

# 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 re-found 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 Alps, 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 Wigginton, 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  $\mu\text{m}$  wide and 150–300  $\mu\text{m}$  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  $\text{cm}^2$ . 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

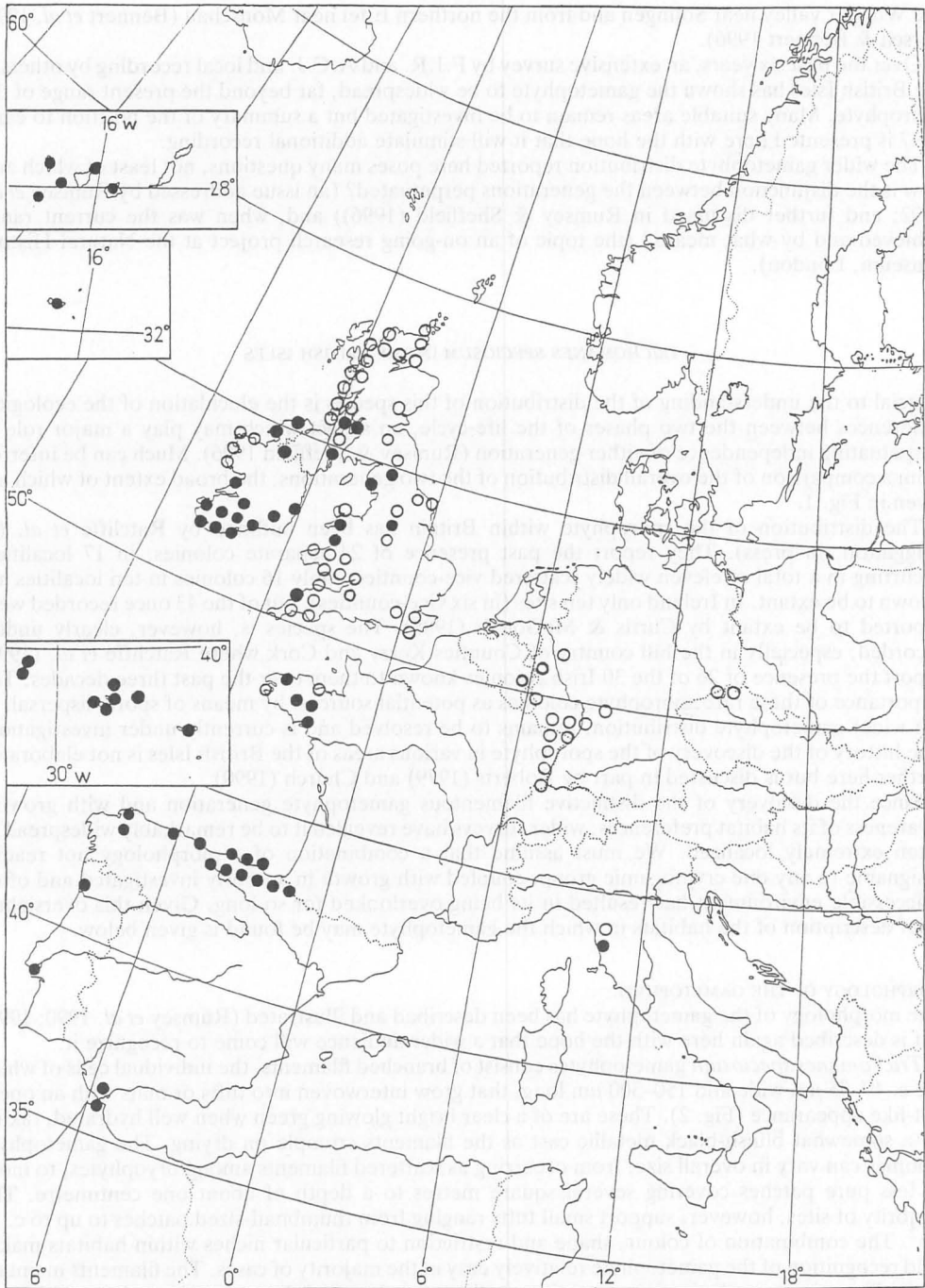


FIGURE 1. World distribution of *Trichomanes speciosum* Willd.: ● both generations; ○ gametophyte only. All known records mapped on the *Atlas florae Europaeae* base map (Jalas & Suominen 1972) amended to include the Canary Islands and Madeira. Dots indicate the presence of the species at any time within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



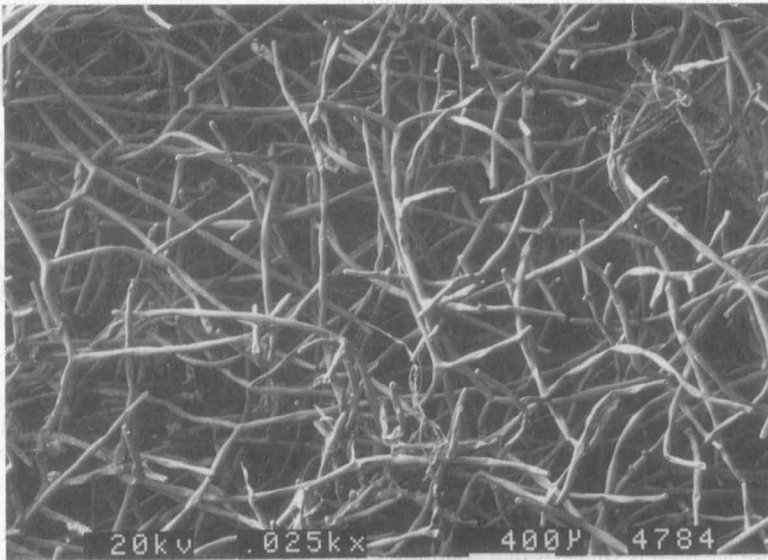


FIGURE 2. Upper. Typical gametophyte habitat under millstone grit boulders at Bell Bank, Yorkshire, 1989. Don Farrar, who first drew attention to the gametophyte in Europe, is holding the torch. (Photograph, A. C. Jermy.) Lower. Scanning electron micrograph of a gametophyte "mat" ( $\times 30$ ). (Micrograph,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

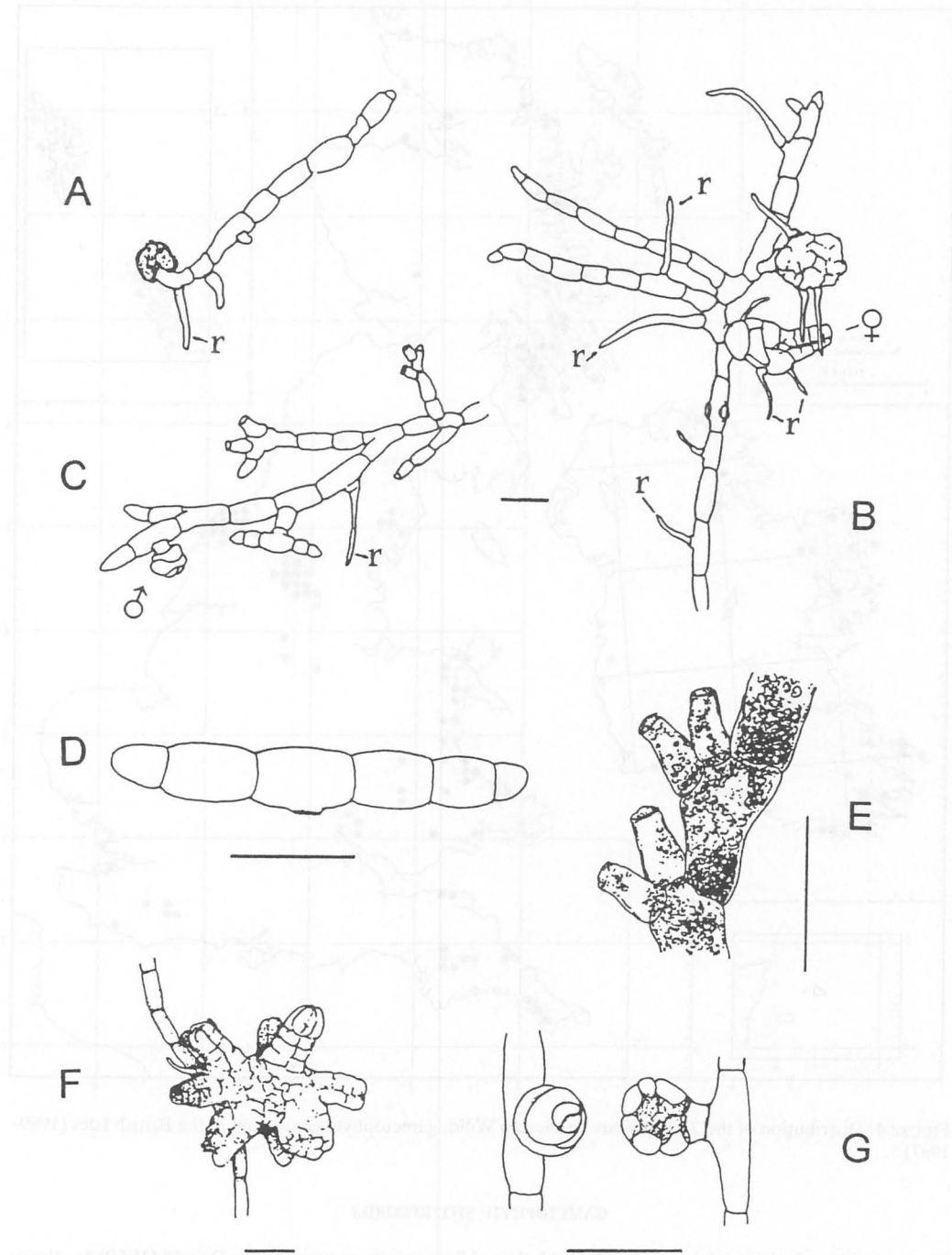


FIGURE 3. *Trichomanes speciosum* gametophytes. A. Germinating spore (r = rhizoid); B. Gametophyte with archegoniophores (♀); C. Gametophyte with antheridium (♂) and gemma; D. Gemma; E. Gemmifers; F. Archegoniophore with archegonia; G. Antheridia. Scale bar = 100 μm.

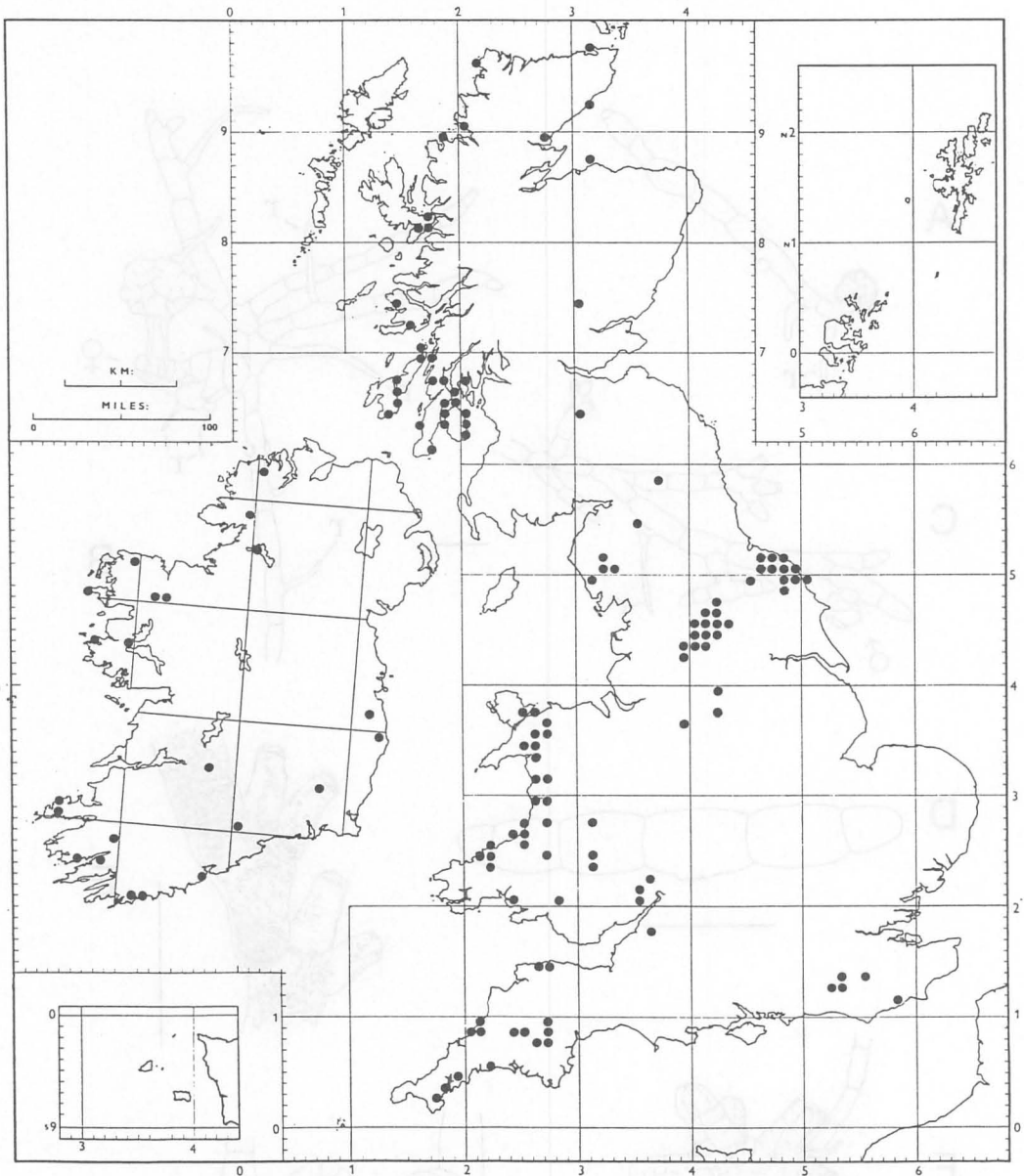


FIGURE 4. Distribution of the *Trichomanes speciosum* Willd. gametophyte generation in the British Isles (1989–1997).

#### 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. Meatyrd; 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. Penyard 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 Carms.  
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 Gwenffrwd, 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 Rheidol 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 Rheidol 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-illin-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 Derbys  
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, Moorholm, 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. 62 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 Crag, 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 Ghyll, 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 Ghyll, 180–190 m alt., ADH, FR & SR, Mar. 1991; SE/15.63 & 15.64. Ravensgill, Beverley, 180–240 m alt., FR & ADH, Jan. 1990; SE/20.63. Braistry 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 Aslaig, 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 streambanks, 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 basic 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 Ganllywd, Merioneth, do not

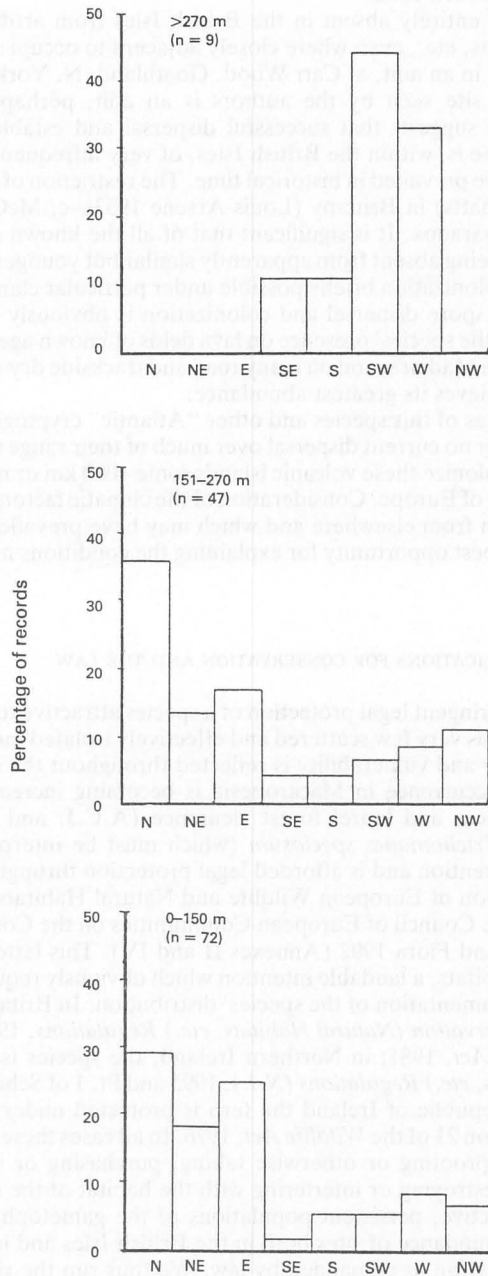


FIGURE 5. Gametophyte of *Trichomanes speciosum* microsite aspect at three different altitudes. Aspects have been simplified to the nearest of eight cardinal points; bar height is proportional to the number of records of that aspect in that particular altitudinal class.

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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## REFERENCES

- ALLEN, D. E. (1969). *The Victorian fern craze. A history of pteridomania*. Hutchinson, London.
- BENNERT, H. W., JÄGER, W., LEONHARDS, W., RASBACH, H. & RASBACH, K. (1994). Prothallien der Hautfarns *Trichomanes speciosum* (Hymenophyllaceae) auch in Nordrhein-Westfalen. *Floristische Rundbrief* **28**: 80.
- BOLTON, J. (1785). *Filices Britannicae: an history of the British proper ferns*. J. Binns, Leeds.
- BUJNOCH, W. & KOTTKE, U. (1994). Der Gametophyt von *Trichomanes speciosum* Willd. im Regierungsbezirk Trier. *Dendrocopos* **21**: 225–230.
- CHURCH, A. R. (1990). Recent finds of Killarney fern (*Trichomanes speciosum* Willd.) in Arran. *Glasgow naturalist* **21**: 608–614.
- CURTIS, T. G. F. & MCGOUGH, H. N. (1988). *The Irish red data book. I. Vascular plants*. Stationery Office, Dublin.
- DANDY, J. E. (1969). *Watsonian vice-counties of Great Britain*. Ray Society, London.
- EDWARDS, M. E. (1986). Disturbance histories of four Snowdonia woodlands and their relation to Atlantic bryophyte distributions. *Biological conservation* **37**: 301–320.
- FARRAR, D. R. (1967). Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the Southern Appalachians. *Science, N. Y.* **155**: 1266–1267.
- FARRAR, D. R. (1985). Independent fern gametophytes in the wild. *Proceedings of the Royal Society of Edinburgh* **86B**: 361–369.
- FARRAR, D. R. (1992). *Trichomanes intricatum*: The independent *Trichomanes* gametophyte in the eastern United States. *American fern journal* **82**: 68–74.
- FARRAR, D. R., PARKS, J. C. & McALPIN, B. W. (1983). The fern genera *Vittaria* and *Trichomanes* in the North-eastern United States. *Rhodora* **85**: 83–92.
- GOEBEL, K. (1888). Morphologische und biologische Studien: II Zur Keimungsgeschichte einiger Farne. *Annales Jardin Buitenzorg* **7**: 74–119.
- JALAS, J. & SUOMINEN, J. (1972). *Atlas florae Europaeae – Distribution of vascular plants in Europe. 1 Pteridophyta (Psilotaceae to Azollaceae)*. Committee for mapping the flora of Europe & Societas Biologica Fennica Vanamo, Helsinki.
- JÉRÔME, C., RASBACH, H. & RASBACH, K. (1994). Découverte de la fougère *Trichomanes speciosum* (Hymenophyllaceae) dans le massif Vosgien. *Le monde des plantes* **450**: 25–27.
- KIRSCH, H. & BENNERT, H. W. (1996). Erstnachweis von Gametophyten des Hautfarns *Trichomanes speciosum* Willd. (Hymenophyllaceae) in Bayern. *Nachrichten des naturwissenschaftlichen Museums Aschaffenburg* **103**: 119–133.
- LOUIS-ARSENE, Fr. (1953a). *Trichomanes speciosum* en Bretagne. *Bulletin de la Société botanique de la France* **100**: 6.
- LOUIS-ARSENE, Fr. (1953b). Nouvelle note sur le *Trichomanes speciosum*. *Bulletin de la Société botanique de la France* **100**: 187–188.
- LOUIS-ARSENE, Fr. (1953c). Les stations des *Trichomanes speciosum* dans la région de Ploemel. *Bulletin de la Société botanique de la France* **100**: 285–290.
- McCLINTOCK, D. (1963). Reports of the Exhibition Meeting, 1962. *Proceedings of the Botanical Society of the British Isles* **5**: 170–171.
- RASBACH, H., RASBACH, K. & JÉRÔME, C. (1993). Beobachtungen über das Vorkommen des Hautfarns *Trichomanes speciosum* (Hymenophyllaceae) in den Vogesen und dem benachbarten Deutschland. *Carolinea* **51**: 51–52.
- RASBACH, H., RASBACH, K. & JÉRÔME, C. (1995). Weitere Beobachtungen über das Vorkommen des Hautfarns *Trichomanes speciosum* Willd. in den Vogesen und dem benachbarten Deutschland. *Carolinea* **53**: 21–32.
- RATCLIFFE, D. A. (1968). An ecological account of Atlantic bryophytes in the British isles. *New phytologist* **67**: 365–439.
- RATCLIFFE, D. A., BIRKS, H. J. B. & BIRKS, H. H. (1993). The ecology and conservation of the Killarney fern *Trichomanes speciosum* Willd. in Britain and Ireland. *Biological conservation* **66**: 231–247.
- RAY, J. (1724). *Synopsis methodica stirpium Britannicarum*, 3rd ed., pp. 119, 127–128. W. & J. Innys, London.
- REICHLING, L. & THORN, R. (1997). *Trichomanes speciosum* Willd., un mystérieux passager clandestin. *Adoxa* **15/16**: 1–4.
- RICHARDS, P. W. & EVANS, G. B. (1972). Biological flora of the British Isles: *Hymenophyllum*. *Journal of ecology* **60**: 245–268.
- RIPLEY, P. H. (1990). National field meetings, 1990: Brittany. *British Pteridological Society bulletin* **4**: 11–14.
- ROBERTS, R. H. (1979). The Killarney fern, *Trichomanes speciosum*, in Wales. *The fern gazette* **12**: 1–4.
- RUMSEY, F. J. (1994). *The distribution, ecology and population biology of Trichomanes speciosum Willd.* Unpublished PhD. Thesis, University of Manchester.
- RUMSEY, F. J., HEADLEY, A. D., FARRAR, D. R. & SHEFFIELD, E. (1991). The Killarney Fern (*Trichomanes speciosum*) in Yorkshire. *Naturalist* **116**: 41–43.



- RUMSEY, F. J., HEADLEY, A. D. & SHEFFIELD, E. (1996). Gametophytic adaptations to low light – how unique are *Trichomanes* species? *American journal of botany* **83** (6) Suppl: 122.
- RUMSEY, F. J., RAINE, C. A. & SHEFFIELD, E. (1992). The reproductive capability of independent *Trichomanes* gametophytes, in IDE, J. M., JERMY, A. C. & PAUL, A. M., eds. *Fern horticulture: past, present and future perspectives*, pp. 299–304. Intercept, Andover.
- RUMSEY, F. J., RAINE, C. A. & SHEFFIELD, E. (1993). *Trichomanes venosum* R.Br. (Hymenophyllaceae: Pteridophyta) in a Cornish garden – with a key to the filmy-ferns established in Britain and Ireland. *Fern gazette* **14**: 155–160.
- RUMSEY, F. J., RUSSELL, S. J., JI, J., BARRETT, J. A. & GIBBY, M. (1996). Genetic variation in the endangered filmy fern *Trichomanes speciosum* Willd., in CAMUS, J. M., GIBBY, M. & JOHNS, R. J. eds. *Pteridology in perspective*, pp. 161–165. Royal Botanic Gardens, Kew.
- RUMSEY, F. J. & SHEFFIELD, E. (1996). Intergenerational ecological niche separation and the 'independent gametophyte' phenomenon, in CAMUS, J. M., GIBBY, M. & JOHNS, R. J., eds. *Pteridology in perspective*, pp. 563–570. Royal Botanic Gardens, Kew.
- RUMSEY, F. J., SHEFFIELD, E. & FARRAR, D. R. (1990). British filmy fern gametophytes. *Pteridologist* **2**: 40–42.
- SCANNELL, M. J. P. & SYNNOTT, D. M. (1987). *Census Catalogue of the flora of Ireland*, 2nd ed. Stationery Office, Dublin.
- SHEFFIELD, E. (1994). Alternation of generations in ferns: mechanisms and significance. *Biological reviews* **69**: 331–343.
- STOKEY, A. G. (1948). Reproductive structures of the gametophytes of *Hymenophyllum* and *Trichomanes*. *Botanical gazette* **109**: 363–380.
- TEESDALE, R. (1800). Supplement to the *Plantae Eboracenses*. *Transactions of the Linnean Society of London* **5**: 75.
- VOGEL, J. C., JESSEN, S., GIBBY, M., JERMY, A. C. & ELLIS, L. (1993). Gametophytes of *Trichomanes speciosum* (Hymenophyllaceae, Pteridophyta) in Central Europe. *Fern gazette* **14**: 227–232.
- WIGGINTON, M. J. ed. (in press), *The British red data book. Vascular plants*. J.N.C.C., Peterborough.
- YOROI, R. (1972). Studies on spore germination and gametophyte of Japanese Hymenophyllaceae. *Science reports of the Tokyo kyoiku daigaku, Section B* **15**: 81–110.

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