Threatened bryophytes: *Didymodon glaucus*

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Status

Didymodon glaucus Ryan (Glaucous Beard-moss), known at a single site in Britain, is Critically Endangered (Church *et al.* 2004) in Britain, fully protected on Schedule 8 of the Wildlife & Countryside Act 1981 (as amended) and is subject to a priority Biodiversity Action Plan (Anonymous 1995). It is a European endemic and is listed as Vulnerable (evaluated using old IUCN guidelines) in Europe (ECCB 1995).

Taxonomic relationships

Didymodon glaucus is a small acrocarpous moss in the family Pottiaceae, although the precise relationship to other species has been the subject of much discussion. Some workers have suggested that it is variety of *Didymodon rigidulus* (Duell 1984) and others (Whitehouse *in litt.*) have noted a resemblance to *Trichostomopsis* (*T. aaronis* has rounded gemmae on branched axillary rhizoids). In *D. rigidulus* M.O. Hill (*in litt.*) correctly observed that the gemmae are on chloronemal filaments (transverse cell walls) whereas those in *D. glaucus* are on filaments with oblique cross walls and lack chlorophyll. *D. rigidulus* gemmae are typically more irregular than in *D. glaucus*, about 35 µm in diameter and often somewhat laterally compressed. Kučera (2002) concluded that *D. glaucus* does not have a close relationship with *D. rigidulus*, but its relationship to another taxon, *D. verbanus* (W.E. Nicholson & Dixon) Loeske, a plant centred on the Italian Lakes region and which grows on the mortar of walls, is unresolved. All populations of *D. glaucus s.s.* known to date are female, whilst those of *D. verbanus* are male. There are quantitative and ecological differences between the two taxa, and it has been suggested that they could be geographically segregated male and female populations of the same taxon (Kučera *op cit.*). DNA sequencing may help to resolve the issue.

Description

Didymodon glaucus forms low growing patches (1-7 mm tall) with a characteristic glaucous-green colour in the dry state, the lower portions of the shoots within the cushion being pale. When dry the narrowly lanceolate leaves are incurved and spreading from an erect basal part when moist (Figure 1). The leaves are up to 2 mm long, sometimes obscurely toothed below and crenulate above. The margin is recurved for 50-90% of the leaf length. Upper leaf cells are rounded-quadrate with low

Figure 1. Habit of *Didymodon glaucus* in moist state. Photo: Ron Porley.

papillae and the hyaline basal cells are rectangular inflated. The lamina is bistratose or occasionally unistratose at the margin and the nerve has 2-4 layers of dorsal stereids. Colour in KOH is yellow. A distinctive feature is the presence of chains of gemmae (moniliform) on modified rhizoids in the upper leaf axils. Gemmae form on side or terminal rhizoid initials, beginning as a colourless swollen protuberance that divides progressively to form a chain. Each cell subdivides giving rise to a 4-6-celled, heavily pigmented, rounded gemmae, ranging from 20 to 30 µm in diameter. Chains may reach up to 175 µm long comprising eight or more gemmae (Figure 2). Occasionally, ellipsoid gemmae occur with a greater number of constituent cells. Abundant gemmae, clumped together, are often evident in the field as dark brown blemishes on the white chalk substrate (Figure 3). Sporophytes are unknown.

Axillary hairs have not received much attention from taxonomists, not only in the Pottiaceae but also in other families (Saito 1975), yet are potentially useful in elucidating relationships. The axillary hairs of *Didymodon glaucus* show some interesting features. They are variable in size, ranging in length from 80-230 µm and in width from 5.4-13.5 µm, and consist of 4-8 (occasionally more) uniseriate cells varying between 10.8-46

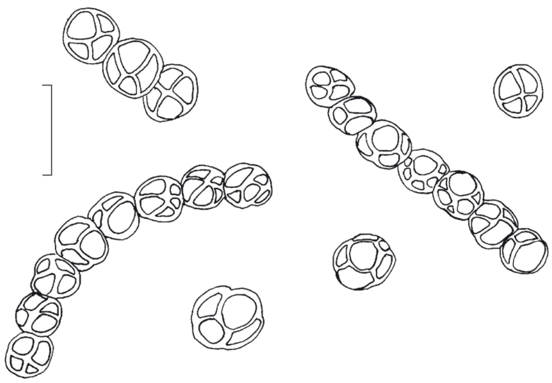

Figure 2. *Didymodon glaucus* chains and single gemmae from modified axillary rhizoids. Scale bar: 50 µm.

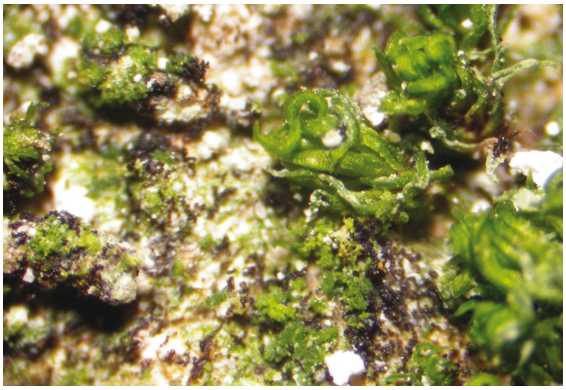

Figure 3. Dark brown gemmae of *Didymodon glaucus* visible on bare chalk with gametophores (dry). Photo: Ron Porley.

µm long, with the terminal cell acuminate. Rarely the axillary hairs have a biseriate portion (*e.g.* Townsend c.2001.022.382) or are forked at the base (*e.g.* Appleyard c.2001.019.8164). The basal cell is hyaline and often inflated, and a key feature is the presence of brown 'bands' (about 4 µm wide) on the distal end wall of the second or third (rarely fourth) cell (Figure 4). The pigmentation is most pronounced on the transverse cell wall, but the immediate longitudinal cell walls are also often lightly diffused with pigment. Occasionally there are two or more heavily pigmented bands. All collections examined from Britain, including material collected in the early 20th century, and a recent Hungarian specimen, show this banded appearance very clearly. Such axillary hairs have not been reported in the Pottiaceae (Saito 1975). By contrast, all specimens of *D. rigidulus* examined have typical *Didymodon*-type axillary hairs (Ah-2 type) (Saito 1975) with a brown basal cell. In length, width and number of uniseriate cells the axillary hairs are otherwise similar to *D. glaucus*. Axillary hairs of eight specimens of *Didymodon verbanus* (including types) were also examined, and all showed the *Didymodon*-type axillary hair with a brown basal cell; this has further implications for the unresolved relationship between *D. glaucus* and *D. verbanus*. *Didymodon* (*Trichosto-*

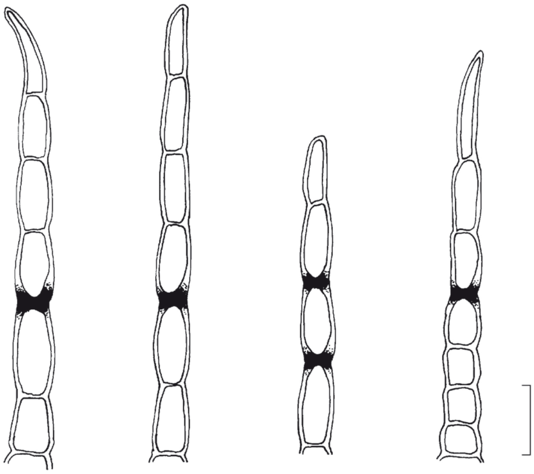

Figure 4. *Didymodon glaucus* axillary hairs. Scale bar: 20 µm.

mopsis) umbrosus has typical *Didymodon*-type axillary hairs, and *Eucladium verticillatum*, another taxon showing some resemblance to *D. glaucus*, has uniformly hyaline axillary hairs (Ah-1 type; Saito 1975). A survey of axillary hairs of the Pottiaceae is clearly desirable.

Ecology

Didymodon glaucus is a pioneer of bare chalk and limestone and a sciophyte (thriving or tolerating lowered light intensity). At its Wiltshire locality the colonies occur on the soft chalk surfaces of a disused chalk pit (Figure 5), in crevices and on small talus-covered ledges. The chalk pit, at an altitude of 160 m and an aspect varying from 250-300˚, sits in a humid hollow surrounded by trees and direct sunlight is excluded. In such shaded microhabitats competition from other bryophytes is minimal; protonemal gemmae of *Eucladium verticillatum* have been detected mixed with *D. glaucus* in deep shaded clefts at the Wiltshire site. *D. glaucus* does not tolerate excessive shading, and under such conditions the leafy gametophore disappears although protonemata often persists. Many mosses produce protonemal gemmae in deep shade, thus providing an opportunity to spread to more favourable locations (Whitehouse 1980). Whitehouse (1987) reported gemmae of similar morphology to those in leaf axils on protonemal filaments in *D. glaucus* cultures but they have not been proven in the wild (it is difficult to distinguish between gemmae giving rise to protonemata and gemmae being formed on protonemata). Where light levels are higher *Fissidens gracilifolius, Didymodon tophaceus, D. rigidulus, Pellia endiviifolia* and *Pohlia melanodon* have been recorded but rarely compete directly with *D. glaucus*. Occasionally, *D. glaucus* grows in less sheltered positions, either on the weathered chalk or on an accumulation of talus on ledges or at the base of the cliff, and is then vulnerable to competition from other bryophytes and vascular plants. Surveillance of a small colony of *D. glaucus* in a moderately exposed position which grew intermixed with *Amblystegium serpens* showed that the latter increased as the former declined to a few moribund gemmae-bearing leafy shoots over a period of about 5 years. In Sussex, where it was last seen in 1915, *D. glaucus* grew in crevices in a small chalk pit and in hollows in a chalk bank near Shoreham; associates included *Didymodon tophaceus*, *Amblystegium serpens*, *Fissidens* cf. *viridulus* and *Bryum* sp. (*in litt*.). In NW Yorkshire, where it was last seen *c*.1914, it grew on carbonif-

Figure 5. Disused chalk pit, Wiltshire. Photo: Ron Porley.

erous limestone walls.

Didymodon glaucus occupies similar shaded microhabitats elsewhere in Europe. In Hungary it grows on limestone walls just inside the entrance of Szeleta cave near Lillafüred in the Bükk Mountains (altitude 370 m), confirmed present in 2006 (Beata Papp, pers. comm.). Szeleta cave is not illuminated by electric light, but Boros (1964) describes a cave (Anna-barlang) in the same area where *D. glaucus* occurs deep inside growing around artificial lights. In the French Alps it occurs on the walls of a cave in calcareous (gypsum) rocks at 2100 m (Skrzypczak 2004) and at another cave about 30 km distant (1500 m), discovered in 2005 (second French record, Renée Skrzypczak, pers. comm.). In Germany, where it is known from about 10 localities (Frahm 2005), several occurrences are from the Brohltal area where it occurs inside cave entrances on base-rich tuff of volcanic origins. In Luxembourg it occurs under rocky overhangs on calcareous sandstone within humid shaded gorges in the Petite Suisse (Werner 1987) and in Norway it occurs below overhanging calcareous cliffs in open pine forest (Kristian Hassel pers. comm.).

Since *Didymodon glaucus* relies solely on vegetative reproduction, and the preferred niche is on sheltered ledges, in crevices or in deep shaded clefts, it is reasonable to conclude long distance dispersal does not occur or is ineffective at best. By contrast, short distance dispersal, over a few metres, seems to be effective. At the Wiltshire locality, a section of fresh chalk exposed in February 2003 was colonised by May 2004 (Porley 2005), several metres away from the nearest known colonies. Rainfall may disperse gemmae but it is also likely that animals play a role. Rabbits have been observed using ledges as 'runs' on the chalk cliff face at the Wiltshire locality. Molluscs, including the snails *Trochulus striolatus* (Figure 6) and *Cochlodina laminata*, are also present in some

Figure 6. The snail *Trochulus striolatus* sliding over *Didymodon glaucus*. Photo: Ron Porley.

quantity on the bare chalk face and may disperse gemmae step-wise over short distances in mucous or possibly by ingestion. Although it seems likely that much of the gemmae evident on the surface of the chalk originate from the modified rhizoids in the leaf axils, protonemal gemmae may also be involved.

The preferred microhabitat of *Didymodon glaucus* disappears unpredictably due to the unstable nature of the chalk, successional changes and excessive shading from growth of *Hedera helix* and other woody and herbaceous species. There is evidence of a persistent diaspore bank (Porley 2005) although the contribution of rhizoidal gemmae or possibly protonemal gemmae is unknown. Surveillance of the Wiltshire population has shown that some colonies can persist as gametophores for at least 19 years (Porley 1993). The life strategy (*sensu* During 1979, 1992) of *D. glaucus* has been variously given as a short-lived shuttle colonist (Hodgetts 1996) and a stress-tolerant perennial (Hallingbäck 1998). However, *D. glaucus* demonstrates the typical attributes of a dioicous colonist: potential life span moderately long, low growth rate and a high reliance on asexual propagules for population maintenance. During (1992) described such a life strategy as a pioneer, differentiating it from a colonist *s.s.* in which the life span is rather short, growth rate high and a high investment in both sexual and asexual reproduction. Colonists *s.s.* tend to colonise open but potentially productive habitats in earlier stages of secondary successions (often a result of disturbance), contrasting with pioneers that colonise very harsh environments usually in the earliest stages of succession.

Distribution

Didymodon glaucus has a Temperate European distribution (Hill & Preston 1998) and until very recently was regarded as a European endemic. It is known from 12 countries in Europe (Figure 7): Austria, Britain, Czech Republic, France, Germany, Hungary, Luxembourg, Norway, Romania, Slovakia, Sweden and Switzerland. The report of *D. glaucus* from Anatolia, Turkey (Çetin 1999), represents the only locality outside of Europe. A report of it from the Azores is erroneous. The centre of distribution is Central Europe, particularly the Czech Republic and Austria, where several new localities have been found recently. In many countries it occurs at a single locality, and is on a Red List where those countries have one. In Germany it is known from at least 10 localities, two relatively recent localities in Norway, and two in France. In Switzerland (two old localities) and Italy the situation is complicated by the occurrence of *D. verbanus*, which is present at several places in the Italian Lakes region, for example at Lake Maggiore and Lake Lugano. Apparently *D. glaucus s.s.* has not been confirmed from Italy (Jan Kučera pers. comm.).

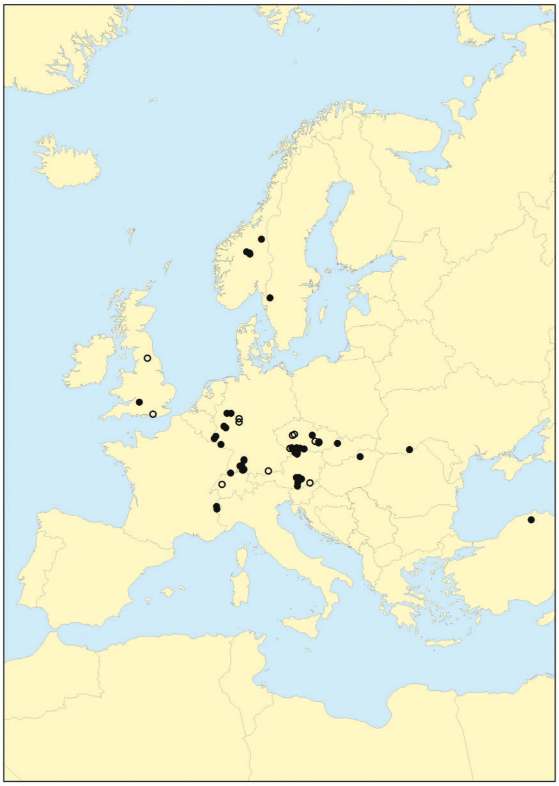

Figure 7. The distribution of *Didymodon glaucus* in Europe. Black dots represent records from 1980 onwards and are mostly still present, open circles are mostly early 20th century and have not been refound.

Conservation

Joan Appleyard discovered *Didymodon glaucus* at the Wiltshire site in 1961. The main colonies occurred within a disused chalk pit, and a few smaller colonies were found on adjacent high cliffs that form an incised green lane running by the chalk pit. One or two other bryologists saw it there soon after, but by 1978 the plant had apparently disappeared. Harold Whitehouse took samples of talus back to the laboratory and detected *D. glaucus*-type gemmae, which was confirmed by growing these on in culture. In 1987, the Nature Conservancy Council (NCC) re-notified the site, including an area of woodland, under the Wildlife and Countryside Act 1981 citing *D. glaucus* as an interest feature. Whitehouse urged the NCC to initiate a programme of habitat restoration in 1988 to remove scrub and talus accumulation. This was pioneering work in the field of bryophyte conservation. As a result, by 1989 a colony of *c.* 15 cm^2 had established in the disused chalk pit and in 1993 it was estimated that *D. glaucus* occupied a total area of 266 cm^2 (Porley 1993), mostly within a deep shaded cleft in a southwest face. Since 1993, the author has monitored the site almost annually. Recent restoration work at the Wiltshire site in 2003, funded by English Nature, utilising a mechanical excavator to expose fresh chalk on a face with a northwest aspect and clearance of trees, resulted in the establishment of further colonies (Porley 2005). By May 2007, the area covered by *D. glaucus* on the northwest face was estimated to be 1080 cm^2, an impressive increase in population size, including some particularly robust patches.

Söderström *et al*. (1992) reported that there was no example of successful conservation programmes where bryophytes have been saved. Thus *D. glaucus* may claim to be the earliest example of direct conservation action preventing the loss of a bryophyte from a country's list. Today there are several examples where conservation action is aimed specifically at threatened bryophytes, for example *Bryum schleicheri* var. *latifolium* (Rothero, Duckett & Pressel 2006).

Historically, *D. glaucus* has been recorded in two other counties in England:

- NW Yorkshire (v.-c. 65): On a carboniferous limestone wall between Richmond and Downholme, Barnes, *c*.1914. There have been no subsequent records and a voucher cannot be traced.

- W. Sussex (v.-c. 13): Hollows in chalk bank between Bramber and Shoreham, Nicholson, May 1908; crevices in a small overgrown chalk pit near Shoreham, Nicholson, March 1915. Vouchers for both are in CGE.

Despite many visits to the historical localities the moss has never been re-found. The entire British population therefore currently resides in the single disused chalk pit in Wiltshire. Although the population here fluctuates in size over time, the number of individual colonies within the Wiltshire site has increased due to management, the estimated area of cover has markedly increased and there are no immediate concerns for the survival of *D. glaucus* at the Wiltshire site.

Translocation and *ex situ* conservation

Many species seem to survive well in small populations in a few special habitats, but if a population is too small stochastic events can exterminate a species (Söderström 2006). The survival of *D. glaucus* is dependent on management and if this were discontinued the species would disappear. It is for these reasons that a translocation programme has been initiated at the Sussex site. The chalk pit in Sussex where Nicholson recorded *D. glaucus* in 1915 was relocated with a high level of confidence based on correspondence held at NMW. Howard Matcham, Rod Stern and the author visited the site in 2006 to assess the condition of the chalk pit. Nicholson remarked that the chalk pit was overgrown in 1915, and in 2006 the chalk pit is scarcely visible due to mature trees, particularly ash, and much scrub and an accumulation of talus. The habitat is therefore currently unsuitable and there was no sign of *D. glaucus*. Restoration of the chalk pit, with the involvement of the Sussex Wildlife Trust, the landowner, and funded by Natural England, will involve tree and scrub removal and exposure of the chalk cliff, due to begin in autumn 2007. The restored site will be visited for at least two seasons following clearance to check for natural re-colonisation from a possible diaspore bank (although as over 90 years has elapsed this is unlikely). If negative, *ex situ* material will be used in a re-introduction trial. A small amount of material from the Wiltshire site was collected under license by Jeff Duckett and the author and has been successfully weaned onto fragments of chalk sourced from the Wiltshire site (Pressel & Duckett 2004). It is envisaged that fragments of chalk carrying *D. glaucus* will be placed in suitable locations within the exposed chalk face. To date there has been no attempt to put rock cultures of

D. glaucus into the wild, contrary to the report in Söderström (2006). An alternative method to placing out chalk fragments may be to inoculate chalk *in situ* with a gemmae suspension; it has recently been confirmed that *D. glaucus* produces gemmae *in vitro* (Pressel & Duckett 2004).

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