Dod 1937).

Heathfield Golf Links (TQ/5.2), Mrs Morton. (Wolley-Dod 1937).

Old Heathfield, corner of Mill Pond, (TQ/5.2?) no date but pre-1980 (BSBI).

Hudlow (Hadlow Down?), "I have found it in hedgerows, scattered for miles, near Hudlow" (TQ5.2), A. E. Branwell (Branwell 1872).

Framfield, Pound Lane, "both sides of lane going north from A272, perhaps 1/3 of distance from main road to fork of lane", (TQ/5.2A), 1949, B. Welch, (BSBI) – this site refers incorrectly to the A272 – the road at those co-ordinates stems from the B2102 and joins the A272 further north.

Framfield, between Pound and Bridgeland Farm (TQ/5.2A), 1974, P. B. Clarke (BSBI). Roadside verge, 1983, P. Donovan (BSBI); site searched in 1986 by FitzGerald, (EN), and in 1987 by E. J. Rich – no plants found.

*Dower House Farm, Blackboys, woodland edge (TQ/5.2F), 1986, P. Donovan (EN); edge of ditch at woodland edge, 1996, D. Gunner.

Possingworth, Waldron Down (TQ/5.2F or K), no date, *J. Woods* (BM); "Borders of Possingworth Wood", Mrs Baines, (Wolley-Dod 1937).

*Tinkers Lane, Cross-in-Hand (TQ/5.2G); “literally 100’s of flowers..”, 1967, E. J. Ashdown (courtesy of T. G. C. Rich), 1970; steep roadside bank off lane called Tinkers Lane, 285 adult plants in 1996 – main concentration at eastern end of lane with smaller numbers spread along verge, 1996, B. R. Wheeler.

Hole Farm, “In the middle of a wood on the Hole Farm in Buxted Parish...”, (TQ/5.2G), 1835, *Bromfield (herb. Roper)* (**BTN**); ‘In Hole Wood on border of field between that and Knight’s in great abundance.’, 1941, *E. Forster* (**BM**).

Loudwell/Little England Farm, Hadlow Down. (TQ/5.2L), – the woods are owned by Little England but often recorded under the nearby Loudwell Farm – “Stream at edge of small wood SE of Loudwell Farm.”, 1974, P. C. Hall (BSBI); 50 plants counted, 1980, E. J. Rich, (BSBI); eight plants found in “overgrown disused coppice”, 1986, N. Stewart and R. FitzGerald, (EN); area searched by B.R. Wheeler in 1996 but no plants found, area very dark.

*Loudwell/Little England Farm, Hadlow Down. (TQ/5.2L), 16 plants found, “..some daylight is needed.”, 1986, N. Stewart and R. FitzGerald, (EN); 5 vegetative plants found in dark overgrown coppice on streambank at Western corner of Homegrove Wood, 1996, B. R. Wheeler.

Mill Lane, Cross-in-Hand, roadside verge (TQ/5.2K), 1973, E. Norman (BSBI); not found in 1980 by R. Minor, (BSBI).

*Malls Bank, Nursery Lane, Cross-in-Hand (TQ/5.2K), 1974, P. C. Hall, (BSBI); plants on a roadside verge where the verge borders Malls Bank Farm – seven plants divided between two small areas of the verge, B. R. Wheeler. This is a reduction from 16 plants in 1980, R. Minor, and 18 in 1987, R. Fitzgerald and E. Wood, (EN).

Selwyns Wood (TQ/5.2K), 1943, *F. Rose* (**NMW**).

A lane east of Hadlow Down (TQ/5.2L or M?), (Wolley-Dod (1937) – this record could be the Knight’s Farm record.

Cross-in-Hand (TQ/5.2Q?), 1832, *W. Christy* (**CGE**); also 1892, *E. H. Farr* (**BTN**); 1924, *Wolley-Dod (BM)*; these could be a number of extinct or extant sites in the Cross-in-Hand area.

*Brown’s Lane, nr Cross-in-Hand, 51 plants. Plants on south bank of lane – not in adjoining field. (TQ/5.2Q), 1980, R. Minor (BSBI); >55 plants in 1986, (EN); only 4 plants by 1994, B. R. Wheeler; overgrown hedge which had been shading verge in recent years had been cut in 1996 – it is possible that the verge may recover.

Tilesmore Wood (TQ/5.2Q or R), 1827, W. Borrer (Wolley-Dod 1937).

Field borders east of Dunsley Wood (TQ/5.2Q or R?), 1827, W. Borrer, (Wolley-Dod 1937) – this is probably Dunly Wood.

East of The Pheasantry, Heathfield. (TQ/5.2W), 1968, H. Hartwell (BSBI); site searched by FitzGerald in 1986, no plants found, (EN).

Warbleton, in the woods at Warbleton in such abundance... (TQ/6.1), 1845, E. Jenner (Wolley-Dod 1937); only remaining Warbleton Parish sites are Rushlake Green and St Dunstan’s Farm.

*St Dunstan’s Farm, three plants in woodland edge (TQ/6.1A), 1994, J. Simes; still extant, 1996, P. Harmes.

Between Herstmonceux and Hellingly (TQ/6.1B?), 1929, *Miss K. M. Morris* (**BM**) – this record could be Park Wood. Park Wood, Hellingly, woodland ride (TQ/6.1B), 1880, *F. C. S. Roper* (**BTN**); “Eastern ride towards Carters Corner.”, 1961, D. P. Young (BSBI).

*Rushlake Green, single plant by path in woodland (TQ6.1J), 1990, M. MacFarlane and G. Stevens (BSBI); 4 flower spikes, 1995, J. Simes; unconfirmed for 1996, but likely to be extant, well known site.

Warbleton Priory (TQ/6.1P) (Arnold 1907).

“Wood near Parson’s Mill” (TQ/6.2), 1835, *W. M. Borrer* (**CGE**) – exact location unidentified.

Street End, Broad Oak (TQ/6.2B), *no name* (**LIV**). 1917, *W. Byrne* (**BM**); 1925, Mr Payne (BSBI).

Conservation of Britain's biodiversity: *Cyperus fuscus* L. (Cyperaceae), Brown Galingale

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ABSTRACT

Cyperus fuscus is a rare plant in Britain and probably always has been. It has been recorded in a total of 13 sites in England and two in Jersey, but is currently known from six sites and one site respectively (c. 50% decline). It is an annual of bare, seasonally exposed, nutrient-rich, base-rich mud on the edges of ponds and ditches. It is at its northern limit of distribution and is probably limited by climate. Population counts for extant sites are given for the period 1993–1996. The numbers of plants vary from year to year and site to site, with many observers noting it is most abundant in hot, drought years. Four sites have numbers below the minimum required to conserve all polymorphic genes with a frequency of 0.05 in the population. Most sites are grazed by stock, but in some, scrub has been removed to improve the habitat. Only one site is not protected.

KEYWORDS: Rare species, conservation.

INTRODUCTION

Cyperus fuscus L. (Cyperaceae), Brown Galingale, is a rare plant in Britain. In 1992, the wild-plant conservation charity Plantlife became concerned that it was amongst the most threatened plants in Britain. It was therefore included in their "Back from the brink" project, which aims to conserve critically endangered plant species through research and management work. About 20 rare plant species have been included in this project between 1992 and 1996, which represents a significant contribution to the conservation of biodiversity in Britain by the voluntary sector. The aim of this paper is to summarize the conservation work carried out on *C. fuscus* to 1996; full details can be found in Rich (1993a, 1993b, 1994, 1995) and Rich *et al.* (1996). Further details about the "Back from the brink" project can be obtained from Plantlife.

DISTRIBUTION

DISTRIBUTION IN BRITAIN

The distribution of *C. fuscus* is mapped in Fig. 1. It has been recorded from 13 native sites in England (some of which have or have had more than one population) and two in Jersey, in a total of eleven 10 km squares. The English sites are concentrated along parts of the valleys of the River Thames and River Avon with outlying sites in Somerset, Dorset and the Weald. It was also introduced to Fulham Common from Swiss material by A. H. Haworth in c. 1819 and was reported regularly until 1865 when the meadow was drained and built on (Gray 1871); this site is not discussed further. A record for Guernsey probably refers to Jersey (McClintock 1975).

The dates of first and last records are summarised in Table 1. It has only been recorded in six sites in England and one site in Jersey since 1990 (c. 50% decline). The reasons for its decline are not always clear, but loss of ponds, drainage, gravel extraction, land reclamation or natural in-filling are possible reasons for loss. Most of the decline took place by the 1920s, and only one site has been lost in the last 50 years.

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FIGURE 1. Distribution of *Cyperus fuscus* in the British Isles. ■ 1990–1996; □ pre-1990; + introduced.

WORLD DISTRIBUTION

Cyperus fuscus is widespread in Europe, adjacent parts of Africa and large parts of Asia (the eastern limits are insufficiently known; Hultén and Fries 1986). It is rare and declining in northern Europe (e.g. extinct in Sweden; Lindberg 1977) but is quite common in parts of central Europe. For instance it is quite frequent along the Rhine in Germany (Haeupler and Schonfelder 1989); in the Czech Republic, it is a characteristic plant of fish ponds in the south of the country (e.g. Husák 1953).

It is rare in the eastern United States of America, occurring westwards to Nebraska and South Dakota (Weedon and Stephens 1969). It was found in Canada in 1970 as an adventive at the edge of a pond in Ontario Province (Gillett 1971).

TABLE 1. DATES OF FIRST AND LAST RECORDS OF SITES OF *CYPERUS FUSCUS* IN THE BRITISH ISLES. EXTANT SITES ARE ONLY LOCALISED TO COUNTY

Site	No. of populations	First record	Last record	Reason for loss
Berkshire 1.	1	c. 1982	1996	-
Berkshire 2. Pangbourne	1	1911	1911	Exact site not known, possibly reclaimed for agriculture
Buckinghamshire 1.	2	1906	1996	-
Buckinghamshire 2. Huntercombe	1	1906	1906	Exact site not known, possibly reclaimed for agriculture
Dorset 1. Bere Regis	1	1893	1893	Site still suitable
Dorset 2. 1–2 miles from Bere Regis	1	1893	1893	Exact site not known, possibly reclaimed for agriculture
Dorset 3. Wimborne	1	1929	1929	Exact site not known
Hampshire 1.	1	1934	1996	-
Hampshire 2.	2	1983	1996	-
Hampshire 3. Blashford	1	1893	1893	Probably lost to gravel extraction
Middlesex 1.	1	1957	1996	-
Somerset 1.	3+	1899	1996	1 population still extant; others possibly lost through succession to fen/swamp vegetation
Surrey 1. Shalford	1	1846	1960s	Seedbank possibly still present, pond rarely dries out
Jersey 1. St Peter's Marsh	1	1842	1842	Site drained
Jersey 2.	1	1989	1996	-

ECOLOGY

LIFE CYCLE

C. fuscus is an annual. It probably germinates from early summer onwards when the seedbank in the mud becomes exposed by seasonal drops in water level. Some germination has been noted as late as August at sites in Hampshire and Buckinghamshire. Plants were seen in flower in early June in the Czech Republic (pers. obs., 1993), but in Britain it flowers later, from about July to September. Plants are wind-pollinated; the anthers are tiny and yellow, and are exerted after the styles.

Plants vary in size markedly. Plants collected at Somerset 1 (see Table 1) last century were often lush and up to 30 cm tall, whilst those seen more recently there and elsewhere have often been only a few centimetres high, although flowering and fruiting freely. It can grow and complete its life cycle within four months, as shown by its persistence in ditches at Somerset 1 over a period of many years where the ditches were cleared out on a four monthly cycle (White 1912). It is possible to obtain two generations in cultivation in one year (R. S. Cropper, pers. comm., 1995).

Plants fruit soon after flowering. Most fruits probably do not disperse outside the pond or ditch system, but fruits have been found in mud attached to birds (Salisbury 1970) and its distribution along river valleys suggests that fruit is also dispersed by water during floods. Evidence from conservation work suggests that it has a persistent seed bank (see below).

HABITAT

The plant occurs on the damp, open, seasonally exposed, muddy margins of small ponds and ditches. Most soils are nutrient-rich (e.g. Lousley 1976), and it may benefit from nutrients from wildfowl droppings. Soil samples measured from four sites ranged from pH 6.6–7.8. It will tolerate some salinity in Europe (pers. obs., 1993), but has not been recorded in saline habitats in Britain.

It is often associated with annuals of disturbed mud such as *Bidens cernua*, *B. tripartita*, *Gnaphalium uliginosum*, *Juncus bufonius*, *Persicaria maculosa*, *P. hydropiper*, *Ranunculus sceleratus*, *Rorippa nasturtium-aquaticum* and *R. palustris*, and perennials such as *Agrostis stolonifera*, *Alopecurus geniculatus*, *Glyceria fluitans* and *Mentha aquatica*. The vegetation is

TABLE 2. SUMMARY OF RECENT POPULATION COUNTS OF *CYPERUS FUSCUS*. NO PLANTS HAVE BEEN SEEN RECENTLY AT SURREY 1, BUT A SEED BANK MAY STILL BE PRESENT. * NOT SURVEYED

SITE	1984–5	1993	1994	1995	1996
Berkshire 1	1,000	250	35–40	30	60
Buckinghamshire 1	0	41	188	96	7
Hampshire 1	1,500	1,000+	10,000	25,000	5,000
Hampshire 2	36,500	c. 500	200	1,061	1,682
Middlesex 1	50	0	200	100	320
Somerset 1	2	5	33	10	1
Surrey 1	0	0	0	0	0
Jersey 2	*	0	0	3	3,000+
Total	39,052	1,796+	10,656	26,300	10,070+

usually open, but *C. fuscus* can sometimes be found under the canopy of taller swamp species, though it will not tolerate deep shade. It is sometimes found with other uncommon wetland species such as *Hottonia palustris*, *Oenanthe aquatica*, *Persicaria minor* and *Rumex palustris*, and in central Europe such communities (*Cyperetalia fusi* and *Cypero Limoselletum*) are regarded as botanical gems (Ellenberg 1988).

CLIMATE

Cyperus fuscus is at the northern limit of its distribution in Britain, and seed production is probably limited by climate indirectly through habitat conditions, and directly through effects on growth and reproduction. Many observers (e.g. Druce 1926) note that it is most abundant in hot, drought years, and this has been confirmed in recent years (e.g. Table 2).

With a generally wet and cool climate in Britain compared to Europe, its wetland habitats are dependent on seasonal lowering of the water table through low rainfall and higher temperatures, thus exposing the mud to allow plants to germinate. Tutin (1953) noted that in cultivation at Leicester it required relatively high temperatures for germination, and set little or no seed in a cool summer. The high nutrient status of many of its sites may also enable rapid growth under suitably warm climatic conditions. It flowers from peak summer onwards in Britain and thus has a very short flowering season before the autumn rains begin and plants are flooded. Plants at Middlesex 1 have been observed to survive short periods of inundation by water, but not longer periods; plants collected in September 1994 after c. 1 week under water and transplanted to the Seed Bank at Wakehurst Place died and set no fruit.

Cyperus fuscus appears likely to benefit from global warming if the climate becomes warmer and drier, but probably not if it becomes warmer and wetter.

POPULATION SIZES

The population sizes at the seven extant sites in 1993–1996 are summarised in Table 2, with some earlier 1984–1985 data for comparison from surveys carried out for the Nature Conservancy Council (Everett 1987; L. Farrell, pers. comm., 1993). It was present in seven sites between 1993 and 1996, and a seed bank may be still present at Shalford Common.

The number of sites present each year depends on the weather and on disturbance. All recorders find that it varies in abundance within sites from year to year. For instance Lousley (1976) noted that *C. fuscus* fluctuated in abundance from year to year at Shalford "from great abundance in years like 1949, when the pond was almost dry, to complete absence when the water is high or the pond is overgrown with tall vegetation".

CONSERVATION

SITE MANAGEMENT

Most sites are usually subject to light disturbance which helps to maintain them in a generally suitable open condition, such as by cattle trampling (though this must not be excessive) (Table 3).

TABLE 3. CONSERVATION STATUS AND CURRENT THREATS TO *CYPERUS FUSCUS* SITES. NNR = NATIONAL NATURE RESERVE. SSSI = SITE OF SPECIAL SCIENTIFIC INTEREST. SSI = SITE OF SPECIAL INTEREST (JERSEY)

Site	Status	Management	Threats
Berkshire 1	SSSI	Cattle grazed. Clearance of willows in pond by English Nature/National Trust.	
Buckinghamshire 1	None	Heavily cattle-grazed common land.	Possible changes in water table due to Maidenhead flood relief scheme; pollution from road run-off; significant increase or decrease in stocking levels.
Hampshire 1	SSSI	Cattle-grazed. Some ditch clearance has been carried out to provide suitable water levels.	Possibly pollution from road run-off; significant increase or decrease in stocking levels.
Hampshire 2	SSSI	Cattle- and pony-grazed common land.	Spread of <i>Myriophyllum aquaticum</i> ; significant increase or decrease in stocking levels.
Middlesex 1	SSSI	Cattle-grazed common. Clearance of willows by Plantlife.	Spread of <i>Crassula helmsii</i> and <i>Myriophyllum aquaticum</i> ; pollution from road run-off; significant increase or decrease in stocking levels; trampling by fishermen; lack of management.
Somerset 1	NNR	Ditch in horse-grazed pasture.	Inappropriate ditch maintenance; marked changes in water table.
Surrey 1	None	Old common no longer grazed. Margins disturbed in 1989 without success; pond dredged in 1992 and some willows cleared, but pond has not dried out since.	Local residents require a fish and duck pond which is in conflict with the <i>Cyperus</i> requirements.
Jersey 2	SSI	Ungrazed common. Reeds cleared in parts annually, and also mown.	Changes to local water table; cess-pit effluent; lack of management.

C. fuscus is not grazed by horses and cattle primarily due to its small size. The associated trampling may result in loss of some individuals, but these losses are probably compensated for by maintenance of short open vegetation which is suitable for other individuals.

It has also benefitted from conservation work at Middlesex 1 and Berkshire 1 which had become overgrown with scrub. Clearance of tall dense willow scrub at Middlesex 1 in September 1993 resulted in the reappearance of the plants in 1994 (no plants had been observed at this site since 1989); further clearances were carried out in 1996. Clearance of willow scrub at Berkshire 1 in 1994 has produced a less spectacular response, but plants are recolonising newly exposed mud. Plants were found at Jersey 1 after clearance of reeds in an old pond.

The timing of management work is critical. Clearly it should not be carried out when plants are growing, but at other times of year ponds are often too wet to work in safely. Experience has shown that disturbance late in the season produces good results the following year. Disturbance could also be carried out immediately the mud is exposed in early summer prior to germination. In Somerset 1, *C. fuscus* was reported to benefit from ditch clearance as late as June (White 1912).

Calculations have shown that a minimum sample size of 172 plants is required to preserve all, or very nearly all, polymorphic genes with frequency over 0.05 in a population (Lawrence *et al.* 1995a, b). It is thus proposed that conservation management should aim to achieve at least 172 *C. fuscus* plants at each site each year. On this basis, three sites have populations consistently above the minimum sizes, and four below (Table 2).

STATUTORY PROTECTION

Table 3 summarises the protection and threats to each site. *C. fuscus* is protected under the Wildlife and Countryside Act 1981, which should prevent deliberate uprooting and collection. Five extant sites are protected as statutory Sites of Special Scientific Interest in England, though only one of these is specifically for *C. fuscus*; one site has no protection. Jersey 1 is a statutory Site of Special Interest.

This species is still under threat in Britain. A Species Action Plan is currently being drawn up by Plantlife for English Nature.

MONITORING AND RESEARCH

It is essential that populations are monitored each year to determine the results of the conservation work, assess natural variation due to weather and to watch out for new threats to sites. Between 1993 and 1996 monitoring was carried out cost-effectively by simply counting plants, taking photographs and making observations on management with the help of volunteers.

In the longer term, population sizes should be correlated against weather patterns and pond water levels to determine how close the links are between population peaks and good weather and *vice versa*. Research should also be carried out into seed set and germination under different environmental conditions (temperature, water-logging, etc.).

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Conservation of Britain's biodiversity: *Salvia pratensis* L. (Lamiaceae), Meadow Clary

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ABSTRACT

A summary of conservation work carried out on the statutorily protected plant species *Salvia pratensis* L. (Lamiaceae) in Britain between 1994–1996 is given. It has been recorded in 138 hectads and 32 vice-counties, mainly in southern Britain. It is accepted as native or probably native in 32 hectads and nine vice-counties, and introduced elsewhere. It has been recorded in 17 native or probably native hectads since 1990, and in another 15 prior to 1990, most of the loss of native sites occurring before 1950. It is a robust, polycarpic, perennial which sets abundant viable seed. It occurs in neutral or calcicolous grassland and scrub on calcareous soils. Sites may be unmanaged, mown regularly or irregularly, or may be grazed by stock or rabbits. It grows and reproduces best in sites which are winter-grazed with plants protected during flowering. Conservation work carried out includes population monitoring, introduction of suitable grazing regimes, soil scarification, scrub clearance, cross pollination and seed bank collections.

KEYWORDS: population sizes, habitat management, distribution, ecology.

INTRODUCTION

Salvia pratensis L. (Lamiaceae), Meadow Clary, is a handsome, blue-flowered, perennial herb which is typically found in unimproved, calcareous or neutral pastures. It was first reported from Kent in 1696 (Druce 1932), and is now known from sites scattered across southern Britain with the majority of the populations in Oxfordshire. It has also been recorded elsewhere as an introduction.

S. pratensis has probably always been rare in Britain. Following concern that it was declining, surveys were carried out by the then Nature Conservancy Council during 1986–1988 (e.g. Everett 1987). It was added to Schedule 8 of the *Wildlife and Countryside Act 1981*, as amended, in 1992, and is statutorily protected. In 1994, Plantlife and the Ashmolean Natural History Society of Oxfordshire began a Species Recovery Programme with partial funding from English Nature to draw up a conservation plan for the species based on the excellent, detailed review of its ecology and conservation by Scott (1989).

The aim of this paper is to summarise the conservation work carried out on the species in Britain between 1994 and 1996. Full details (which have been up-dated here) are given in confidential Plantlife reports (Rich 1995, Rich & McNab 1996, Rich *et al.* 1997). A full Species Action Plan is being implemented in England by Plantlife with funding from English Nature (Rich *et al.* 1997), and in Wales by the Countryside Council for Wales (L. K. Wilkinson, pers. comm., 1996). Various

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studies are also being carried out in Holland where the plant is also locally endangered (Ouborg, Van Treuren & Van Damme 1991; Van Treuren *et al.* 1991, 1993; Ouborg & Van Treuren 1995).

DISTRIBUTION

About 450 records of *S. pratensis* were traced in the literature, major herbaria (**BM**, **BRISTM**, **CGE**, **K**, **LIV**, **MNE**, **NMW** and **OXF**), Biological Records Centre and correspondence with various botanists, statutory agencies and Wildlife Trusts. Only a few records have been rejected as the plant is easily identified and many records are supported by herbarium specimens.

The distribution of all records is summarised by 10-km squares in Fig. 1. *S. pratensis* has been recorded in 138 hectads (10-km × 10-km squares) and 32 vice-counties. The records pick out the main areas of chalk on the North and South Downs, the Chilterns, the Hampshire-Wiltshire plains and the limestone of Oxfordshire and Gloucestershire, reflecting its general requirement for calcareous substrates.

Whilst there is little doubt that *S. pratensis* is native in some localities in Britain and introduced to others, its status at some sites will probably never be resolved. The records have been revised as far as possible, noting the opinions of authors of the local Floras and other information. In general, *S. pratensis* is accepted as native in long-recorded sites or areas on chalk or limestone, and as introduced elsewhere. The presence of a single plant at a site may indicate that it is introduced, especially off calcareous soils, but the characteristic way in which single plants appear on suitable soils close to other records could also indicate a long persistent, native seed bank. Squares where *S. pratensis* is accepted as native are also shown in Fig. 1; it is native in 21 hectads and possibly native in another eleven hectads. In terms of vice-counties, it is native in vcc. 8, 15, 16, 17, 23, 24 and 34, and probably native in vcc. 13 and 35. This interpretation of the native distribution differs significantly from that presented in the *Atlas of the British flora* (Perring & Walters 1990).

There has been some debate about the status of the Monmouthshire population (e.g. Riddelsdell 1916). Kay & John (1995) investigated the population genetics and demographic ecology of 32 species of lowland grassland and related habitats in Wales including *S. pratensis*. Nine loci in six enzyme systems were analysed in *S. pratensis*, of which five were variable. The pattern of heterozygosity was variable and unexpected, suggesting that recombination might be restricted by a degree of structural heterozygosity. An unrooted phylogenetic tree indicated that there was a high degree of correlation between geographic and genetic inter-relationships, with very little differentiation within the sub-divided population but relatively large distances between populations (N.B. one locality in Kent is erroneously treated as two localities). There was some evidence of a cline of decreasing genetic variability from the more variable populations in south-east England to the least variable population in Monmouthshire. This pattern indicated that the surviving genotypic composition of the Monmouthshire population could be regarded as a typical edge-of-range population, perhaps derived from the Cotswold plants. This suggests that it could indeed be native or introduced from the Cotswold populations; based on the information available to date it is accepted as native. Further work on the genetics in relation to European material may provide more information on the status at this and other sites.

There appear to be several modes of introduction. *S. pratensis* has been specifically noted as introduced with foreign grain to many sites in Britain, especially during the period 1880–1930. It is locally common in Europe and was a regular seed contaminant of imported grass/clover permanent pasture seed mixtures but was rare in grain from annually-cultivated arable fields.

Salvia spp. have also been widely grown as herbs or salves (though *S. pratensis* is not especially noted for its medicinal uses). The name “Clary” appears to be derived from “clear-eye” – a practice by which mucilage from wetted seeds was put into eyes to “cleanse them” (this is not recommended practice). It was also used as a gargle for sore throats and as a cleanser of the teeth. The plant is now also fairly widely available in garden centres and its seed is present in so-called “wild-flower” seed mixtures. Some introduced records may therefore be a result of escapes from cultivation.

Sturt (1995) has recently drawn attention to the association of *Salvia verbenaca* L., Wild Clary, with churchyards where it was sown on graves in the belief that it conferred immortality. At least eight records of *S. pratensis* are associated with churches, and this association may also account for some introduced records.

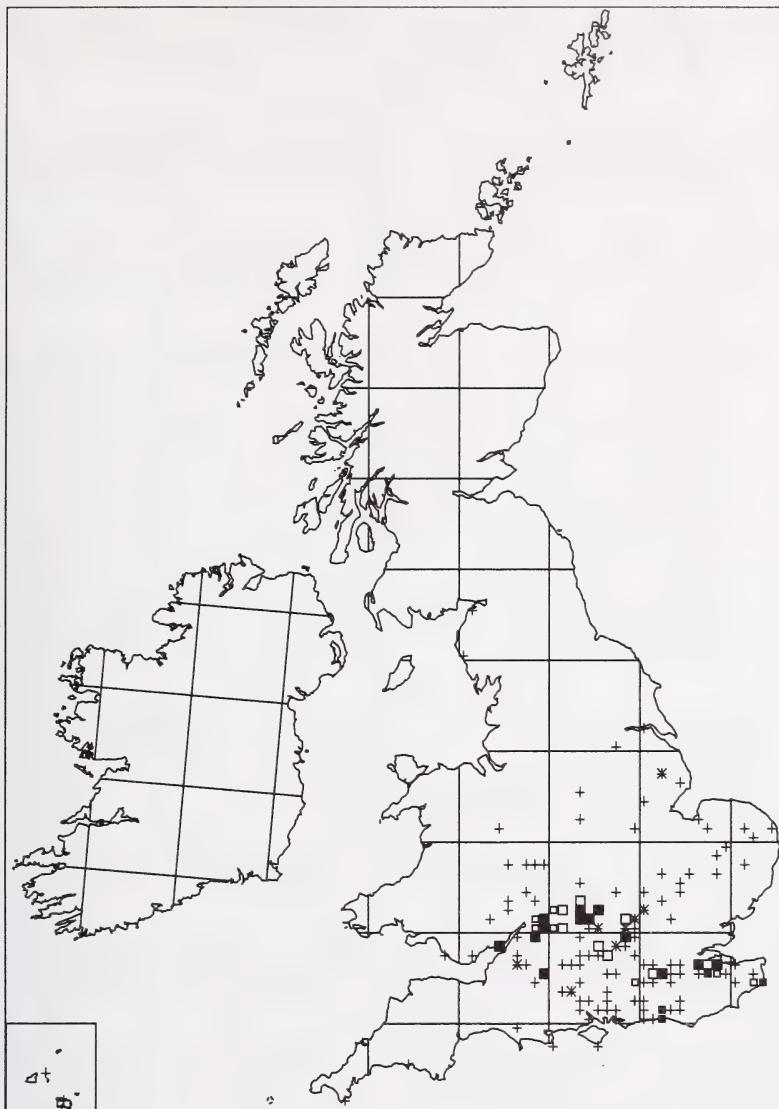


FIGURE 1. Distribution of *Salvia pratensis* L. in Britain. ■ Native 1990 onwards; □ native, pre-1990; ▨ possibly native, 1990 onwards; ▨ possibly native, pre-1990; * introduced, 1990 onwards; + introduced, pre-1990.

POPULATION SIZES

At a national scale *S. pratensis* has been recorded as native or probably native in 17 hectads since 1990, and in another 15 prior to 1990. It has been recorded as an introduction in nine hectads since 1990. The plant should now thus be regarded as a Nationally Scarce species (cf. Stewart *et al.* 1994). Most of the loss of native sites appears to have taken place prior to 1950, and there is little evidence of significant decline in recent years; it is hoped that its statutory protection coupled with conservation work summarised below will prevent further losses.

Populations were counted at each site at least once between 1994 and 1996; the maximum counts are shown in Table 1. Populations were usually counted by walking around sites, but at one large

TABLE 1. MAXIMUM POPULATION COUNTS FOR NATIVE *SALVIA PRATENSIS* L. SITES
RECORDED AT LEAST ONCE BETWEEN 1994 AND 1996. SITES ARE
ONLY LOCALISED TO COUNTIES

Site	Year	Population
Buckinghamshire 1	1996	1
Gloucestershire 1	1994	200
Gloucestershire 2	1994	3
Gloucestershire 3	1996	1
Kent 1	1994	20
Kent 2	1996	c. 13
Monmouthshire 1	1994	3
Oxfordshire 1	1994	4000–5000
Oxfordshire 2	1994	408
Oxfordshire 3	1995	43
Oxfordshire 4	1994	8
Oxfordshire 5	1995	1270
Oxfordshire 6	1996	20
Oxfordshire 7	1995	19
Oxfordshire 8	1995	4
Oxfordshire 9	1995	358
Oxfordshire 10	1996	6
Oxfordshire 11	1996	211
Oxfordshire 12	1996	8
Oxfordshire 13	1996	20
Surrey 1	1996	11
Sussex 1	1994	200
Sussex 2	1995	1
Wiltshire 1	1994	1

site a more detailed systematic grid was used. In general each discrete clump was assumed to be one plant, but some clumps may have consisted of more than one individual. Counts included seedlings, vegetative and flowering plants.

The population sizes vary enormously from single plants to a few thousands. An unusual feature of *S. pratensis* is the survival of a single plant in one remote locality for long periods, perhaps for 30 years or more. There are about 7000 plants in 23 native sites (Table 1), and about 2000 introduced plants in Britain (Rich 1995).

An analysis of change in Oxfordshire indicates that 1994 populations are markedly below those of 1986–1988 censused by the Nature Conservancy Council (Everett 1987), though no sites have been lost (C. R. Lambrick in Rich 1995). The same appears to be true for some of the other populations elsewhere, indicating longer term climatic conditions may be important in regulating population sizes. It is likely that the management of sites is also critical.

Ouborg & Van Treuren (1995) examined the relationship between population size and fitness in *S. pratensis* in the Netherlands. In theory small populations would be expected to have lower fitness than large populations as higher levels of genetic drift and inbreeding would occur leading to a reduced viability and fecundity of the population. To test the theory, they cultivated plants from two large and two small Netherlands populations under similar conditions, and measured various components of seed size, germination, growth and reproduction. Contrary to the predictions, they found no evidence for reduced fitness in small populations, nor was there any evidence in the small populations for genetic erosion of fitness. It is possible that the small populations were at an early stage of genetic erosion where the allozyme diversity was low but the quantitative genetic variation underlying the fitness traits had not (yet) been affected. Applying these results to British populations, it may mean that even the small ones are viable in genetic terms. The evidence at the moment suggests that environmental or stochastic processes have more significant effects on populations than genetic processes.

ECOLOGY

The population biology and ecology of *S. pratensis* in Oxfordshire, and at a few sites in Gloucestershire and Hampshire was described in detail by Scott (1989), from which the account below has largely been taken, with additional data from other sites (Rich 1995; Rich & McNab 1996).

S. pratensis is a long-lived, polycarpic, perennial. Plants are relatively compact in growth form even when growing at high density (up to 50 plants per m²) and may be distinguished from one another by distinctive morphological characteristics which include the sex, length and colour of flowers.

The peak flowering period is from late May to early July; Scott (1989) found 32–94% of the plants flowered on unmanaged sites. It is gynodioecious and self-compatible, though insects are required for within-flower selfing. Populations contain 1–9% of male-sterile plants and their frequency increases under intense shade or after damage from herbicides. Male-sterile plants have aborted stamens and smaller flowers than hermaphrodites. Flowers were visited by five species of pollinating bumblebees, and by pollen beetles, robber bumblebees and two species of butterflies.

Scott (1989) found that seed-set exceeded 90% on most sites, but was slightly reduced where all plants were robbed (84%) or when fewer pollinators were available in mid-August (83%). Late flowering male-sterile plants set 67–74% of seed suggesting that even hermaphrodites are substantially out-crossed. Seed took one month to ripen and was released from mid-July onwards. Laboratory experiments showed that 72% germinate immediately after wetting in daylight or darkness, though after-ripened seed is less viable. Seed can germinate after at least one year of dormancy in the soil seed bank.

Seedlings successfully establish where disturbance and stress generate gaps in the sward, exposing bare, uncompacted mineral soil. Short swards maintained by rabbit grazing provide very favourable conditions for seedling establishment and it is in these areas that the density of seedlings and mature plants is highest. Suitable niches for seedling establishment include worm casts, old ant hills, small mammal runs and rabbit scrapes. Establishment is generally unsuccessful in tall undisturbed grassland where more than 1 cm of moss or leaf litter accumulates under vigorous species such as *Brachypodium pinnatum* and scrub. Reproduction is also unsuccessful where plants are mown or intensively grazed by stock while flowering, as their inflorescences are destroyed (Scott 1989).

Many populations occur on flat to steeply sloping sites facing south or west, which provide a warm, sunny microclimate. They generally grow on shallow, calcareous soils overlying oolitic limestone or chalk, but may also occur (and persist) on mesotrophic, freely-drained soils. Plants have deep roots which extend into the C horizon of the soil.

S. pratensis occurs in hay meadows, grazed pastures, scrub and open woodland, and on banks, verges and tracks. It has been recorded in a range of communities of the National Vegetation Classification (Rodwell *et al.* 1991 *et seq.*). It mainly occurs in unimproved species-rich calcicolous grasslands (CG2 *Festuca ovina* – *Avenula pratensis* grassland, CG3 *Bromus erectus* grasslands, CG4 *Brachypodium pinnatum* grassland, CG5 *Bromus erectus* – *Brachypodium pinnatum* grassland) but surprisingly also occurs and persists in mesotrophic grasslands (MG1 *Arrhenatherum elatius* coarse grassland, MG7 *Lolium perenne* leys). Scrub or woodland edge communities in which it occurs are usually W21 *Crataegus monogyna* – *Hedera helix* scrub.

Sheep and cattle at a high stocking density graze off all inflorescences and defoliate plants. In Oxfordshire, plants grazed in late June fail to flower later in the year, but 13% of flowering plants cut during hay making in mid-June flowered again in mid-August (Scott 1989). It appears that roe and muntjac deer browse inflorescences while rabbits ignore *S. pratensis* entirely. On some sites significant damage was caused by sawfly larvae and small mammals to flowers and unripe seed respectively. The plant is also grazed by slugs and snails, which may cause significant mortality in damp situations. Dormant basal buds on the rootstock develop rapidly if the main axis is damaged by grazing or cutting, and as part of the seasonal growth-cycle from July onwards.

CONSERVATION MANAGEMENT

S. pratensis survives for long periods under various management regimes. Sites may be neglected or unmanaged, mown irregularly (e.g. road verges) or annually (e.g. hayfields), or grazed by rabbits or stock. In general, the plants seem to grow best and increase where the sites are winter-grazed with plants protected during flowering. Unfortunately this regime is not practicable for many sites such as road verges.

Scott (1989) has drawn up a series of recommendations to maintain and encourage the expansion of populations in existing sites; disturbance is required to maintain an open grassland sward, prevent plant litter and moss accumulating, and control the spread of invasive species. For site-specific conditions, the following management regimes were recommended:

1. Unmanaged sites should have a grazing or cutting regime introduced.
2. Mown sites should be cut in late July (early August) and the cuttings raked off. Soil scarification may also be required.
3. Sheep grazed sites should be grazed until early May, and then again from late July (early August) onwards. Grazing with cattle may be possible all year provided the stocking density is not too high. Plants can be protected by small enclosures during the summer if necessary. Every 4–5 years, the sites can be summer grazed.

These recommendations are being applied in various sites under the Species Action Plan and the results will be documented in due course. In addition, scrub clearance has been carried out at four shaded sites which has resulted in improved flowering performance. Soil disturbance has also been carried out at three sites but as yet has failed to produce more plants from the seed bank. At one site a single female plant has been cross-pollinated with another plant of known origin from another site.

Reinforcement of populations is being carried out at two sites with stochastically-threatened populations to increase the populations to this size.

Seed has been collected under licence from English Nature from six sites and deposited at the Seed Bank at the Royal Botanic Gardens, Wakehurst Place; further collections are planned.

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Rumex *× akeroydii* – a new Dock hybrid

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ABSTRACT

A new *Rumex* L. (Polygonaceae) hybrid is described and illustrated. A single robust plant of *R. × akeroydii* Rumsey **hybr. nov.** (*R. palustris* Sm. × *R. cristatus* DC.) was discovered growing with its parents on the Inner Thames Marshes SSSI, Rainham, S. Essex in 1991.

KEYWORDS: hybridisation, Essex.

INTRODUCTION

While surveying the distribution of locally and nationally scarce taxa on the Inner Thames Marshes SSSI (Site of Special Scientific Interest) at Rainham Marshes, S. Essex (Grid reference TQ/5.8) in the summer of 1991, a striking *Rumex* hybrid was discovered at the head of a then dry drainage ditch. The area, previously used as rifle ranges, grazing marsh and silt lagoons, borders commercial transport and light engineering works. At the time of the visit in late August, the site was very dry and appeared somewhat derelict as a result of the apparent cessation of grazing and other management. Scarce ruderal species of open vegetation such as *Puccinellia rupestris* (With.) Fernald & Weath., previously present in cattle-poached areas by drainage dykes, were absent. The drainage dykes which cross the grassland did, however, still locally support healthy populations of the nationally scarce docks *R. maritimus* L. and *R. palustris* Sm.

The areas bordering on Ferry Lane, which skirts the site on two sides, support a rich alien flora and have long been a hunting ground for those interested in such plants. A *Heracleum* sp., identified as *H. mantegazzianum* Sommier & Levier, but perhaps not that species, has been naturalized here since at least the 1920s and the alien dock species *Rumex obovatus* Danser and *R. patientia* L. (as subsp. *patientia*) have both been reported in this general area (Jermyn 1974). The most frequent (and perhaps only) member of the *R. patientia/R. cristatus* group present in 1991 was *R. cristatus* DC. (specimens confirmed by Dr J. R. Akeroyd). Whether this is the result of an earlier mis-identification, or more recent colonisation and perhaps ousting of *R. patientia* by *R. cristatus* is impossible to state in the absence of any earlier voucher specimens. *R. cristatus* is, in my experience, much the commoner on waste ground on the clay soils along the Essex side of the Thames estuary and would seem to still be increasing.

R. cristatus was infrequent away from the roadside but scattered plants could be found extending onto the grassland area at Rainham previously used for the rifle ranges and grazing. One such plant, a rather depauperate example at the head of a drainage ditch, was growing with an unfamiliar, striking, robust plant recognized in the field as a hybrid due to its intermediate appearance and sterility. The base of the ditch supported an open vegetation dominated by a large stand of *R. conglomeratus* Murr. with scattered plants of *R. palustris* and *R. maritimus* occurring within 25 m, further down the same ditch. A single example of the hybrid *R. conglomeratus* × *R. palustris* (*R. × wirtgenii* Beck), conspicuous by virtue of its highly abortive fruits, and apparently unrecorded previously in S. Essex, also occurred in this ditch.

The stature of the ditch-head hybrid, with shoots up to c. 1.5 m tall, and its close proximity to *R. cristatus* clearly implicated that as one parent. In leaf and shape of the perianth segments the plant was clearly intermediate between this taxon and *R. palustris*; the dentation of the margins of the perianth-segments (valves) ruled out *R. conglomeratus* and the teeth were coarser than would be expected had *R. maritimus* been involved. Furthermore, the plant did not show any sign of the distinctive golden coloration that *R. maritimus* assumes when fruiting. Somewhat surprisingly,

given the ease with which *Rumex* species hybridise and the researches of many in the detection of such hybrids (e.g. Rechinger 1964; Lousley & Kent 1981), the cross between *R. cristatus* and *R. palustris* has apparently not hitherto been found. This is probably because their native ranges barely overlap (Jalas & Suominen 1979; Akeroyd 1993). Accordingly a name and illustrated description of this plant are given here.

TAXONOMIC DESCRIPTION

***Rumex × akeroydii* Rumsey, hybr. nov.**

(*Rumex cristatus* DC. × *R. palustris* Sm.) (Fig. 1)

Hybrida inter *Rumex cristatus* DC. et *R. palustris* Sm., characteribus inter parentes variantes; planta robusta, valvae fructiferae 4–7 mm longa, acute et irregulariter denticulatae, dentibus angustibus ad summum 2 mm, seminibus praecipue sterilibus.

Robust, erect perennial herb up to c. 1·5 m tall, the basal leaves narrowly ovate-lanceolate, cuneate. Inflorescence moderately dense, with erecto-patent to patent branches, leafy throughout. Valves cordate, suborbicular to triangular, 4–7 mm long, denticulate to dentate with spreading narrow teeth to c. 2 mm long. All valves with distinct tubercles, one larger, the other two subequal.

HOLOTYPUS:, Rainham Marsh, at head of drainage ditch, S. Essex, v.c. 18, TQ/520.813, putative parents close by, 27 August 1991, F. J. Rumsey (RNG); isotypus (BM).

The specific name honours Dr John Akeroyd, who confirmed the identity of this hybrid, has done much to raise interest in this genus in Britain and Ireland, and like this taxon is a robust denizen of waste places.

DISCUSSION

This new hybrid is only likely to be confused with *R. palustris* × *R. patientia* (*R. × peisonis* Rech.), a hybrid as yet unreported from the British Isles. *R. × akeroydii* would be expected to show more irregularly dentate valve margins, but might only reliably be discriminated by cytological studies, *R. cristatus* having $2n = 80$, *R. patientia* $2n = 60$ (Lousley & Kent 1981).

The recognition of *R. cristatus* as specifically distinct from *R. patientia* has been questioned (Stace 1997). Akeroyd (1993) adopted a conservative approach and maintained it, with some reservations. In its consistently dentate valve margins, darker nutlet colour and leaf venation more nearly at right angles to the midrib, *R. cristatus* can always clearly be morphologically separated from the variable *R. patientia*. These characters and the cytological differences referred to above argue for their continued recognition at specific level.

R. × akeroydii could occur anywhere in the sympatric range of the parent species (Fig. 2). *R. palustris* has a wide range across central and southern Europe, extending northwards to Denmark and southwards to central Greece. *R. cristatus* is restricted to Greece and the Aegean region, southern Albania, Cyprus and Sicily. The two only naturally overlap in the southern Balkans, where *R. palustris* is rather uncommon. The apparent lack of this obvious hybrid in the region may be the result of under-recording but probably reflects a genuine absence, the species being effectively isolated by habitat preferences. This is also largely true in Britain, where neither species is at all common but both may be locally abundant. In Britain *R. palustris* is almost restricted to wet nutrient-rich mud exposed in the late summer and autumn (Mountford 1994), whereas *R. cristatus* is a plant of dry ruderal waste places. In only a few localities will the species grow in close enough proximity for pollination and hybridisation to occur. The grazing marshes of the Thames estuary, with their cattle-disturbed wetlands, often in proximity to industrial sites, railways, roads, etc., provide suitable habitats for the formation and establishment of such *Rumex* hybrids. A range of very rare hybrids, such as *R. crispus* × *R. maritimus* (*R. × fallacinus* Hausskn.), *R. conglomeratus* × *R. maritimus* (*R. × knafii* Celak) and *R. obtusifolius* × *R. cristatus* (*R. × lousleyii* Kent) have been recorded from the Rainham, Pitsea-Bowers Gifford and Hadleigh Marshes further east (see Jermyn 1974, Stace 1975), to which can now be added *R. × akeroydii*.



FIGURE 1. *Rumex* \times *akerøydii*. A. Fruit, i.e. perianth enclosing nutlet. B. Diagrammatic section through fruit to show relative size of tubercles. C. Basal leaf. D. Inflorescence.

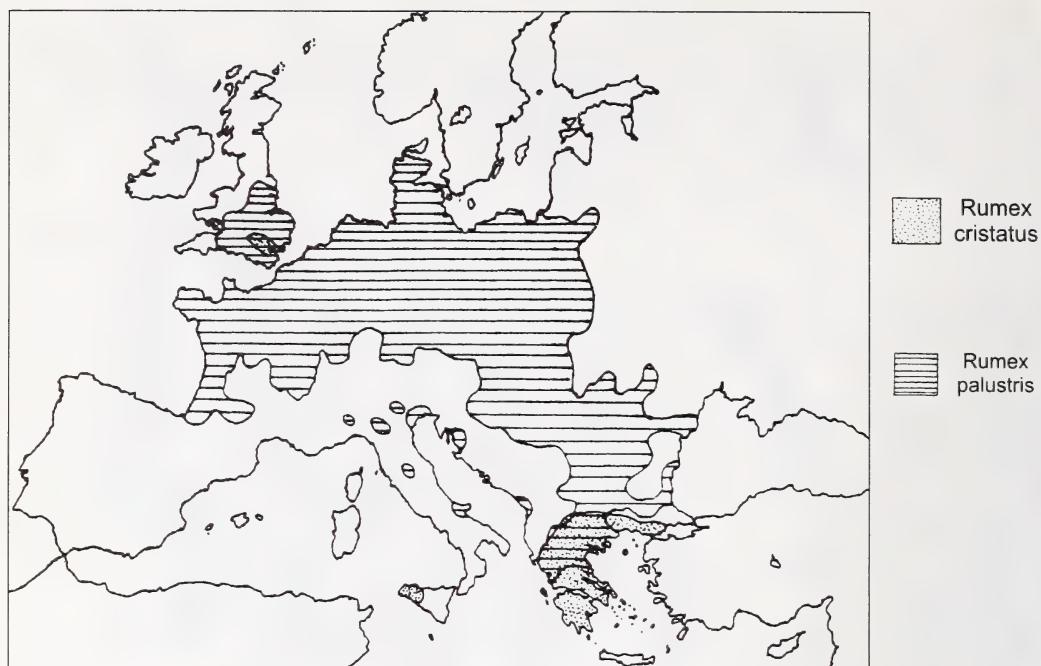


FIGURE 2. Distribution of *R. palustris* and *R. cristatus* (somewhat diagrammatic – based on Jalas & Suominen (1979)).

The current status of the plant seen in 1991 is uncertain, as is the future of the site upon which it grew. Once foreseen as part of the route of the Channel Tunnel rail-link, then considered as the possible site of a theme park, the area is, in part, now the subject of a development proposal by Havering Council.

ACKNOWLEDGMENTS

I am very grateful to John Akeroyd for determining the specimen and for his enthusiastic attempts to encourage my interest in this genus.

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A new *Epilobium* hybrid from Scotland, *E. pedunculare* A. Cunn. × *E. montanum* L.

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ABSTRACT

A new hybrid, *Epilobium* × *kitcheneri* McKean hybr. nov. (Onagraceae), between a widespread British species, *Epilobium montanum* L., and a much more local alien species *E. pedunculare* A. Cunn. is described from its one wild location in West Perthshire, v.c. 87. This new taxon more closely resembles the New Zealand parent but is generally larger in its parts and the shoots are ascending towards the apex instead of being prostrate as in *E. pedunculare*.

KEYWORDS: New Zealand, Onagraceae

INTRODUCTION

One new hybrid *Epilobium* (Onagraceae) is described, which now brings the number of hybrids involving New Zealand species in Britain to six (Kitchener & McKean 1998). The others all have *E. brunnescens* (Cockayne) Raven & Engelhorn as the New Zealand parent but this latest hybrid has the much less widespread *E. pedunculare* A. Cunn. (*E. linnaeoides* Hook. f.) as one of the parents. This latter species is found on wet ground in open habitats mainly in W. Perth (v.c. 87), W. Galway (v.c. H16) and W. Mayo (v.c. H27); in England and Scotland it is a very local weed in gardens (Stace 1997). The other parent, *E. montanum*, is widespread throughout Britain and Ireland. The few well formed seeds of the hybrid (Fig. 1F) are similar in size and sculpturing to those of *E. montanum*, with the papillae evenly distributed. The seeds of *E. pedunculare* are about 0.8 mm long, uniformly papillose on the convex side, and the ends are pointed, with the apex obtuse and the anterior end pale in colour and more acute, similar in shape to *E. ciliatum* Raf. seeds (cf. Stace 1997, Fig. 445 no. 4). The flat side is smooth except for a pale-coloured ridge between the two ends.

This hybrid is fairly distinct from the hybrids with *E. brunnescens* because the leaves are much larger and the leaf margins are sharply toothed as in *E. pedunculare*.

E. × kitcheneri McKean, hybr. nov. (*E. pedunculare* A. Cunn. × *E. montanum* L.)

Hybrida inter *E. pedunculare* A. Cunn. et *E. montanum* L., characteribus inter parentes variantibus; planta semi-prostrata, effusa; stigmata lobis clavatis vel breviter lobatis ferentia; caulis pilis crispatis brevibus uniformiter obtectis, folia glabra, margine ciliato, ovario pilis ad pedicellum subtentum extensis; florum colore pallide roseo, et seminibus praecipue sterilibus sed interdum fertilibus tum plus quam 1 mm longis.

A semi-prostrate straggling herb c. 20 cm long and 8 cm tall, rooting at the lower nodes and occasionally branching. Stem terete, generally clothed in dense short crisped hairs. Lower leaves opposite, upper ones alternate, ovate with prominent teeth, 4–11 on each side, slightly bronze coloured on the underside, largest 2.5 × 1.8 cm, glabrous except margins ciliate, base more or less rounded, attenuate to petiole; petiole 3–5 mm long. Sepals linear-lanceolate, c. 0.35 mm; corolla light pink, c. 1.1 cm across with veined petals 7 mm long; 4 short stamens just reaching the stigma base and capable of shedding pollen there, 4 long stamens slightly overtopping stigma. Ovary c. 1.3 cm long with scattered short crisped hairs becoming denser on the pedicel. Style 0.4 mm, bearing clavate or shortly 4-lobed stigma. Capsule c. 1.7 cm, with scattered short crisped hairs, fruiting pedicel c. 2 cm long. Seeds mainly sterile, but with a few well developed ones c. 1.0–1.3 mm long.

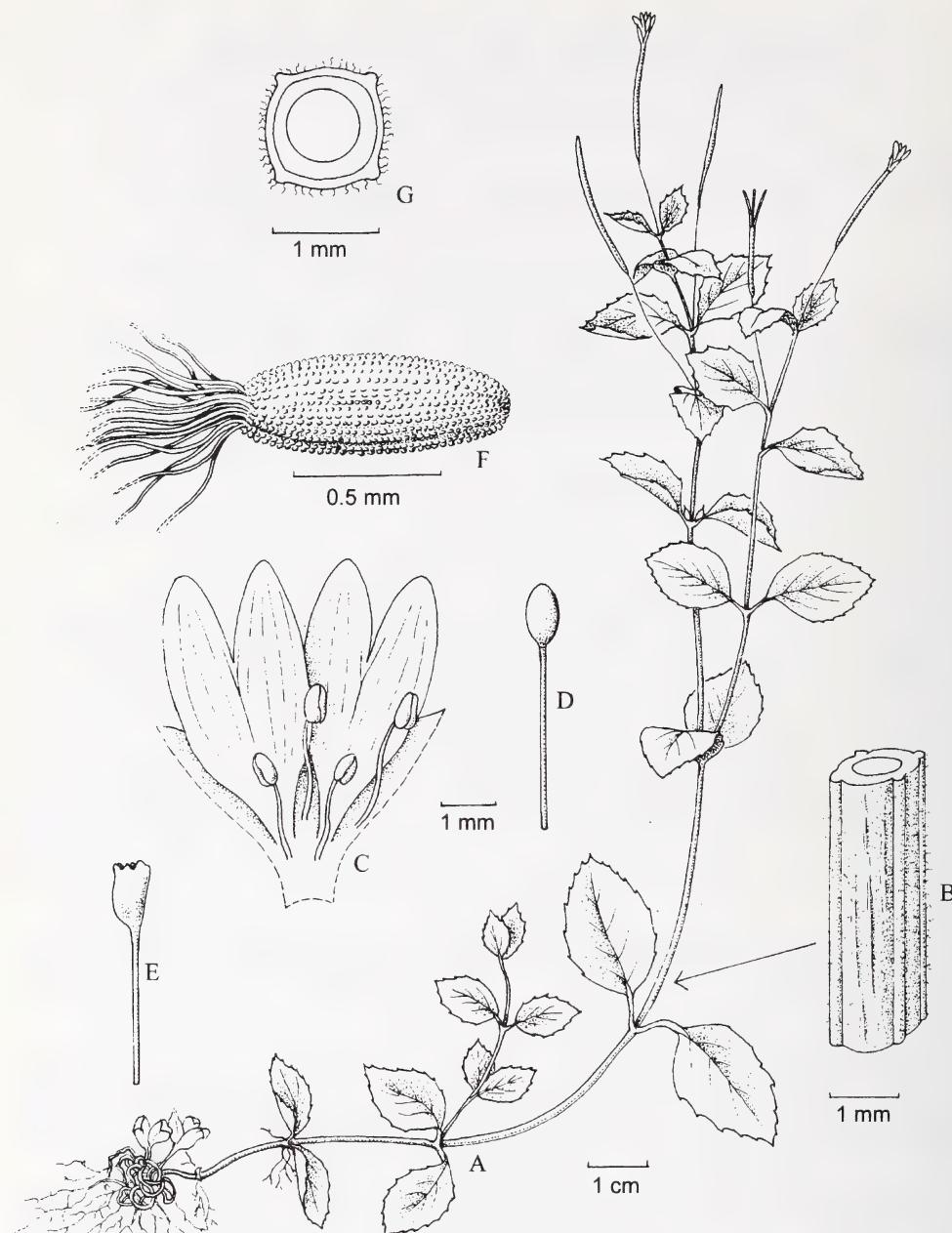


FIGURE 1. *Epilobium* × *kitcheneri*. A. plant; B. mid-stem; C. flower (half cut away); D. clavate style; E. 4-lobed style; F. seed; G. transverse section of capsule.

HOLOTYPE: Scotland, West Perth, v.c. 87, near Aberfoyle, off Duke's Pass Road, dampish hillside track in oak wood, leading to abandoned quarry, grid reference NN/516.016, 18 August 1996. G. D. Kitchener, s.n., bar-code no. 00076122 (E).

Paratypes (2) were cultivated from basal shoots of the wild plant and grown on to fruiting condition: 9 August 1997. G. D. Kitchener s.n., bar-code nos. 00076120 & 00076121 (E).

The plant was growing in patches of *Epilobium pedunculare* (abundantly naturalised in the vicinity of Duke's Pass) and both *Epilobium montanum* and *E. obscurum* Schreber grew nearby.

The hybrid is named in honour of its finder, Mr Geoffrey Kitchener, an amateur botanist, who has been involved in the study of New Zealand willowherbs hybridising with British species.

ACKNOWLEDGMENTS

I would like to thank a local artist, Ms Louise Olley for her excellent illustration of the plant. I am also grateful to the finder, Geoffrey Kitchener who cultivated the plant and sent me much information about it. R. R. Mill gave advice and provided assistance with the Latin description and the Royal Botanic Garden (Sibbald) Trust provided a grant to pay for the art work.

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Notes

ELYTRIGIA REPENS (L.) DESV. EX NEVSKI SUBSP. *ARENOSA* (SPENNER) Á. LÖVE (POACEAE) IN SOUTH-EAST YORKSHIRE (V.C. 61)

The account of *Elytrigia repens* (L.) Desv. ex Nevski subsp. *arenosa* (Spennner) Á. Löve in north-western Europe (Trist 1995) prompted searches for this taxon on the north bank of the Humber estuary, including the Spurn peninsula, during the period 1995–1998. The following new records represent a significant extension to the known distribution on mainland Britain:-

Haverfield Quarry, TA/323.200; Welwick Bank, TA/335.193; Winsets Bank, TA/380.177; Easington, near Firtholme Clough, TA/398.167; Spurn Bird Observatory, TA/420.148 and Spurn Warren, TA/408.117.

Trist (1995) commented on the variable incidence of awns and both awned and awnless forms of this grass were recorded.

At each location, *E. repens* subsp. *arenosa* occurs on consolidated sand of low salinity, cohabiting with at least four of the following: *Erodium cicutarium* (L.) L'Hér., *Galium verum* L., *Potentilla reptans* L., *Ononis repens* L., *Allium vineale* L., *Carex arenaria* L., *Festuca rubra* L., *Agrostis stolonifera* L., *E. repens* subsp. *repens* var. *aristata* (Döll) P. D. Sell, *E. atherica* (Link) Kerguélen ex Carreras Martinez, *Ammophila arenaria* (L.) Link and, on Spurn only, *Potentilla anserina* L., *Plantago coronopus* L., and *Hippophaë rhamnoides* L. These species indicate established and forming sand dune communities in the National Vegetation Classification SD7 through to SD10.

DISCUSSION

Knowledge of the distribution as presented by Trist (1995) suggests *E. repens* subsp. *arenosa* is rare in Britain and in north-western Europe. However, the ease with which these new records were taken suggests that *E. repens* subsp. *arenosa* may be yet under-recorded.

Taxonomic rank as high as subspecies is considered doubtful by some, e.g. Stace (1991). However, as Trist (1995) shows, the taxon has had a "chequered history" ranging in rank from variety through subspecies to species.

The Welwick Bank, Winsets Bank and Easington locations, each of an area less than 400 m², represent approximately 50% of the total SD7 to SD10 resource in v.c. 61. Each location is at risk of damage as a result of proposed reconstruction of flood defence structures.

Local rarity of habitat type alone may not be enough to protect these locations, even though they appear to be characterized, in part, by a low-rank taxon which can still be regarded as rare in Britain and north-western Europe.

ACKNOWLEDGMENT

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THE POTENTIAL FOR SEED DISPERSAL BY SEA WATER IN *COINCYA WRIGHTII*
(O. E. SCHULZ) STACE AND *C. MONENSIS* (L.) W. GREUTER & BURDET
SUBSP. *MONENSIS*

The two endemic *Coincyta* taxa in Britain have restricted distributions (Rich 1991). *C. wrightii* (O. E. Schulz) Stace is confined to sea cliffs on the island of Lundy in the Bristol Channel. *C. monensis* (L.) W. Greuter & Burdet subsp. *monensis* occurs on maritime sands around the east side of the Irish Sea from the Clyde to the Wirral and on the Isle of Man and has disjunct localities on Mull (extinct) and on the Gower and North Devon (the latter extinct). As both taxa have essentially maritime distributions, it might be expected that their seeds could be dispersed by the sea like other specialised maritime crucifers such as *Cakile maritima* Scop., *Crambe maritima* L. and *Raphanus maritimus* Sm. (e.g. Praeger 1913).

An experiment was set up to investigate the potential for seed dispersal by sea water in the laboratory. In *Coincyta* the fruits have two distinct parts which might have different dispersal capacities; the lower part is composed of twin loculi covered by dehiscent valves each with numerous seeds, and the upper part is an indehiscent beak with a few seeds. When the fruits are ripe, the valves dehisce to release the seeds in the loculi whilst the beaks remain intact until the infructescences break up. The experiments investigated the length of time for which individual seeds and beaks floated and the capacity for germination after periods of immersion in sea water and rain water. Only small numbers of seeds were available as both plants are rare.

FLOATATION EXPERIMENT

100 seeds and 50 beaks of each taxon were placed in separate beakers of sea and rain water, and the number remaining floating recorded with time. The beakers were shaken at irregular intervals to simulate wave action. A small amount of domestic detergent (washing-up liquid) was added to some additional beakers to test if surface tension helped the seeds float.

All beaks of both taxa floated for at least 12 hours, and some for up to four days, but most seeds sank immediately (Table 1). In both cases the proportion of beaks or seeds floating was higher in sea water than rain water as might be expected. Detergent caused all seeds and beaks to sink more rapidly (data not presented).

GERMINATION EXPERIMENT

Sub-samples of ten seeds were taken at intervals from beakers with sea water and fresh water, rinsed and placed on moist tissue paper in beakers to germinate in the light at room temperature. Controls were sown directly onto moist tissue without being immersed in water. Total germination (i.e. emergence of the radicle) was counted after 28 days. A few seeds in rain water went mouldy before germinating.

The number of seeds germinating after immersion in rain and sea water for different periods of time is shown in Table 2. The first seeds germinated after six days when completely immersed in rain water. Seeds which had been immersed in sea water were generally much slower to germinate than seeds immersed in rain water.

Germination was significantly lower in *C. monensis* than *C. wrightii* (ANOVA, all treatments lumped, d.f. = 1, p < 0.001). No seeds of either taxon germinated when immersed continuously in sea water for 28 days; dissection of the seeds in sea water showed that they had partially hydrated compared to dry seeds, whilst seeds in rain water appeared to have completely hydrated. There are no significant differences in germination after different periods of immersion in either sea or rain water for either taxon.

CONCLUSIONS

The floatation experiment shows that beaks float for longer periods than seeds in both taxa, and thus dispersal in sea water is more likely to occur by beaks than seeds. However, the length of time for which beaks float is very short, in general up to three tidal cycles (though one beak of *C. monensis* did float for four days in sea water), which may explain why both taxa have restricted distributions.

TABLE 1. NUMBER OF *COINCYA* BEAKS OR SEEDS FLOATING WITH TIME IN BEAKERS OF RAIN AND SEA WATER.

Hours	<i>Coincyta monensis</i>				<i>Coincyta wrightii</i>			
	Rain water		Sea water		Rain water		Sea water	
	Beaks	Seeds	Beaks	Seeds	Beaks	Seeds	Beaks	Seeds
n	50	100	50	100	50	100	50	100
0	50	17	50	24	50	17	50	34
1	50	3	50	8	50	14	50	26
2	50	1	50	5	50	1	50	19
3	50	1	50	2	50	1	50	3
12	50	1	50	0	50	1	50	1
24	0	0	20	0	48	0	45	0
36	0	0	11	0	7	0	10	0
48	0	0	5	0	0	0	0	0
72	0	0	3	0	0	0	0	0
96	0	0	1	0	0	0	0	0
120	0	0	0	0	0	0	0	0

TABLE 2. NUMBER OF *COINCYA* SEEDS GERMINATING AFTER IMMERSION IN SEA OR RAIN WATER FOR PERIODS OF TIME (N = 10).

Time immersed	<i>Coincyta monensis</i>		<i>Coincyta wrightii</i>	
	Rain water	Sea water	Rain water	Sea water
0 days (control)	2		10	
Continuous sea water	0		0	
1 day	4	1	8	9
2 days	3	2	9	7
3 days	3	1	10	9
7 days	2	2	7	5

Seeds will not germinate in sea water, but seeds of both taxa retain viability even after seven days immersed in sea water, over twice the maximum floatation time. Presumably, as in *Cakile* (Hocking 1982), the high sodium chloride levels inhibit germination until seeds are washed ashore and leaching by rain lowers the salt content.

ACKNOWLEDGMENT

I would like to thank Ron Groom for supplying material of *C. wrightii*.

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SOUTHWARD RECOLONISATION BY *MERTENSIA MARITIMA* (L.) GRAY ON THE COAST OF NORTH-EASTERN SCOTLAND

The distribution of *Mertensia maritima*, a beach plant growing in the strandline zone reached by highest tides, has fluctuated markedly since 1800 in northern Britain (Stewart 1994), with patterns quite different in the half-centuries 1800–1849, 1850–1899, 1900–1949 and 1950–1992. On the east coast between Fraserburgh and Berwick, the range of *Mertensia* contracted sharply after 1900, there being 28 occurrences in 10-km squares for the 1800–1899 period compared to just three occurrences for the 1950–1992 period (Stewart 1994). This author suggests that human recreation and shingle removal are the likely causes of this decline.

Since about 1980, *Mertensia maritima* has been recolonising the east Aberdeenshire coast (v.c. 93) (Table 1, Fig. 1). Probably the species was totally extinct after 1950 between Fraserburgh and Aberdeen, since no records were made during the B.S.B.I. Maps Scheme (Perring & Walters 1962), but some stretches of this coast are remote and might not have been thoroughly examined. However, other shores would have been visited often, e.g. Craig Ewan by Peterhead Golf Course, or are in conservation areas (Sands of Forvie National Nature Reserve and Loch of Strathbeg R.S.P.B. Reserve) and got regularly recorded; for some of these shores there is no doubt that *Mertensia* was absent, then one to several plants colonised, and now numerous plants occur (Table 1).

TABLE 1. POPULATION SIZE AND DATES OF RECORDING OF ELEVEN COLONIES OF *MERTENSIA MARITIMA* ON A 50 KM SECTION OF THE ABERDEENSHIRE AND KINCARDINESHIRE COAST

Colony	1 km square	Distance (km) from Craig Ewan	Year of recording	Number of plants (plt) and seedlings* (sdlg)	Recorder
Craig Ewan	NK/12.48	0	1989	40 plt and sdlgs	M. Innes
			1991	35 plt and sdlgs	M. Innes
			1998	37 plt and sdlgs	M. Innes
Gadle Braes	NK/13.46	1	1994	23 plt and sdlgs	M. Innes
			1998	50 plt and sdlgs	M. Innes
Sandford Bay	NK/12.43	4	1985	5 plt	D. Welch
			1990	10 plt	D. Welch
			1998	3 plt	D. Welch
Furrah Head	NK/13.43	5	1988	c. 10 plt	M. Innes
			1998	c. 840 plt and sdlgs	M. Innes
Boddam	NK/13.42	6	1989	7 plt	D. Welch
			1992	16 plt	D. Welch
			1998	absent	D. Welch
Whinnyfold	NK/08.33	16	1992	few plt	C. Millar
			1998	absent	M. Innes
Perthudden	NK/03.28	24	1991	3 plt + 25 sdlgs	T. Dargie
			1998	2 plt	D. Welch
Poor Man	NK/03.27	24	1989	1 plt	B. Davis
			1992	14 plt + 83 sdlgs	L. Farquhar
			1998	19 plt + 4 sdlgs	D. Welch
Broadhaven	NK/03.27	25	1992	9 plt + 32 sdlgs	L. Farquar
			1998	2 plt	D. Welch
Sanyne-Rockend	NK/02.26	26	1992	73 sdlgs	L. Farquar
			1998	absent	N. Harding
Nigg Bay	NO/96.04	48	1996	1 plt	B. Ballinger
			1998	1 plt	D. Welch

*seedlings were arbitrarily defined as having <10 leaves and being <10 cm² in area.



FIGURE 1. Map of the coastal area of north-eastern Scotland showing main towns, the site of the long-standing colony of *Mertensia maritima* at Strahngles Point, and the section of coast between Craig Ewan and Nigg Bay being presently colonised.

Evidence for a southward direction in the recolonisation is given by the first dates of observation in Table 1. At Craig Ewan the 40 plants present in 1989 indicate an initial colonisation c. 1980–1984; at Nigg Bay (v.c. 91) colonisation was almost certainly in 1996, judging from the small size of the single plant in that summer and the regular searching along this shore since 1992 made by botanists checking on a colony of *Lathyrus japonicus*. The source of the sea-borne seed initially producing these colonies could have been the large Orkney populations (Randall 1988; Stewart 1994) or the populations on the northern coast of Aberdeenshire and Banffshire (v.c. 94); the nearest of these populations extant after 1970 is at Strahngles Point, Aberdeenshire (NJ88.64), where 101 established plants and 66 seedlings were counted in 1987 (John Edelsten, pers. comm.).

Differences in trends between sites over the study period are probably related to the coarseness of their substrate material. The colony at Furrah Head, which has increased spectacularly, occupies rocks and stones that have slumped to the beach from the boulder clay slope above, and at Poor Man the plants grow among large pebbles (mean diameter of c. 20 cm) but rooted in gravel. In contrast, sandy beaches have either not been colonised, e.g. the 22 km of coast between Rockend and Nigg Bay, or their colonies have remained tiny, e.g. at Sandford Bay. Here the three plants grow at the top of the beach, very close to a dense stand of *Leymus arenarius* which perhaps restricts colonisation; these plants may also suffer from being covered by sand during storms.

The few seedlings observed at the Forvie sites in NK/0.2 in 1998 suggest that establishment is difficult and variable between years. At Poor Man the largest plant had a diameter of 1 m in 1998, and the 18 other adult plants averaged about 50 cm diameter, so considerable quantities of seed should have been produced in the previous few years. Perhaps there was more germination in 1998 than was apparent at the September monitoring visit, and the seedlings failed to survive.

Explanations for the observed distribution changes are necessarily speculative in the absence of monitoring on plant growth, longevity, fruiting and dispersion. With the species classified as scarce (Stewart 1994) and a total British population estimate of only c. 11,000 plants and seedlings in the 1980s (Randall 1988; Farrell 1989), determination of the controlling factors is very desirable. Low winter temperatures to stimulate seed germination, and relatively low summer temperatures to avoid drought for juvenile plants, have been put forward as controls on the broad range of *Mertensia* (Randall 1988). At the local scale other factors may be important. For the Nigg Bay colony, so strong in the nineteenth century that 20 separate specimens are known in British herbaria, Trail (1923) considered the cause of extinction was removal of shingle to make concrete for the south breakwater adjoining Aberdeen beach. Randall (1988), from visits to a wide range of colonies, considered that burial by sand in summer, grazing by sheep and rabbits, and trampling by humans could all severely deplete populations. But, with *Mertensia* now increasing at some sites with quite heavy public recreation pressures, it seems that even more factors may be affecting populations. We suggest that variable fruiting in response to climatic trends and shifts in the direction of sea currents also merit investigation as well as the factors advanced by previous workers.

ACKNOWLEDGMENTS

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ERICA CILIARIS L. (ERICACEAE) DISCOVERED IN THE BLACKDOWN HILLS, ON THE SOMERSET-DEVON BORDER (V.C. 3)

Erica ciliaris L. is a European near-endemic, with a world distribution extending from the north-western tip of Morocco northwards through Portugal, western Spain and France, and reaching its northern limit in southern England, with one site in western Ireland. It is a member of the Oceanic Southern-temperate element of the British and Irish flora (Preston & Hill 1997). In Britain it has a curiously disjunct distribution, being almost entirely restricted as a native to the Purbeck area of Dorset (v.c. 9) and Cornwall (v.cc. 1 & 2). Isolated records - usually of just a few plants – from Dartmoor, the New Forest and Anglesey are generally presumed, or known as in the case of Dartmoor, to have been introductions (Ivimey-Cook 1984; Rose *et al.* 1996; L. Spalton,

pers. comm.). In a few locations in the New Forest it is thought to be native and is extending its range naturally into suitable habitat in this area from its Dorset stronghold (Chapman & Rose 1994; Brewis *et al.* 1996).

On 27th August 1998, during a routine visit to a Site of Special Scientific Interest (S.S.S.I.) in the Somerset part of the Blackdown Hills, the writer noticed a strange-coloured heather looking like *E. ciliaris*. A careful search revealed that *E. ciliaris*, along with *Erica tetralix* L., was the commonest dwarf-shrub species over about 0.5 ha of wet heath and mire. The colony was clearly a long-established one, many plants being 0.4–0.6 m tall with shoots probably 15–20 years old. The total population of *E. ciliaris* was difficult to estimate, but was thought to be in the order of 1,000–10,000 plants.

The following day the author returned to the site with Paul Green and Ian Green, B.S.B.I. recorders for v.cc. 5 and 6 respectively, who confirmed that it was indeed *E. ciliaris*. Many plants of the hybrid between *E. ciliaris* and *E. tetralix* (*E. × watsonii* Benth.) were noted, with considerable variation in flower colour and foliage. Specimens of both *E. ciliaris* and *E. × watsonii* were sent to D. McClintock, who confirmed the identifications.

Is it possible that *E. ciliaris* is native at this site, representing a geographical “missing link” between its strongholds in Dorset and Cornwall? The site is at an altitude of 210 m A.O.D., which makes it higher and further north than any other “native” English site. There is no evidence of *E. ciliaris* having been introduced – indeed, to those of us who have seen it there, the plant has every appearance of being native, occurring in an area of high-quality mire vegetation, with *Molinia caerulea* (L.) Moench., *E. tetralix*, *Eriophorum angustifolium* Honck., *Succisa pratensis* Moench., *Narthecium ossifragum* (L.) Hudson and *Sphagnum* spp. as common associates. In phytosociological terms the vegetation is mainly *Narthecium ossifragum* - *Sphagnum papillosum* valley mire (M21) with *Potamogeton polygonifolius* - *Hypericum elodes* soakways (M29), grading into *Molinia caerulea* - *Cirsium dissectum* fen-meadow (M24) on slightly drier ground (Rodwell 1991). This appears to be similar to the kinds of vegetation in which *E. ciliaris* occurs in Dorset (Rose *et al.* 1996).

It is surprising that such a large and evidently long-established population of *E. ciliaris* could have been overlooked for so long. However, there may be several good reasons for this. Firstly, the general area is seldom visited by natural historians as it is not obviously *en route* to any of the region’s well-known botanical hunting grounds. Secondly, the site has no public access, and is not visible from any public right of way. Thirdly, even supposing one had the good fortune to visit the site, the difficult terrain and tussocky nature of the vegetation would cause many fieldworkers to avoid the area in which *E. ciliaris* grows. Even so, it is extraordinary that the plant has been missed until now, given that over the last 15 years – during which time it *must* have been present – the site has received several visits from experienced field botanists, including Nature Conservancy Council and English Nature staff. On more than one occasion the area was visited in late August-early September, at a time when *E. ciliaris* should have been *in flower*!

If, as suspected, its occurrence on this S.S.S.I. is a truly native one, there is a possibility that *E. ciliaris* will be recognised elsewhere in this region. There is other suitable-looking habitat in the Blackdown Hills, in both S. Devon (v.c. 3) and S. Somerset (v.c. 5), as well as on the East Devon Pebblebed Heaths, near Budleigh Salterton (v.c. 3).

The newly discovered site for *E. ciliaris* lies close to the Somerset-Devon border, in a part of Somerset that actually falls within v.c. 3 (S. Devon). The site is on privately owned farmland, and the owners have requested that details of its exact location should not be published. Anyone wishing to visit the site should contact the writer at the address below.

ACKNOWLEDGMENTS

I thank the owners for permission to visit the site and for their help in producing this note. Thanks also to Ian Green and Paul Green for their assistance with the field survey, to David McClintock for so promptly determining the specimens sent to him, to Laurie Spalton (B.S.B.I. Recorder for v.c. 3) for comments on the final draft and to Simon Leach for extensive and very helpful comments on an early draft.

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GENTIANELLA ULIGINOSA (WILLD.) BÖRNER (GENTIANACEAE) REDISCOVERED IN NORTH DEVON

Dune Gentian *Gentianella uliginosa* (Willd.) Börner is a European endemic and regarded as a “priority species” within the UK Biodiversity Action Programme. Rich (1996) reported previously unknown herbarium specimens collected at Braunton Burrows in North Devon (v.c. 4) prior to 1849 and in 1927 (all in BM), and suggested that it should be searched for again. Elsewhere in Britain it is known at five sites in south Wales (Kay 1972; Ellis 1983) and three on the island of Colonsay off western Scotland (Gulliver 1998; Rose 1998).

On 28 August 1998 *G. uliginosa* was rediscovered at Braunton Burrows (SS/4.3) during a survey of all the slacks of this extensive dune-system. Over 130 plants of *G. uliginosa* were found in an area of several square metres in part of one dune-slack. A series of voucher specimens was collected (NMW) and numerous photographs were taken. The plants identified as *G. uliginosa* were 2–4 cm tall, some reaching 6 cm, with one or two (rarely three) internodes; they all showed the long terminal pedicel (> one-half of total height to pedicel apex), and calyx lobes often of uneven size and spreading away from corolla, that are characteristic of this species.

About 60 plants of *Gentianella amarella* (L.) Börner were growing intermixed with the *G. uliginosa*, and this species is widespread in numerous dune-slacks and grassland elsewhere at Braunton Burrows. Compared to *G. uliginosa*, *G. amarella* had much shorter terminal pedicels and mostly appressed calyx lobes that were all of similar size; they also included much larger plants (up to 21 cm tall) with more numerous internodes (4–10). However, at least seven plants of *Gentianella* associated with the population of *G. uliginosa* appeared intermediate between that species and the closely adjacent *G. amarella* in respect of pedicel length, number of internodes and calyx characters. The latter were judged to be hybrids between *G. amarella* and *G. uliginosa*, as were small numbers of plants seen during 24–30 August 1998 in other dune-slacks at Braunton Burrows accompanying *G. amarella* but not *G. uliginosa*. Hybrids with *G. amarella* are known from most colonies of *G. uliginosa* in south Wales, where they are reported to be fertile and to show “all grades of intermediacy” (Stace 1991), but they have not hitherto been reported from England.

G. anglica (Pugsley) E. F. Warb. and its hybrids with *G. amarella* also occur in the same dune system (Rich *et al.* 1997), although in different slacks to *G. uliginosa*. Since Braunton Burrows is the only locality with both *G. anglica* and *G. uliginosa*, both of which grow alongside *G. amarella*, and the flowering seasons of all three species partly overlap, the possibility exists of other hybrids. Further investigations of the intermediate plants at Braunton Burrows are therefore planned.

The *G. uliginosa* plants at Braunton Burrows were growing in almost closed cover of low vegetation (mainly c. 3 cm, tallest stems to 10 cm), on the nearly flat, humic sand of the floor of the dune-slack. The turf had numerous grasses and herbs, the commonest being *Agrostis stolonifera* L., *Leontodon saxatilis* Lam., *Lotus corniculatus* L., *Holcus lanatus* L. and *Hydrocotyle vulgaris* L.; only sparse *Salix repens* L. was present. Grazing by rabbits appears to be important at present in

maintaining the short sward at this location. However, rabbit numbers at Braunton Burrows have been much reduced over recent decades by myxomatosis and the consequent reduction in grazing has contributed to loss of much of the herb-rich turf for which this S.S.S.I. is famous (Breeds & Rogers 1998). Monitoring of *Gentianella* populations at Braunton Burrows is therefore needed to ensure timely management intervention where grazing pressure from rabbits declines.

ACKNOWLEDGMENTS

Field research at Braunton Burrows was carried out under contracts from English Nature and with access permission from the Ministry of Defence. Thanks are also due to John Breeds, Geraldine Holyoak and Martin Willing for assistance in the field, to Richard Gulliver for information on *G. uliginosa*, and to Tim Rich for checking voucher specimens.

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RUBUS CAMPANIENSIS WINKEL EX BEEK (ROSACEAE) IN BRITAIN

In 1977 I came across a large population of an unfamiliar glandular bramble with cupped pink flowers and distinctive leaf shape and prickle development on an overgrown old common near Emsworth, S. Hants., v.c. 11. A. Newton, to whom a specimen was shortly afterwards submitted, did not recognise it as any named species known to him, suggesting that it was perhaps a hybrid of *R. sprengelii* Weihe. Subsequent discovery of what was clearly the same bramble in two further localities in that district, however, rendered that suggestion less likely.

Around 1982 a search of CGE brought to light a series of specimens matching this Hampshire plant from Hosey Common, near Westerham, W. Kent. v.c. 16, labelled as *R. adornatiformis* Sudre, a species recorded as frequent in that locality by Watson (1958). That name, however, was known to have been applied by Watson to British material doubtfully correctly; moreover, specimens from other localities in south-east England in BM, NMW and SLBI so determined by him are not only all different from his Hosey Common plant but mostly from one another as well. Edees & Newton (1988) were clearly well justified in relegating the taxon to an appendix listing names applied to British Isles *Rubi* dubiously at best.

A further match was then made with two Dutch specimens in BM labelled as *R. drymophilus* Mueller & Lef., and a further one queried as *R. granulatus* Lef. & Mueller, all collected in 1951 and sent by Kern & Reichgelt to F. Rilstone in an exchange. Again, however, neither of those names were judged to be applied correctly. The discovery that the plant was evidently present in the Low Countries nevertheless suggested that it would be worth sending specimens to the Belgian specialist in the group, H. Vannerom, and this was accordingly done in 1992. Vannerom at once recognised it as a bramble well known to batologists there. It had first passed for some years under

one or other of the two names used by Kern & Reichgelt and later put into wider currency by Beyerinck (1956), but, those having been found to be erroneous, the epithet *campaniensis* – after the Kempens district which straddles the Dutch-Belgian border in the vicinity of Antwerp, where the bramble had turned out to be rather common – had been adopted instead. In the confident expectation that it would shortly be described as a new species by J. van Winkel, that name had already made at least one informal appearance in print (Vannerom 1986). Having examined a large number of sheets of the plant in 1986 in the Rijksherbarium at Leiden (**L**), I felt similarly safe in subsequently introducing the manuscript name into the British literature, attributing it to van Winkel (Allen 1996). In the event, however, van Winkel died before realising his intention, and it has fallen to van de Beek (1998) to publish the description. The holotype has been deposited in **L**, and an isotype donated to **BM**.

Although van de Beek refers *R. campaniensis* to ser. *Radula* (Focke) Focke, the markedly variable expression of the armature, including its near-total suppression, seem to make it more appropriately placed in ser. *Anisacanthi* H. E. Weber (as in Allen 1996). In addition to the Kempens district the distribution is described as extending to Gelderland and Zeeland in the Netherlands, though much more thinly, and to Kent (locality unspecified) in England. However, as the following list of British exsiccatae indicates, its range in south-east England is actually much wider than that:

- v.c. 11, S. Hants.: abundant in chestnut plantations, Emsworth Common, SU/74.08, 23 July 1977 (**BM**), 19 June 1983 (herb. **D.E.A.**, herb. **H. Vannerom**), 19 July 1992 (**BM**, **BON**), *D. E. Allen*. One patch, Havant Thicket, SU/715.113, 9 July 1977, *D. E. Allen* (**BM**).
(The Emsworth Common population extends a short way into v.c. 13, W. Sussex).
- v.c. 15, E. Kent: east part of Denstead Wood, near Canterbury, TR/091.570, 14 July 1964, *B. A. Miles*, indet. (**CGE**).
- v.c. 16, W. Kent: Hosey Common, TQ/45.52, 13 Aug. 1905, anon. (but in handwriting of C. E. Britton), det. W. M. Rogers as *R. pallidus* var. *leptopetalus* forma, det. A. Newton 1977 as possibly *R. praetextus* (**BM**); 12 July 1934 (**NMW**), 21 July 1938 (**CGE**, **SLBI**), 6 July 1949 (**CGE**, **NMW**), 28 Aug. 1951 (**SLBI**), *W. C. R. Watson*, all as *R. adornatiformis*; 2 July and 10 Aug. 1954, 13 July 1955, 16 July 1957, *W. H. Mills*, all as *R. adornatiformis* (**CGE**); 2 July 1961, *B. A. Miles* as *R. adornatiformis* (**CGE**).
- v.c. 17, Surrey: Tilburstowhill Common, TQ/355.505, 16 July 1962, *B. A. Miles* (**CGE**).

Hosey Common and Tilburstowhill Common are both on the Lower Greensand within 10 km of each other. It should be noted that specimens collected on the former by J. E. Woodhead in 1948 and 1951 and labelled *R. adornatiformis* (**CGE**), and on the latter by C. Avery in 1951 and labelled *R. rotundifolius* (**SLBI**), are not *R. campaniensis* but represent other, unnamed morphotypes.

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SEPARATION OF *CAREX VULPINA* L. AND *C. OTRUBAE* PODP. (CYPERACEAE)
USING TRANSVERSE LEAF SECTIONS

A rare plant in Britain, *Carex vulpina* is listed as vulnerable (Wigginton 1999) and is thought to have significantly declined in the last 20 years (Stewart *et al.* 1994). In recognition of its threatened status an Action Plan has been produced (Anon 1995) as a framework to prevent further decline and plan for recovery. *C. vulpina* is superficially very similar to *Carex otrubae* and both are in the same subgenus *Vignea* (Stace 1997). The taxonomy of these two species in Britain was not elucidated until relatively recently (Nelmes 1939), but their separation remains problematical. Several morphological characters have been used to distinguish between the two species (Rich & Jermy 1998; Jermy, Chater & David 1982), but these can be variable, leaving the botanist with a degree of doubt over the plant in question. Hitherto, one of the most reliable characters has been the shape of the adaxial epidermal cells of the utricles, but even here there is some overlap between *C. vulpina* and *C. otrubae* and often material is difficult to place.

Fundamental to the delivery of the conservation objectives is the ability to reliably distinguish this species from *C. otrubae*. Using material determined as *C. vulpina*, a comparison was made with *C. otrubae*, investigating a number of potentially useful morphological characters. It was noted that internal leaf anatomy, observed in transverse sections about half way up the leaf, differed markedly between the two species. Leaf sections were cut by hand with a double-edged razor blade using the tip of the forefinger as a cutting guide. Sections were mounted in water and observed under a compound microscope. An examination of many specimens, collected from Oxfordshire and Kent, showed that these differences remained constant.

Leaf anatomy, as seen in transverse sections of the lamina, has been used extensively in taxonomic investigation of the Cyperaceae, including *Carex*, and many of the characters can be used for diagnostic purposes at the species level (Metcalfe 1971). Metcalfe's book should be consulted for an explanation of the terms used in this note. The most useful anatomical feature in separating the two plants are the bulliform cells that overlie the midrib. In *C. vulpina* (Fig. 1) they are only slightly inflated, up to 70 µm long (usually less), and are 3-tiered (sometimes 4-) and not strongly differentiated from the neighbouring chlorenchymatous cells. In *C. otrubae* (Fig. 2) the bulliform cells are strongly inflated, up to 85 µm long, extending from the adaxial epidermis to the median vascular bundle, and arranged in a single tier forming a quite distinct group. In addition, the adaxial (upper surface) epidermal cells in *C. vulpina* are relatively small, about 20 µm wide, whilst those in *C. otrubae* are larger, about 40 µm wide. These and further differences are summarised below.

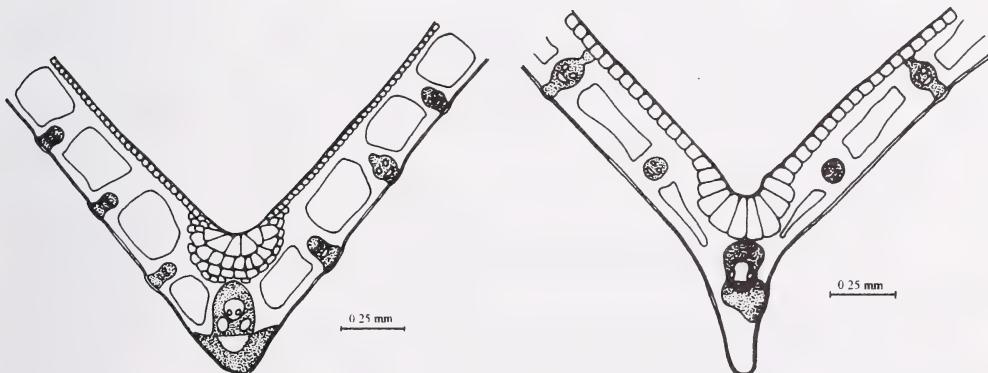


FIGURE 1 *Carex vulpina*, Otmoor, Oxfordshire 1998.
T.S. of keel region of leaf (sclerenchymatous tissue stippled).

FIGURE 2 *Carex otrubae*, Otmoor, Oxfordshire 1998.
T.S. of keel region of leaf (sclerenchymatous tissue stippled).

<i>Carex vulpina</i>	<i>Carex otrubae</i>
bulliform cells numerous, not strongly inflated and at least 3-tiered	bulliform cells few, strongly inflated and single tiered extending from adaxial epidermis to median vascular bundle
adaxial epidermal cells small, 20 µm wide	adaxial epidermal cells about twice as large, 40 µm wide
air cavities within mesophyll ± quadrate	air cavities ± elongate
sclerenchyma associated with median vascular bundle sits evenly in keel	sclerenchyma associated with median vascular bundle offset
sclerenchyma girders usually positioned abaxially	sclerenchyma girders usually span width of lamina
margin often incurved and filled with sclerenchymatous tissue in extreme lamina margin	margin flat and sclerenchyma not in extreme leaf margin
keel blunt	keel sharp

Leaf sections are easy to prepare and provide an unequivocal way of distinguishing between *C. vulpina* and *C. otrubae*. Furthermore, vegetative plants can be named obviating the need for inflorescences. Other large sedges sometimes grow with *C. vulpina*, including *C. riparia* Curtis and *C. acutiformis* Ehrh. These two species are morphologically distinct, particularly in ligule shape, but if there is any doubt they can be separated on leaf anatomy, both plants having a papillose abaxial epidermis seen most easily in transverse section.

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Book Reviews

Dorset's disappearing heathland flora. A. J. Byfield & D. A. Pearman. Pp. 37 (text) + 47 (annexes). Plantlife, London & Royal Society for the Protection of Birds, Sandy. 1996. £10.00, ISBN 9-780903-138987.

This document does not, thank goodness, describe again the demise of Dorset's heathlands. That particular story is already well-known, with large tracts of heathland lost – and those remaining much fragmented – due to agricultural “improvement”, forestry, mineral extraction and urban expansion. Rather, it reports on the status of rare vascular plants on surviving areas of heathland.

The authors visited 390 heathland stands originally recorded by Professor Ronald Good as part of his remarkable floristic study of Dorset's vegetation in the 1930s. They found 137 (35.1%) had been “destroyed”, while 253 (64.9%) had “survived” insofar as they still supported some kind of heathland or other semi-natural vegetation. In Good's day each of these “surviving” stands supported at least one rare species (defined by the authors as including national *Red Data Book*, nationally scarce and Dorset R.D.B. species, plus a few other “species of note” – 41 species in all). The purpose of the new survey, carried out between 1990 and 1993, was to see how many of Good's populations of these species were still extant.

It was my Botany teacher at school who first pointed out to me that not finding a plant in a particular place was not the same as it not being there. Even so, the figures in this report are alarming. Of a total of 644 populations of rare species recorded by Good, the authors of the present study re-located only 163 (25.3%) – almost three-quarters had apparently been lost. This was more than double what one would have expected due to habitat loss alone. Take *Radiola linoides* as an example: Good recorded it in 74 stands, yet in the 38 of these stands still surviving in 1990–93 Byfield & Pearman could find *Radiola* in only two.

For a few species the situation may not be quite as bleak as suggested in the body of the report. For example, *Crassula tillaea* is given as having suffered a 100% decline in Table 5, as it had disappeared from all seven of the sites in which Good found it in the 1930s; yet in Annex 3 there are records of it from four of Good's stands in which he had not recorded it. Nevertheless, for most rare species the losses far outweigh the gains, for example: *Anagallis minima*, lost from eleven “surviving” stands and gained in just three; *Cicendia filiformis*, lost from nine, gained in two; *Lycopodiella inundata*, lost from 33, gained in none; and *Radiola linoides*, lost from 36, gained in four.

As the report highlights, very few of these rare heathland species are found in heath plant-communities (*sensu* N.V.C.). Most occur in mire, or in ephemeral or early-successional vegetation within the heathland mosaic – along footpaths and cart-tracks, around the margins of seasonal pools and in puddles, in summer-parched sandy grasslands, on village greens and tightly grazed “lawns”. The authors consider that lack of management, or insufficient management – and especially the decline of grazing – has been the main reason for the observed declines, allowing patches of open species-rich vegetation to become increasingly overrun by *Molinia*, *Juncus acutiflorus* and ericoid shrubs.

This report should be read by all those involved in the conservation of lowland heaths, not just in Dorset but elsewhere in the U.K. Its publication is timely, given the emphasis these days on biodiversity action plans and species recovery programmes. Management for rare species is a tricky business. Different species and groups of species – birds, reptiles, invertebrates and lower plants – have differing ecological needs. As this document makes crystal clear, on the Dorset heaths some major adjustments are required if the rare vascular plants are to survive. English Nature's Wildlife Enhancement Scheme for the Dorset heathlands, established in 1994, has already succeeded in getting grazing back onto many areas (about 2000 ha and 25 sites by September 1998) – just in the nick of time, let us hope, and an initiative very much in line with this report's view of what is needed. The authors do not beat about the bush: “in the long term we believe that only [through] the reinstatement of extensive pony and cattle grazing regimes over large tracts [of heathland] can the future of these plant species of nature conservation value be assured”.

Natives and Aliens – The wild flowers and trees of the Langdon Hills. Rodney L. Cole. Pp. 204. Basildon Natural History Society. 1996. £10.00, ISBN 0-9527849-0-4.

Since its inception in 1968 the Basildon Natural History Society has achieved much in promoting a greater awareness of the wildlife that surrounds the new town of Basildon, and the publication of this work marked its thirtieth anniversary. An evocative introduction includes the author's childhood memories of a time when it was safe for children to roam the local fields and woods unconsciously absorbing the natural world and, no doubt, coming home in a disreputable state.

The first part of the publication covers not only the geography and geology of the Langdon Hills, but also an interesting account of its history and of how the landscape and the people have affected the area leading to the mixture of natives and aliens that make up the flora that is present today. Part II is a list of the plants present, with a very readable account for each species which shows the author has an eye for detail, an extensive knowledge of the area and that he understands the factors that have resulted in the plants present today. Colour plates of some of the rarer flowers are included, but there are only two depicting the landscape, both of historical interest; perhaps a modern one for comparison could also have been included.

In summary, as a local Flora written for the local people, it serves its purpose admirably.

T. TARPEY

Wildflower Safari: the life of Mary Richards. W. Condry. Pp. 237. Gower Press, Llandysul, Ceredigion. 1998. £17.99, ISBN 1-85902-558-7.

There cannot be many B.S.B.I. members who have been the subject of a full-length biography, but when I finished reading this absorbing account, I felt that there would be few who would deny Mary Richards' worthiness for the honour.

Many readers will know of Richards only for her share with Peter Benoit in the "Contribution to the Flora of Merioneth" (2nd ed. 1963), but that is only a small part of her life. William Condry's warm and sympathetic account, which is based on her diaries, supplemented by her papers, letters and the memories of many friends, begins in her childhood and bowls along well, past her marriage in 1907 and extensive terms abroad before and after the First World War. There is no mention of funds, but they must have been quite liberal to allow these trips plus extensive travel within the British Isles as a keen member of the B. S. B. I. and the Wild Flower Society.

Her husband died in 1941, when Mrs Richards was 56. Up to this point, and for the immediate post-war years, her life is energetic, seemingly impervious to the elements and thus like that of many others of our members. But in 1951, at age 66, and less than halfway through the book, she leaves for Central Africa, at first for an extended holiday, but soon to live there. Her life departs from the ordinary, and the prose of the author changes too. The account of early days is well-written, but because he is relying extensively on diaries it becomes just a little a series of unconnected events. Year follows year with selected highlights. With the arrival in Africa the pace relaxes and the canvas broadens. I have done only a little botanising in Africa but the descriptions are right, the atmosphere is perfectly caught and with the accounts of the incredibly long days in the bush and then the ensuing hours of pressing and writing up, the reader is filled with amazement at her energy, stamina and achievement. She continued long, arduous collecting trips for over 22 years, until just short of her 89th birthday, collecting around 20,000 specimens for Kew. We are not told how many new species were discovered by her and her African assistants, but she had one genus - *Richardsiella* (Poaceae) - and 28 species named after her. Each year she made trips to Britain, taking up her botany here again!

William Condry says in his preface that years (20 in fact) have passed since the material was entrusted to him. We are fortunate that he completed the work just before his death and, indeed, saw the finished product. This is a nicely produced work with apposite photographs in colour and black and white.

D. A. PEARMAN

Flora of County Dublin. D. Doogue, D. Nash, J. Parnell, S. Reynolds, P. Wyse Jackson (eds.). Pp. 560. Dublin Naturalists' Field Club, Dublin. 1998. IR£25, ISBN 0-9530037-0-1. Special limited edition IR£ 150, ISBN 0-9530037-1-X.

It is said that the O'Connell monument in Dublin's main street was designed by a committee and that it is none the worse for that. The new *Flora of County Dublin* has been written by no less than 19 members of the Dublin Naturalists' Field Club, five of whom are credited with compiling and editing the work.

The county has been well served by Nathaniel Colgan's Flora of 1904 and a *Supplement* of 1961. The successful *Flora of the Inner Dublin* (P. Wyse Jackson & M. Sheehy Skeffington 1984) established a fieldwork team and a modus operandi which was used to good effect for the recent project. Fieldwork for the project continued until the early nineties though some more recent records are included.

Dramatic urbanisation together with afforestation, peat erosion, drainage, roadmaking and coastal exploitation have all taken their toll on the "wild" county though much of interest and value remains. Sixteen colour photos of good habitats are included in the Flora. Coastal habitats, gravel ridges, estate and semi-natural woodland, rivers and the mountains preserve the essential character of the flora as Colgan knew it.

Prager's 1919 obituary of Colgan is reprinted, emphasising his outstanding contribution and his palpable presence to students of Dublin's flora. A portrait of Colgan here would have been an enhancement.

The introductory chapters on topography, climate, geology, soils, history of the study of the flora, botanical districts and 18 habitat accounts are written by specialists or particularly knowledgeable members of the Field Club. Some are short factual accounts, some didactic and some discursive and provocative.

The account of the history of recording by Declan Doogue is a delight. There is a real sense of the author writing about kindred spirits. Some insecure references do not detract from this fine chapter: Wade's discovery of *Pastinaca* at Finglas Bridge predates the founding of the Glasnevin Gardens; caution should attach to any assessment of David Orr's record of *Centaurium pulchellum*, however "native" it looks now on the Bull Island. Orr perpetrated a large number of frauds, deliberately planting and subsequently finding rare plants or allowing others to find them!

The Flora is intended to stand alone. Colgan's 1904 records are repeated for the rarer plants. Tetrad dot maps are included for species with interesting or curious distributions, not wastefully for ubiquitous or very rare species. Colgan's irritating but justifiable use of an appendix for casuals and aliens not fully naturalised is followed.

The help of experts was enlisted for the critical genera, *Rubus*, *Salix*, *Rosa*, *Potamogeton*, *Taraxacum* and *Chara*.

I wondered whether *Sparganium erectum* records might not be almost all subsp. *microcarpum*. "Circaeal alpina", weed at Blackrock" was surely *C. × intermedia*.

Epilobium obscurum, "occasional in base-poor wetlands" is also a common and troublesome garden weed, not at all particular about nutrient status. *Mercurialis perennis* may look native in several places in Ireland but is clearly spreading and a classic case of a relatively recent introduction. Colgan recognised it for what it is. *Trifolium fragiferum* survives at the Glasnevin pond by the River Tolka as McArdle reported it in 1902. *Hydrocharis* survived at Curragha at least until the mid-eighties.

The Flora has been handsomely produced. What a joy to have it at last between covers. It is a credit to the Club. The "Committee" approach has delivered a fascinating selection of introductory essays and a meaty and detailed account of Dublin's wild plants. Like Colgan's Flora, which was its model and inspiration, and the aforementioned O'Connell monument, it will become another of Dublin's worthy institutions.

Dandelions of Great Britain and Ireland. B.S.B.I. Handbook No. 9. A. A. Dudman & A. J. Richards, ed. P. H. Oswald. Pp. 344. Botanical Society of the British Isles, London. 1997. £15.00, ISBN 0-901158-25-9.

This fine and scholarly Handbook is the fruit of a quarter of a century's intensive study of the genus since Richards published his first attempt to bring order to British dandelions (*The Taraxacum Flora of the British Isles* 1972). The book is dedicated to the memory of the late Chris Howarth who played a major role in this revision. 235 species are described, a more than two-fold increase on the 132 in the earlier work since 34 of the latter are no longer recognised. There are excellent dichotomous keys, both to the Sections and to individual species or clusters of similar species. Bearing in mind the extreme difficulties of constructing keys to large apomictic genera this is as much as one can expect. There is also an ambitious multi-access key; it would be interesting to know just how useful such keys are in practice. 105 of the species are treated as "lead species", with closely similar species being given the same number followed by a letter. The descriptions are full and detailed and points of comparison between related species are clearly indicated.

The descriptions are augmented by silhouettes of whole plants and involucral drawings by the late Olga Stewart. There are interesting and helpful comments on apomixis, dandelion evolution and sources of variation, and invaluable advice on identification and on how, and how not, to collect. Distribution maps are provided for 178 species although these inevitably highlight the whereabouts of the relatively small number of dandelion enthusiasts. Sectional running heads are provided for the map section; it is a pity they are omitted in the main text.

96 (about 40%) of the species are thought to have been introduced and most of these are in the very large Section Ruderalia. The information on the extra-British distribution of the native species is patchy. There is a list (p. 15) of single species representative of phytogeographical areas. It would have been nice to have this expanded. The terms Western and Southern Atlantic hardly seem appropriate! One wonders whether, as in brambles, there are distinctive regional florulae.

There is a cryptic reference (p. 7) to a "*Taraxacum* herbarium of the British Isles" built up by Richards and later augmented by Haworth but with no reference to its present whereabouts. It is in the care of A. A. Dudman.

This is a first-rate Handbook, a worthy addition to the series and one of which the authors can be justifiably proud.

G. HALLIDAY

The Atlas Flora of Somerset. P. R. Green, I. P. Green & G. A. Crouch. Pp. xxiv + 292. Published by the authors. 1997. £25.00, ISBN 0-9531324-0-4.

There have been two previous Somerset Floras, one by R. P. Murray in 1896 and the other by R. G. B. Roe in 1981. Neither was furnished with distribution maps which are such important features of the present work. An even more impressive feature, which becomes clear as the book is studied, is the remarkably complete coverage of a large county over the last ten years. The area includes 977 tetrads and the average number of species recorded per tetrad is 311, which exceeds that in almost all recent Floras. The authors are to be congratulated on the exceptional thoroughness of their fieldwork, as well as on their presentation of the data. Perhaps all authors of Floras would benefit from being twins!

The initial information concerning methods, botanists, tetrad totals, geology and topography has been pruned to a minimum. It is supplemented by a summary of the 23 best botanising sites in the county, which at once demonstrates the breadth of the authors' local knowledge. Throughout the text there are helpful hints as to where to find good colonies of the less common species. The text itself is set out on A4-sized paper in twin columns, with inset maps for about half of the 2300 or so taxa mentioned. This large number of taxa includes many aliens. There are 16 pages of colour plates in the central section of the book, all taken by the authors, and a comprehensive index.

Although Somerset is conventionally divided into v.c.c. 5 and 6, its inland botany can be broadly described in three parts, West, Central and North. These parts are illustrated by many distribution maps in this Flora. To the west are the hills of Exmoor, with outliers in the Quantocks and the

Brendon Hills. These have high elevations, correspondingly high rainfall and acid soils. They are well provided with heath, bogs and *Quercus petraea* woodland, with plants such as *Agrostis curtissii*, *Eriophorum vaginatum*, *Listera cordata*, *Nardus stricta*, *Oreopteris limbosperma*, *Sibthorpia europaea* and *Wahlenbergia hederacea*. The authors conclude that *Leucojum vernum*, found in the lowlands here, is an ancient introduction. The central part includes the famous levels, where woods and even hedges are scarce, but the rhynes have a wealth of aquatics, e.g. *Alisma lanceolatum*, *Ceratophyllum demersum*, *Hottonia palustris*, *Hydrocharis morsus-ranae*, *Utricularia vulgaris* and *Wolffia arrhiza*. Here drainage and peatcutting have destroyed almost all the wet fen habitats, and *Lathyrus palustris* is all but extinct. If global warming does not trigger marine transgression during the coming century, this region may be further exploited to grow osiers for fuel. The northern part of Somerset is the least homogeneous, but it includes the botanically exciting limestone areas of Brean Down, Cheddar and the Mendips, with their relict populations of *Carex montana*, *Dianthus gratianopolitanus*, *Helianthemum apenninum*, *Koeleria vallesiana*, *Potentilla neumanniana*, *Saxifraga hypnoides*, *Thlaspi caerulescens* and rare *Hieracia*. Of course some species have distributions which do not fit this oversimplified picture, examples being *Cruciata laevipes* and *Rubia peregrina*; the latter is frequent inland in this county.

This Flora could be criticised for its omissions, the main being that it does not include that part of v.c. 6 which was part of the political county of Avon for the duration of the current survey. The reason was that a Flora for that ephemeral county was in preparation. The lack of sections on ecology and cryptogams can be remedied by future workers. The maps do not plot old records, but the text clearly states which species are thought to be increasing or decreasing. Conifers are perhaps less well covered than are other aliens, and the accounts of critical groups, such as *Rubus*, *Hieracium* and *Taraxacum*, are understandably incomplete. But these are minor quibbles. The Atlas Flora of Somerset can take its place as a first-rate modern County Flora, and is thoroughly recommended to residents and visitors alike.

H. J. M. BOWEN

The Flora of Oxfordshire. J. Killick, R. Perry & S. J. Woodell. Pp. xii + 386. Pisces Publications, Newbury. 1998. £45, ISBN 1-874357-07-2.

Oxfordshire has been a fortunate county, having had a series of Floras beginning in 1794 with *Flora Oxoniensis* by J. Sibthorp, updated by a series of later works. The last, published in 1927 was by G. C. Druce. Work started on this new one for v.c. 23 in 1968, the year Humphrey Bowen published his *Flora of Berkshire* for the adjacent v.c. 22 (which includes a substantial portion of present-day political Oxfordshire). However, the fieldwork behind this new volume has been executed extremely thoroughly over 28 years by an incredible number of botanists (duly acknowledged). Careful searching of herbarium and literature sources appears to have been carried out. There are some 90 pages of introductory material which give a good review of the topology, geology, palaeobotany (!), soils, climate, vegetation history and present-day communities (sumptuously illustrated in colour). A chapter entitled 'The Vascular Plants of Oxfordshire' actually gives details of some former Oxfordshire botanists, Floras, methodology of the recording exercise undertaken, inferences from the maps, dioecious species in the Oxfordshire flora and details of the structure and presentation of the species accounts. The lack of a decent topographical map is surprising.

The main body of the Flora (212 pages) enumerates the species systematically with clear tetrad distribution maps for all but the most ubiquitous and those found in less than eight tetrads. Nomenclature follows Stace, including his usage of English vernacular names. Clear and helpful notes are given on abundance and ecology. Herbarium specimens for interesting, rare or unusual records are cited. Casuals are included and noted in smaller type, as also are species unrecorded but which might be expected as they occur just outside the border (e.g. *Dactylorhiza traunsteineri* (Sauter ex Reichb.) Soó).

This Flora unusually contains a substantial (60pp) account of the bryophytes by A. Roy Perry and the late Eustace W. Jones. This is in the same format with similar details and again with sumptuous colour illustrations (43 on 8 pages). No account of the lichens is provided. The work ends with a useful gazetteer, bibliography and index to scientific and vernacular names.

Modern county Floras are no longer produced by a single enthusiast and expert, but by a team. The three well-known and distinguished authors have not only been supported by the experts on bryophytes, soils, geology, etc., but by very many distinguished amateur and professional botanists to give an authoritative full treatment.

The book, A4 size and heavy, is an altogether quality production. It is naturally going to be compared with the recent *Flora of Cumbria* by Geoffrey Halliday (University of Lancaster, 1997), which has set an incredibly high standard of both scientific content and production. The *Flora of Oxfordshire* comes up to this standard.

All the illustrations – line drawings, colour paintings (four full-page by Andrew Brown) and colour photographs are extremely good and beautifully printed. The book is not one to carry about, but for admiring and extensive reference in the library, office, study, etc. At £45 it is expensive, and it is to be hoped that botanists and plant-minded people will buy it. The authors, collaborators and publishers are to be congratulated on producing such a fine work. It is a shame we had to wait so long for it! Other workers currently producing county Floras must be intimidated about following these productions.

S. L. JURY

Scottish Wild Plants. Philip Lusby and Jenny Wright with photography by Sidney J Clarke. Pp. 116. Royal Botanic Garden, Edinburgh. 1996. Hardback £19.95, ISBN 1-8722091-17-1. Paperback £12.95, ISBN 0-11-495802-5.

This is a good book, ideal for dipping into for solace and inspiration in the winter and giving a fund of information for botanical excursions during the summer. It is the second in what is hoped will become a series on Scottish plant life and follows a broadly similar format to the book on Scottish orchids. In the foreword, David Ingram makes it clear that the aim of the book is to have professional botanists tell the story of some of Scotland's plants in such a way as to foster concern on the part of an increasingly conservation-conscious public.

The text consists of an introductory section which gives a brief history of the Scottish vegetation since the disappearance of the glaciers, an overview of the geographic elements represented in the Scottish flora and a discussion of the special features of the plants of the five broad regions of Scotland, often with reference to the plants included in the accounts. This is followed by a short section on the human influences on our flora, a sensible explanation of "rarity" and a too-brief discussion of practical conservation measures. The "meat" of the book follows with an account of some 45 plants. There does not appear to be a theme to the selection of species – except that it would seem that grasses and sedges are deemed not interesting or, more likely, not photogenic enough (or perhaps another book is already under consideration!). Many of the plants included are rare, some are quite frequent, but all have a good story well told.

As we have come to expect, the photographs are wonderful, but the reproduction is far too small to do them justice although it will have kept production costs down. The frontispiece of *Saxifraga oppositifolia* is mouth-watering and the inside-cover of the hardback edition, with a wide-angle shot of *Oxytropis halleri* and *Scilla verna*, is stunning. The design of the cover is rather odd, with a fine picture of Coire Ba and the west end of Rannoch Moor superimposed by a picture of *Moneses uniflora*.

The species accounts have a broadly consistent format detailing the history of the discovery of each plant, its British distribution, ecology, population biology and, where appropriate, conservation. As in the book on Scottish orchids, the distribution of each species is illustrated by a map of the botanical vice-counties in Scotland. For the rarer species, this scale is not very useful and can be very misleading – look at the distribution map of *Phyllodoce caerulea* and compare it with the distribution that is clearly explained in the text. Some explanation of the record of *Moneses uniflora* from Kintyre would also have been interesting!

The amount of information condensed into a couple of pages is impressive as is its diversity, ranging from historical anecdotes to seriously complex sex-lives. This is the main strength of the book: the amalgamation, in a very readable format, of information for each species that would otherwise require many different sources. Inevitably some accounts generate as many questions as

they answer and there are a few factual errors. One wonders whether a few references within the text would really have been such a disruption. For most people who have looked at plants in Scotland there will be some personal connection with the text; I was delighted to read that the first record for *Minuartia sedoides* in Britain was from Ben Klibreck, where I saw it in abundance a few months ago.

G. P. ROTHERO

The Ferns of Britain and Ireland. C. N. Page. Second edition. Pp. 540. Cambridge University Press, 1997. Hardback £95, ISBN 0-521-58380-2. Paperback £40, ISBN 0-521-58658-5.

Anyone already interested in ferns has seen this book before; it was first published in 1982. It was then (and still is) the "bible" for all pteridologists – describing, in a loquacious but very readable style, (almost) all the pteridophytes found in the British Isles, and their habitats and associated plants. General chapters (including 19 maps of environmental parameters) and multi-access and chart keys give a useful background. However, for those who already have the first edition, I find myself asking: "Do the changes/additions warrant the outlay this book requires?"

There are 100 or so extra pages; 20 on bracken alone with illustrations and descriptions of recent new taxa; three newly discovered *Equisetum* hybrids. Descriptions of taxa within *Dryopteris affinis* agg. have been brought into line with other recent authors but the hybrid *D. × complexa*, now included, is somewhat oversimplified. There is a useful discussion on *Asplenium adiantum-nigrum* and its serpentine form that is usefully recognised at subspecies level, [*corruncense* (Christ) Rivas-Mart., probably more correctly called subsp. *silesiacum* Milde]. What have been added and indeed, enhance the book are some of Chris Page's excellent black-and-white photographs of plants in the field (e.g. *Equisetum sylvaticum* on p. 469). The silhouettes (printed with greater contrast than in the first edition) of leaves and whole plants certainly help to give the "jizz" of a species but in some cases this has been over-done (e.g. for *Selaginella selaginoides*, 19 plants over two pages). This is one case where the paler, but greater detail, "xerox" reproduction in ed. 1 is more effective.

Some things could have been improved, and indeed expected, if users' feedback had been listened to. Alien ferns are not treated, even in passing, and this is particularly sad in the case of *Azolla* (we may have two species), and *Equisetum ramosissimum*, the presence of which in Somerset may be natural. Field botanists need to be acquainted with these plants. There is still a major gap in the absence of stem T.S. diagrams of the *Equisetum* hybrids, a group on which Page is undoubtedly a world authority. The small sketch-maps of the British Isles are infuriating and in many cases, among the rarer taxa where new records have been made, the fact is not recorded – or the map is changed and the text not, or vice versa. There are errors in authors of Latin names which hinders its use as a standard reference and it is clear that Page has revised some paragraphs but not others which would have benefited from it (e.g. taxonomic concepts on p. 5). Taxonomic concepts have changed a lot in the last 15 years. There is no doubt that Chris Page's field observations are outstanding, and most of them are in this book. However, if he (and the publishers) are to achieve their aim of being really user-friendly, some serious editing to make the descriptive text *comparative* between close species or hybrids would be a great improvement.

Perhaps this edition was revised in a hurry; and maybe the publishers should take some blame too. To answer the question I posed above: the keen fern enthusiasts will want this edition, regardless, but this reviewer feels that the full potential of both the subject and the author has not yet been fully realised.

A. C. JERMY

The Natural History of Pollination. M. Proctor, P. Yeo & A. Lack. Pp. 479. Harper Collins, 1996. Hardback £35, ISBN 0-00219905-X. Paperback £16.99, ISBN 0-00219906-8.

The study of pollination biology has come a long way since the publication of Michael Proctor & Peter Yeo's *The pollination of flowers* (1973). So much so that the authors invited Andrew Lack to join them in writing an extensively revised and updated version of their earlier work. The result,

rather than going out as a second edition, has been published under a new title. The chief difference between the two works, apart from the enormous number of references to new studies, is that the new version adopts a rather more functional view of the phenomena involved and discussions are couched in terms of the costs and benefits to the various organisms involved. The subject matter covered, however, is similar between the two works, although the new version has a somewhat broader geographical scope, dealing with situations not only in the British Isles, but also on a world-wide basis – as the topic dictates; this is particularly noticeable in the improved coverage of the various vertebrate pollination syndromes.

Like its predecessor, this volume is packed with information and provides a fascinating and lucid discussion of the material in a style that is accessible to the intelligent layman as well as the professional. The topics that have benefited from updating are numerous and range from nectar composition and the chemistry of floral fragrances to late-acting self-incompatibility, the pollination biology of "primitive" angiosperms, and the ecology of pollination in plant communities; there is also a better account of the interrelationship between pollination biology and the genetical structure of populations. As a check on the extent to which new studies have been incorporated, I looked carefully at the section on water-pollination and found that all those discoveries that I knew about, including internal geitonogamy and underwater outcrossing in the Callitrichaceae, bubble-pollination in *Potamogeton* and new observations of members of the Zosteraceae, were indeed dealt with. The treatment of orchid pollination is now more integrated, being addressed in a single chapter rather than being split between two as before, where British and European species were separated from the exotics; much more is also made of floral deception and brood-site pollination. Another innovation that I liked was the presentation of certain topics and definitions in "boxes" that can be read more-or-less independently of the text.

Not surprisingly, in order to accommodate all the new material, some topics in the first edition have been omitted. Readers of this book who have an interest in the British & Irish flora will be disappointed to find that the short summaries of the pollination biology of selected plant species have gone, although some of the relevant data can still be found if searched for in the chapter on insect-pollinated flowers. Also gone is the discussion of speciation and reproductive isolation as promoted by different pollination syndromes. This is a pity because it is an important topic from an evolutionary point of view, although it is adequately covered in other books.

The photographic illustrations, including eight composite coloured plates, of both flowers and pollinators are first-class, and complement the text beautifully. In short, this is an excellent book and I can recommend it unreservedly to anyone with an interest in the natural history of pollination.

R. J. GORNALL

Plant Crib 1998. T. C. G. Rich & A. C. Jermy, with the assistance of J. L. Garey. Pp. vii + 392. Botanical Society of the British Isles, in association with the National Museums & Galleries of Wales and the British Pteridological Society, London. 1998. Paperback £15.00, ISBN 0-901-15828-3.

The concept of *Plant Crib 1998* can be traced back to Franklyn Perring's 'Blue Book' entitled *Hints on the determination of some critical species, microspecies, subspecies, varieties and hybrids in the British flora*, which was published in *Proc. B.S.B.I.* in September 1962 (Vol. 4, pp. 359–383) and also pre-published (March 1962) as a separate (price 3/6d) that was much used during recording for the *Critical Supplement to the Atlas of the British Flora* (1968). The more obvious predecessors of *Plant Crib 1998* (Wigginton & Graham's 1981 *Guide* (which was itself a revision of a 1976 work), Jermy & Camus's 1987 *The BM Fern Crib*, and Rich & Rich's 1988 *Plant Crib*) are outlined in the current work. This claims to have "been prepared to provide guidance with recording and identification of plants for the *Atlas 2000* project", but in fact it has turned out to be more than such a guidance, for it contains a lot of information which is not directly relevant to the *Atlas 2000* work. For example, it carries sections on *Taraxacum*, *Hieracium* and *Rubus*, it includes many additional species (e.g. two in *Gilia*, three in *Amelanchier*) including a number not even known from the British Isles, and it covers several varieties (e.g. in *Galeopsis* and *Fumaria*), none of which will be included in *Atlas 2000*.

Plant Crib 1998 contains a large amount of very useful information that is certainly of enormous assistance in identification, and it should, if used wisely, greatly improve the accuracy of recording for *Atlas 2000*. The authors have performed an extremely valuable service in producing such a large and informative compendium in a very short time. The limiting time factor explains the rather loose editing that is evident throughout. The authors have been forced largely to accept what they have received, so that there are many cases where the treatment could have been more usefully much shorter (e.g. *Hymenophyllum*, *Oenothera*) or much longer (e.g. *Limonium*, *Melampyrum*, *Agrostis*), where glaring gaps in coverage exist (e.g. *Trichophorum* subspecies), where important references appear to have been overlooked (e.g. *Cerastium fontanum* and *Arenaria serpyllifolia*), and where there are obvious inconsistencies (especially in nomenclature) and even errors (e.g. *Deschampsia*). Such imperfections are to be expected rather than criticized, but the user needs to be aware of them. A corrigenda sheet is now available.

There are other important caveats for the reader to heed, all of which are hinted at by the authors in various places in the text. Firstly, this is not a book for beginners, but for the fairly experienced field botanist who will already have a good botanical vocabulary and will know how to distinguish each of the groups covered from taxa outside that group. Secondly, many of the "extra" characters used (i.e. those not usually considered diagnostic for the taxa concerned, but which are useful guides supplementing the strictly diagnostic features) are **not** absolutely diagnostic and must be used with great caution if they are not to mislead. The text must be scrutinized carefully to identify these, but sometimes they have found their way into the keys and tables, where they are liable to cause misidentifications.

I personally found the accounts of *Equisetum*, *Ranunculus* subg. *Batrachium*, *Alchemilla*, *Sorbus*, *Myriophyllum*, *Epilobium*, *Hedera*, *Callitrichie* and *Carex* particularly valuable, but other readers will have their own favourite sections. No field botanist will fail to find a great deal of value in the latest *Crib*. It is not so much a permanent reference work as a commentary on the current state of knowledge on British plant taxonomy, a situation which is still changing rapidly and which will call for rather frequent new editions (rather than supplements) in future years. As the authors acknowledge, much further research, testing and updating needs to be carried out before *Plant Crib 1998* can be used as the basis for a Critical Flora of the British Isles. The latter is as distant a goal in 1998 as it was in the 1930s when first mooted.

C. A. STACE

Obituaries

JOHN HESLOP-HARRISON
(1920–1998)

One of the most innovative botanists of our time, John Heslop-Harrison will be sadly missed by his colleagues and admirers. He held three professorships (Belfast, Birmingham and Wisconsin), in addition to visiting professorships and many medals, fellowships and honorary degrees from learned societies and universities.

In addition to being Director of the Royal Botanic Gardens, Kew (1971–76) he kept up a strong research programme, often with his wife Yolande and his son Pat, with some 300 publications in learned journals. I had the privilege of knowing him and working with him during his time at Birmingham (1960–67), and admired him greatly.

In his early days he worked on orchids, especially the dactylorhizid populations in the Inner and Outer Hebrides, some of his work being published jointly with his father, J. W. Heslop-Harrison. He was also interested in the general aspects of Irish vegetation and post-glacial history. His book entitled "New Concepts and Flowering Plant Taxonomy" (1953) was an important landmark in plant evolution and classification concepts.

In the late 1950s and early 1960s he was publishing, with his wife, Yolande on flowering-plant growth and organogenesis as shown in *Cannabis sativa* and other plants. He was also experimenting on apomixis and aspects of photoperiodic effect, and that of growth hormones, on sexuality and development. This led in the mid-1960s to investigations on pollen growth, cell walls and chloroplast structure, as well as sex expression in flowering plants. Thus, he was never content to describe *what* he saw but needed as a true scientist to investigate *why* it took place and the mechanisms which controlled such phenomena. These aspects of *why* and *how* things took place were published by him and with several of his research students and his wife in the mid- to late-1960s. Thus, the *what* of taxonomy led to the *why* of physiology – what and why certain morphological and physiological phenomena took place. Many of these publications showed collaborative work with his students, particularly with Bruce Knox and Hugh Dickinson. He was always anxious to indicate his collaborators, though naturally the impetus came from Jack himself.

In the 1970s Jack's interest turned even more to the *why* and *how* of processes such as pollen-stigma interaction, incompatibility, and organelles, this work being the result of constant collaboration with Yolande. At this time he also wrote on the ever more important topic of species and ecosystem conservation, though at the same time, and into the 1980s, he was still investigating pollen growth and pollen-stigma interactions (again, with Yolande), as well as the phenomenon of heterostyly.

Jack Heslop-Harrison's contact with the B.S.B.I. will be well-known to older members, and particularly to those interested in dactylorhizids and flora studies of Britain. His work and interests in so many other aspects of plant studies also will not be forgotten.

Jack died of a heart attack on May 7th, 1998. Our deep sympathy goes out to his wife Yolande, his son Pat and other family members.

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J. HAWKES

OLGA MARGARET STEWART
(1920–1998)

Olga Margaret Stewart (*née* Mounsey), who died on 6 August 1998, was inextricably linked with the botany of Scotland. She had been a member of both the B.S.B.I. and the Wild Flower Society since 1965, and soon became close friends with Mary McCallum Webster, who had just settled in Morayshire. Olga was quick to learn from her mentor and, as her knowledge increased, so did her enthusiasm. In 1975 she was invited to become Recorder for the Stewartry of Kirkcudbright (v.c. 73), and it is for her thorough work there that most of her British botanical friends will remember her.

She was born in Edinburgh on 1 July 1920. Her father was an Edinburgh lawyer, James L. Mounsey, and her mother a Canadian from Nova Scotia. Her first school was in Edinburgh and at the age of 12 she moved to a boarding school in Kent, where she had a successful career, winning several academic prizes and representing the school at hockey, lacrosse and tennis, and ending up as joint Head Girl. She returned to Edinburgh to study architecture at the Art College, and at the end of her first year was on holiday in Nova Scotia visiting her grandfather when World War II broke out. It was decided that she should stay there, and she enrolled into Dalhousie University in Halifax, where she found herself the only female studying Engineering. Her professors soon noticed her drawing capabilities and, after a year, they offered her a job with the National Research Council of Canada in the Naval Dockyard at Halifax. When the first German acoustic mine was discovered and defused off the coast of Nova Scotia, it was Olga who was given the task of producing sectional drawings of it for military scientists to study.

In 1943, in spite of hostilities both in the North Atlantic and Western Europe, Olga decided to return to the U.K. and was given a research job with the Royal Navy in Edinburgh. Three years later, on 28 November 1946 in Edinburgh, she married Frank Stewart, a pre-war friend who had spent the last five years as a Prisoner of War in Germany; they enjoyed a very happy life together for over 51 years. Frank was yet another Edinburgh lawyer, so it was there, in between bringing up four children, that Olga started on her botanical 'career'. This had a curious beginning. In 1947 she and Frank went on their first holiday together, to Aviemore, where, as she wrote later, (1983) *Wild Flower Society Magazine* 39: 15 "While climbing a hill, rather slowly and rather pregnant I collected flowers on the way and sat down to draw them ... So began my passion to draw practically every plant, wild and naturalised that I have seen since". Her reputation as an artist soon spread and she was asked to draw black-and-white flower illustrations for books and journals. Examples are to be found in McCallum Webster's *Flora of Moray, Nairn & East Inverness* (Aberdeen University Press, 1978), and the late Princess Grace of Monaco's book, *My Book of Flowers* (Doubleday, 1980), and many other articles on British plants. Most recently (1997), she drew the involucres of British dandelions in the B.S.B.I. Handbook 9, by Andrew Dudman and John Richards; to use the authors' own words, "She has graced the present volume with delightful and accurate drawings ... and we thank her for the dedication and hard work that these have entailed". She also left, unpublished, a number of hawkweed drawings, and a collection of water-colour drawings of more than 3000 British plants, which is indeed unique, and well worth publishing in its own right. Her drawing of the bluebell has become well-known being incorporated into the Society's logo.

It is Olga's botanical fieldwork in Kirkcudbrightshire for which she will be best remembered. She and Frank had enjoyed summer holidays around New Abbey for some years and in 1962 had the opportunity to build a holiday home, 'West Maryfield', on the north-east of the village. She had got to know the local flora well, so on Dr Humphrey Milne-Redhead's demise in 1974, she was the obvious choice to carry on as B.S.B.I. Recorder for the vice-county. Characteristically, she took up her duties seriously and enthusiastically, scouring the area from the top of the Galloway Hills to the Solway, often three days a week between March and October, sometimes alone and sometimes with friends. Her *Check List of the plants in Kirkcudbrightshire* was published in 1990, by the Dumfries & Galloway Natural History and Antiquarian Society, of which she was an active member. Her card index with detailed records and her maps at tetrad level destined for later publication will be completed, we must hope, and brought to fruition. Stimulated by the lack of expertise available to identify problems in the smallreed (*Calamagrostis* spp.) complex she took up the cudgels and studied plants from elsewhere in Britain and Europe (including type specimens) in the National Herbaria at Edinburgh and the Natural History Museum, London. She became the B.S.B.I. Referee for the group and the characters she listed as useful for the five species in 1988 were re-published in the *Plant Crib* 1998, as being still the authoritative account.

Paintings, publications and records are lasting tributes to some of her endeavours which can be enjoyed by those that study plants in the future. But to the large coterie of friends she leaves behind – the many who enjoyed hospitality at West Maryfield, on their way from the South to northern Scotland – it will be those warm and happy memories of botanical forays, long walks to re-find a rare plant, or to check the status or identity of an old record; memories of botanical discussions in the kitchen, poring over maps and checking grid references over pre-dinner gins and tonic, unobtrusively administered by Frank, whose silent support for all she did allowed Olga to develop

her hobby to the full. After dinner, there would be the checking of taxonomic queries with lens or microscope, and Olga would carefully put those little vouchers, invariably shrivelled, into the plant-press which, when dry, would be sent to specialists at home or abroad to confirm the record; or taken to the R.B.G. at Edinburgh to compare with herbarium material. Then, later in the evening, replete in body and relaxed in mind, her guests would retire, leaving Olga sketching a wanted plant before the petals fell or dried. Next morning she was the first up, and breakfast (and packed lunch!) would be ready by the time we came down.

If Olga thought a species should be in 'her area' she would not rest until it was found, and confirmed. Invariably she succeeded, or manoeuvred her botanical friends into the right habitat so that they could "find" it. I don't know how many scraps of *Dryopteris dilatata* I was shown before the true mountain buckler fern (*D. expansa*) was found, but found it was! The challenge at the time of her death was to find the hybrid between *Isoetes echinospora* (not common in Kirkcudbrightshire) and *I. lacustris*. This enthusiasm for something new was infectious, and her presence at any meeting was welcomed with real pleasure. The B.S.B.I. Exhibition Meetings in Scotland were never, or rarely, missed, and for many years she also regularly attended – and exhibited at – the Society's Annual Meeting in London. On the rare occasion when she did not, her absence was the concerned comment of many who had looked forward to seeing her. Over a period of 50 years she acquired a great knowledge of flowers, and she was, without doubt, one of the best field botanists in Scotland, if not Britain. She was concerned about nature conservation and encouraged landowners and other environmental managers to do their best for plants. As a Regional representative on the B.S.B.I. Conservation Committee for S.W. Scotland, she was particularly concerned about the water management at Loch Ken, and produced a thorough survey of the area (1988. *Transactions of the Dumfries & Galloway Natural History & Antiquarian Society* 63: 1–4) to draw attention to the plight of the pillwort (*Pilularia globulifera*).

Olga was always interested, too, in other people, young and old alike, and from time to time worked for charities helping elderly people. She helped run a Badminton Club for young people in Edinburgh in the 1960s but her main sporting love was curling. She joined the Edinburgh Ladies Curling Club in the mid-1950s and, as in everything she took up, she soon became an expert. Olga won many competitions and, in 1967, was chosen to go on a curling tour of Western Canada, from Winnipeg to Victoria, as one of 20 ladies representing Scotland. She was forced to retire from curling only two years ago, after slipping and hitting her head on the ice.

She had the ability to impart her great knowledge of botany to beginners in her own unassuming way; she always saw the good side of a person's character and never criticised others. Her integrity and generosity of spirit is something that all of us who have had the good fortune to know her will remember most. Olga leaves husband Frank, daughter Rosemary, and sons Alan, John and Nick, the last of whom, having graduated in Geology at Cambridge, followed in her footsteps and is now a professional botanist in his own right. They, and their families, have lost a loving wife, mother and grandmother and our sympathies are with them. There are also botanical friends who have enjoyed many a happy day exploring Kirkcudbright with Olga. We too have lost a most knowledgeable and lovable field companion.

A. C. JERMY

KARL-HEINZ RECHINGER PHIL. DOC. (VINDOB.) FMLS
(1906-1998)

Karl-Heinz Rechinger, author of *Flora Aegaea*, founder, editor and for many parts also author of *Flora Iranica*, died in Vienna on 30 December 1998, aged 92. He has increased our knowledge of the flora and vegetation of the Balkan peninsula and South-west Asia more than anyone in this century. Since 1938 he has been a member of the B.S.B.I., and was later elected to honorary membership. The combination of three qualifications made Rechinger a most remarkable man. He acted for almost 35 years as director of the Department of Botany at the Natural History Museum in Vienna and for eight years served as "Erster Direktor" of that institution. At the same time he was also a prolific scientist who left behind a vast oeuvre of the highest merit with scores of new taxa described, of which many have stood the test of time. Thirdly, Rechinger was an extremely active plant collector who repeatedly travelled to some of the remotest corners of the world.

When the first instalment of *Watsonia* was published in January 1949 it contained a contribution by Rechinger which had first been presented at a meeting of the British Association in Dundee. Entitled "Lines of evolution and geographical distribution in *Rumex* subgen. *Lapathum*", its introduction offers a good insight into his mind: "The docks, having no showy flowers, do not awake aesthetic feelings as do, for instance, brightly coloured flowering plants or plants distinguished by a particular habit. The more intimate beauty which lies in the various shades of red, brown and yellow of the ripe fruiting panicles, contrasting with the dull green willows accompanying the river banks is not so obvious. Nevertheless it belongs undoubtedly to the general impression of a landscape in autumn. On the other hand, when looked at with a certain attention the amazing variability in size and shape of the inner perianth segments at the fruiting period offers a great deal of pleasure".

Pleasure meant for Rechinger travelling and collecting plants in dry habitats, with the Aegean area and the Near East being his favourite hunting grounds. Travelling in Iran, Iraq, Afghanistan and Pakistan was at that time an uncomfortable experience and required much dedication. He has brought home more than 100,000 collections, mainly flowering plants, many in several duplicates, and almost always deposited the first set in the Natural History Museum in Vienna. Pleasure meant for Rechinger analysing the endless variety of plant life, and describing it with great care and accuracy, *Cousinia*, *Rumex* and *Salix* being among his special friends. But pleasure also meant for Rechinger synthesising his observations and those of others in Floras, of which he produced three: *Flora Aegaea*, his first magnum opus, published in 1944; *Flora of Lowland Iraq*, printed in 1964; and his second magnum opus, *Flora Iranica*, of which the first fascicle came out in 1963. So far 173 fascicles have been published, a most remarkable achievement, with the treatment of a single family, a single tribe, and a single, albeit large, genus (*Astragalus*) still outstanding. A eulogy in *Annalen des naturhistorischen Museums in Wien* 75:1-16 (1971) and a paper in *Proceedings of the Royal Society of Edinburgh* 89B: 3-5 (1986) are major sources of information about his numerous publications.

Rechinger visited England and Scotland several times, maintaining long-term contacts with several botanists, notably at Edinburgh and Kew. Through his close co-operation with Peter Davis, editor of *Flora of Turkey and the East Aegean islands*, he strove for consistency with *Flora Iranica* despite there being, at times, varying perceptions of taxonomic rank. For many members of the B.S.B.I. he was their first contact when dealing with queries concerning the very rich holdings of the Natural History Museum in Vienna. There was a considerable involvement of British botanists in *Flora Iranica*: the account of Papaveraceae was written by J. Cullen, Rutaceae by C. C. Townsend, Guttiferae by N. K. B. Robson, Capparidaceae, Aizoaceae and Molluginaceae by I. C. Hedge and J. Lamond, Gramineae by N. L. Bot, several mainly aquatic monocot families by J. E. Dandy, and Balsaminaceae by C. Grey-Wilson. Several British botanists (A. J. C. Grierson, I. C. Hedge, J. Lamond, J. A. Ratter and P. F. Yeo) also contributed generic treatments to individual families, and the most recently published two fascicles of *Flora Iranica* were edited by I. C. Hedge instead of the ageing Rechinger. Some of his expeditions to Afghanistan, Pakistan and Iran were done in the company of two Scottish botanists, I. C. Hedge and J. Lamond.

Rechinger was one of the original advisory editors to the monumental *Flora Europaea* project, and although his original contributions were restricted to accounts (notably *Salix* and *Rumex*) in the first volume, published in 1964, his works on the Flora of Greece continued to provide a major foundation for studies of the flora of that country.

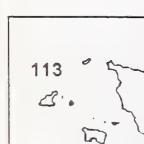
Rechinger grew old enough to be able to reap what he had sown, and he could reflect many of his undertakings in two autobiographical papers transmitting something of the flavour and fascination of travelling in the Levant and the Near East. They were published in the *Annales Musei Goulandris* in 1978 and the *Davis & Hedge Festschrift* in 1989 by Edinburgh University Press. Music was also very important to him, both playing the piano and listening to classical music, a pleasure from which deafness deprived him late in life.

Apart from many other distinctions like the Omajou Order Third Class from the Shah of Iran, Rechinger was honoured by being elected Foreign Member of the Linnean Society of London in 1966 (restricted to 50 botanists and zoologists), and was appointed an Honorary Fellow of the Royal Society of Edinburgh in 1987. His many friends will remember his benevolent, gentlemanly nature and his puckish yet kindly sense of humour. He is survived by his widow, Wilhelmina, without whose support in all facets of his life he would never have achieved so much.

without whose support in all facets of his life he would never have achieved so much.

His was a very rich and remarkable life, reaching the utmost end of what nature has accorded to man. British botany, and British botanists with their colleagues on the Continent and worldwide, will miss Karl-Heinz Rechinger.

H. W. LACK



NAMES OF VICE-COUNTIES IN WATSONIA

ENGLAND

- | | | |
|---------------------|--------------------------|--------------------------|
| 1. West Cornwall | 21. Middlesex | 54. North Lincolnshire |
| 1b. Scilly | 22. Berkshire | 55. Leicestershire |
| 2. East Cornwall | 23. Oxfordshire | 55b. Rutland |
| 3. South Devon | 24. Buckinghamshire | 56. Nottinghamshire |
| 4. North Devon | 25. East Suffolk | 57. Derbyshire |
| 5. South Somerset | 26. West Suffolk | 58. Cheshire |
| 6. North Somerset | 27. East Norfolk | 59. South Lancashire |
| 7. North Wiltshire | 28. West Norfolk | 60. West Lancashire |
| 8. South Wiltshire | 29. Cambridgeshire | 61. South-east Yorkshire |
| 9. Dorset | 30. Bedfordshire | 62. North-east Yorkshire |
| 10. Isle of Wight | 31. Huntingdonshire | 63. South-west Yorkshire |
| 11. South Hampshire | 32. Northamptonshire | 64. Mid-west Yorkshire |
| 12. North Hampshire | 33. East Gloucestershire | 65. North-west Yorkshire |
| 13. West Sussex | 34. West Gloucestershire | 66. Co. Durham |
| 14. East Sussex | 36. Herefordshire | 67. South Northumberland |
| 15. East Kent | 37. Worcestershire | 68. North Northumberland |
| 16. West Kent | 38. Warwickshire | 69. Westmorland |
| 17. Surrey | 39. Staffordshire | 69b. Furness |
| 18. South Essex | 40. Shropshire | 70. Cumberland |
| 19. North Essex | 40. Shropshire | 71. Isle of Man |
| 20. Hertfordshire | 53. South Lincolnshire | |

WALES

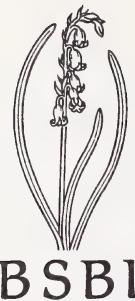
- | | | |
|---------------------|---------------------|----------------|
| 35. Monmouthshire | 45. Pembrokeshire | 50. Denbyshire |
| 41. Glamorgan | 46. Cardiganshire | 51. Flintshire |
| 42. Breconshire | 47. Montgomeryshire | 52. Anglesey |
| 43. Radnorshire | 48. Merionethshire | |
| 44. Carmarthenshire | 49. Caernarvonshire | |

SCOTLAND

- | | | |
|-----------------------|-------------------------|----------------------|
| 72. Dumfriesshire | 86. Stirlingshire | 99. Dunbarton |
| 73. Kircudbrightshire | 87. West Perthshire | 100. Clyde Isles |
| 74. Wigtownshire | 88. Mid Perthshire | 101. Kintyre |
| 75. Ayrshire | 89. East Perthshire | 102. South Ebudes |
| 76. Renfrewshire | 90. Angus | 103. Mid Ebudes |
| 77. Lanarkshire | 91. Kincardineshire | 104. North Ebudes |
| 78. Peeblesshire | 92. South Aberdeenshire | 105. West Ross |
| 79. Selkirkshire | 93. North Aberdeenshire | 106. East Ross |
| 80. Roxburghshire | 94. Banffshire | 107. East Sutherland |
| 81. Berwickshire | 95. Moray | 108. West Sutherland |
| 82. East Lothian | 96. Easterness | 109. Caithness |
| 83. Midlothian | 96b. Nairnshire | 110. Outer Hebrides |
| 84. West Lothian | 97. Westerness | 111. Orkney |
| 85. Fife | 98. Main Argyll | 112. Shetland |

IRELAND

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



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