hills around us, but our chosen ground remained dry. After a succession of strenuous days in the hills, we languidly pottered about on shingle and soil banks at Delvine – a fine, open, peaceful place by the River Tay, a few miles downstream from Dunkeld – keeping company with Sand Martins, who flickered and wittered quietly by.

A few minutes into the morning's exploration, Seán found *Syntrichia papillosa* on an oak tree, and then *Pohlia filum* appeared on the riverbank near to *Archidium alternifolium**. *Riccia canaliculata** and *R. cavernosa* sprawled over damp mud in a drying lagoon, alongside a little *Ephemerum serratum* var. *minutissimum*. Mudwort (*Limosella aquatica*) and the aquatic cabbage Awlwort (*Subularia aquatica*) were both in bloom, and another patch of damp mud by sequestered water in an old oxbow carried Needle Spike-rush (*Eleocharis acicularis*).

With arable bryophytes so topical at present, we felt obliged to close the week's fieldwork with a few minutes on our knees in a field of arable set-aside. Prayers were answered in the forms of *Fossombronia pusilla*, *Marchantia polymorpha* subsp. *ruderalis* and *Phaeoceros carolinianus**.

Summary

In the course of our week, we recorded six species that were either new to the vice-county or had not been seen there for over 50 years. *Riccia canaliculata* and *Phaeoceros carolinianus* from our day at Delvine are both Red Data Book species, reminding us that many bryophytes are rare because their favoured haunts are rare too. In turn this prompted the reflection that while bryologists understandably head straight for the hills when they go north, in doing so we unjustifiably neglect low-lying habitats and places that may yield uncommon species. Scotland surely has much to offer on low ground as well as high, a notion that we can test again when we sally into north Aberdeenshire next summer.

AGM and Bryological Symposium 2003, London

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The Annual General Meeting and Bryological Symposium were held at Queen Mary College, University of London on 5-7 September, with Prof. Jeff Duckett as local secretary. This, the first autumn meeting to have been held at the College, proved to be a popular venue for the bryological diaspora, with a total of 54 members attending the symposium and 20 going on to join the Sunday excursion. Participants were housed in the College's halls of residence at the Mile End Site overlooking the Regent's Canal in whose murky depths they were both surprised and delighted to find the local bryological jewel *Octodiceras fontanum*.

Bryological Symposium

The Symposium, held in the School of Biological Sciences at Queen Mary, and chaired by David Long and Jeff Duckett, comprised a remarkably eclectic and enjoyable selection of presentations, as can be seen from the abstracts on pp 32-44.

There are many ways of making water-conducting cells but what about stomata?

Prof. Jeffrey G. Duckett (Queen Mary College, University Of London) & Prof. Roberto Ligrone (Seconda Università Di Napoli, Caserta, Italy)

Introduction

In the 50 years since Watson and Crick (with more than a little help from Rosalind Franklin) elucidated the structure of DNA, studies of land plant phylogeny have moved from a backwater of futile speculation based almost entirely on comparative morphology, to a position in which cell and molecular biology have made massive new contributions. In this paper we present a critical evaluation of two major characters used in interpreting bryophyte phylogeny: water-conducting cells (WCCs) and stomata.

Water-conducting cells

In the 1970s, Charles Hébant (Hébant, 1977, 1979) described a suite of characters apparently common to both hydroids in mosses and tracheary elements in vascular plants. Since then, the vexed question as to whether or not these similarities indicate homology has been a crucial issue in arguments concerning a possible direct phyletic relationship between mosses and tracheophytes. The key character in these dead cells is the resemblance between wall breakdown during vessel element ontogeny and the supposedly hydrolysed walls in hydroids (Ligrone, Duckett & Renzaglia, 2000). Careful study of Hébant's works reveals that the assumption that the walls of hydroids are hydrolysed (and hence supposedly freely permeable) is based solely on their appearance in transmission electron micrographs. There are no data on the presence of wall-degrading enzymes in hydroids, nor on the permeability properties of their walls. Thus we decided to investigate further the physiology and wall chemistry of hydroids.

The movement of dyes in hydroids is considerably slower than through tracheary elements. The higher the molecular weight of the dye the slower the rate of movement; particles in suspension (e.g. Indian ink) do not move at all. These are hardly the properties of freely-permeable walls. Dye movement is inhibited by aldehyde fixation in hydroids, but not in tracheary elements. 'Hydrolysed' hydroid walls are completely disrupted by both carbohydrate-degrading and protein-degrading enzymes, after which dyes and particulate matter move much more freely. These discoveries suggest that, far from being hydrolysed, the walls have a complex structure whose functional integrity depends on both carbohydrate and protein moieties. Our subsequent immunocytochemical demonstration of several carbohydrate epitopes in hydroid walls (Ligrone *et al.*, 2002) also runs counter to the notion of maturational hydrolysis of the walls. Cryo-scanning electron microscopy of hydroids in dehydrated mosses reveals that they still contain water. Air bubbles are, however, formed in hydroids when enzyme-treated specimens are dehydrated. We therefore conclude that the unique carbohydrate and protein composition of hydroid walls, along with the absence of perforations (plasmodesmata disappear during the elongation of developing hydroids), renders these cells highly resistant to cavitation, a characteristic almost certainly linked to desiccation tolerance.

Remarkable diversity in the structure, development and immunocytochemical characteristics of the walls of WCCs in bryophytes (Ligrone *et al.*, 2000, 2002) is consistent with the notion that WCCs in *Takakia* are not homologous with hydroids in other mosses, nor with WCCs in *Haplomitrium* and metzgerialean liverworts. Overall there is now no good evidence for homology between any of the WCCs in bryophytes and tracheary elements. The independent origins of WCCs in different groups of bryophytes parallels the situation in recently-described Devonian mesofossils (Edwards, Axe & Duckett, 2003).

Stomata

These new insights into the absence of homology between WCCs in bryophytes and tracheophytes point to the need for a critical evaluation of the widespread assumption that all stomata are homologous. The absence of stomata, and some molecular data, are the chief features placing liverworts as the basal lineage in land plants (Kenrick & Crane, 1997; Raven, 2002). However, all other features point to hornworts as the more comfortable occupants of this position (Renzaglia *et al.*, 2000). Compared with the complex developmental processes associated with WCC differentiation, making a stomatal pore, by dissolution of the middle lamella between two guard cells, would seem to be simple. But, as we have seen for WCCs, unequivocal demonstration of homology requires developmental and physiological data. So what do we know about these in bryophyte stomata?

Ultrastructural data for bryophyte stomata are limited to *Funaria* (Sack & Paolillo, 1983), comparisons between stomatal development in bryophytes and in vascular plants do not exist, and the composition of guard-cell walls is unknown. As in higher plants, the stomata in *Funaria* open and close and are sensitive to abscissic acid

(Garner & Paolillo, 1973). Stomata in *Phaeoceros* show neither of these properties. Whether or not guard cell movements in bryophytes involve potassium fluxes, and whether or not bryophyte stomata regulate gaseous exchange, have yet to be investigated. In the absence of this vital information the grounds for assuming homology appear most flimsy – all the more so when set against the distribution of stomata in mosses and in hornworts. In vascular plants, absence of stomata is a feature more or less restricted to submerged aquatics. In bryophytes, presence and absence are much more sporadic. Thus stomata occur in *Phaeoceros* and *Anthoceros* (interestingly, in very low densities similar to Devonian vascular plants that flourished when the concentration of atmospheric carbon dioxide was much higher than subsequently (Beerling & Royer, 2002)), but not in *Megaceros*, *Dendroceros* and *Notothylas*. They are present in *Polytrichum* (but absent in *Atrichum* and *Pogonatum*), present in *Dialytrichia mucronata* (but absent in *Cinclidotus fontinaloides*), and present in *Tetrodontium* (but absent in *Tetraphis*) (Paton & Pearce, 1957).

These data would seem to indicate that, in bryophytes, stomata may have a primary function other than gaseous exchange. Schimper's (1858) drawings of *Sphagnum* suggest that stomata may possibly have a key role in drying out mature capsules prior to spore discharge. Though it is often stated in textbooks that the stomata covering the capsules of *Sphagnum* may be non-functional, the supporting evidence is never cited. Schimper's drawings, confirmed by our own observations, clearly show that *Sphagnum* stomata simply cannot function in gaseous exchange since throughout sporophyte ontogeny they are completely covered by the calyptra. Only when this withers and dies, as the mature capsules change in colour shortly before spore discharge, are the pores exposed to the external environment.

These considerations underline a pressing need for experimental studies on bryophyte stomata. Until physiological and developmental data become available the assumption of stomatal homology in plotting phylogenies should come with a severe health warning.

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Evolution and composition of bryophyte primary cell walls

Zoë Popper, Ian Sadler & Stephen Fry (University of Edinburgh)

Introduction

Evolution has a major influence on plant cell walls, and variation in primary cell wall (PCW) composition is known to exist between different angiosperm taxa. However, the PCWs of lower land plants have not been well studied. We have therefore investigated PCW composition in a wide variety of land plants (bryophytes, lycopodiophytes, eusporangiate and leptosporangiate ferns, gymnosperms and angiosperms) and the closely related charophycean green algae.

Results

Major differences in PCW components between non-vascular plant taxa are reported.

Xyloglucan
Driselase digestion yielded isoprimeverose (the diagnostic repeat unit of xyloglucan) from PCW-rich material of the hornwort *Anthoceros*, mosses, both leafy and thalloid liverworts, and numerous vascular plants, showing xyloglucan to be a PCW component in all land plants tested (Popper & Fry, 2003). Contrastingly, charophycean green algae (*Klebsormidium*, *Coleochaete* and *Chara*) did not yield isoprimeverose. Additionally, charophyte material was not digestible with XEG (xyloglucan–specific endoglucanase (Pauly *et al.*, 1999)) or cellulase to give xyloglucan-derived oligosaccharides.

Uronic acids
Galacturonic acid was consistently the most abundant uronic acid in PCWs, but was present in higher concentrations in bryophytes and charophytes than in any of the vascular plants. Acid hydrolysis of PCW-rich material from charophytes, *Anthoceros*, thalloid and leafy liverworts, and a basal moss (*Sphagnum palustre*) yielded higher concentrations of glucuronic acid than were found in other land plants, including the less basal mosses (Polytrichales, Dicranales, Bryales, Isobryales, Hookeriales and Thuidiales). Polysaccharides of *Anthoceros* contained an unusual repeat unit, α-D-Glucuronosyl-(1→3)-L-galactose, not found in high concentration in any other plants tested (Popper, Sadler & Fry, 2003). Mannuronic acid was not detected in any of the species surveyed.

Mannose
Acid hydrolysates of charophyte and bryophyte PCW-rich material yielded appreciably higher concentrations of mannose than were found in vascular plant PCWs.

Methyl-sugars
3-*O*-Methyl-D-galactose was present only in acid hydrolysates of lycopodiophytes (Popper, Sadler & Fry, 2001). In contrast, 3-*O*-methylrhamnose was present in acid hydrolysates of charophytes, bryophytes and homosporous lycopodiophytes, but was absent from heterosporous lycopodiophytes (Popper, Sadler & Fry, 2004).

Conclusions

Xyloglucan was present in the PCWs of all land plants investigated but appeared to be absent from the closely related charophytes (Popper & Fry, 2003). The presence of xyloglucan in the early ancestor of land plants may have been a pre-adaptation for land colonisation. The evolution of a vascular habit and the leptosporangiate condition occurred along with major changes in PCW composition. We have shown that variation in PCW composition appears to be particularly pronounced between monophyletic groups of plants, and may correlate with changed ecological pressures.

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In vitro culturing of rare bryophytes

Silvia Pressel & Prof. Jeffrey G. Duckett (Queen Mary College, University of London)

Background

As recently outlined in Church *et al.* (2001), the rich bryophyte flora of Great Britain is vulnerable. Several dozen species have Red List status, and 37 species are listed on Schedule 8 of the Wildlife and Countryside Act 1981, i.e. plants which enjoy special protection against picking, uprooting (where uprooting is defined as

removal from the site), destruction and sale. The conservation of rare and endangered taxa is therefore extremely important. Until recently, efforts have relied heavily, if not solely, on an *in situ* approach, whereby conservation of threatened taxa has translated directly into the conservation of their habitat. A novel approach, designed to complement traditional habitat preservation, is *ex situ* conservation. An *ex situ* programme has recently been developed for the conservation of rare and endangered British bryophyte species. This is a collaborative venture between the Royal Botanic Gardens Kew, English Nature, Scottish Natural Heritage and the Countryside Council for Wales. This novel approach focuses on the development of cryopreservation protocols as a valuable means for the long-term storage of rare and endangered bryophytes (Burch & Wilkinson, 2002).

Our project builds on this collaborative programme. *In vitro* culturing of an extensive number of different taxa, including many Schedule 8 and specially-protected species (Church *et al.*, 2001), has so far been achieved, and is providing an invaluable means of 'bulking up' material of rare and endangered species for possible reintroduction trials as well as for experimental manipulation. *In vitro* culturing also offers unique opportunities to study the juvenile stages of moss development, thereby revealing new characters that can be used to clarify taxonomic problems and providing new insights into the reproductive biology and ecology of bryophytes. Cytological studies aimed at understanding cellular responses to desiccation and rehydration of moss protonemata have been initiated, and will soon be applied to understanding the ultrastructural consequences of cryopreservation and the cellular events associated with regeneration following cryotreatment.

We have, to date, successfully cultured a wide range of bryophyte taxa. These *in vitro* cultures can be maintained, via careful sub-culturing, almost indefinitely and thus provide an invaluable databank of rare bryophyte material, should certain taxa become extinct in the wild. Furthermore, since protonemata are the first structures to develop, *in vitro* culturing allows rare material to be bulked up in relatively short periods of time, once axenic cultures have been obtained. Axenic cultures can then be used for a variety of purposes: experimental manipulation, cryopreservation, molecular studies, and reintroduction trials (Duckett *et al.*, in press).

Reintroduction trials

An advantage of the *in vitro* approach is that some taxa produce asexual propagules in culture. Suspension of gemmae could prove ideal inocula for reintroduction trials. The discovery that *Zygodon gracilis* (an endangered and specially protected species (Church *et al.*, 2001)), *Didymodon glaucus* (critically endangered and specially protected) and *Seligeria carniolica* (critically endangered and specially protected) all produce gemmae *in vitro* was most welcome news.

As well as the use of gemmae as inocula, other means of reintroduction into the wild have also been explored. The establishment of axenic cultures using fragments of parent substrata seems most promising. So far, this has been successfully achieved for the two saxicolous species *Z. gracilis* and *D. glaucus*, and trials will soon commence for *S. carniolica*. These 'rock cultures' (a method first developed by Paul Fletcher at Queen Mary College, University of London) consist of surface-sterilised fragments of parent substratum in nutrient-free Phytogel on which the desired species is allowed to establish and grow. This year, 'rock cultures' of *Z. gracilis* have been used for reintroduction trials at one of only two British sites where this moss still survives in the wild. At first sight *Z. gracilis*, although very restricted in its distribution, appears to be thriving – large cushions of this species cover extensive areas of Carboniferous Limestone walls on the slopes of Penyghent in Yorkshire. However, a close examination reveals the presence of mature colonies only, with little or no sign of new ones being established. This, coupled with the absence of gemmae in nature and the extreme rarity of sporophyte production (Fred Rumsey, pers. comm.), could prove fatal to the survival of *Z. gracilis* should a catastrophic event (e.g. the destruction of the rock walls) lead to the death of the existing colonies. If our reintroduction trials prove successful the survival of *Z. gracilis* will be guaranteed against such eventualities.

Taxonomic studies

The taxonomic rewards of *in vitro* culturing are best exemplified by the recent work of Newton *et al.* (2000). By elegantly combining morphological and molecular data these authors were able to link, on the bases of protonemal plates and nucleotide sequences, *Tetraphis* with *Oedipodium* (i.e. the reassignment of *Oedipodium* from the Funariales to the Tetraphidales), and to separate *Andreaea* from other mosses, based on the presence of massive parenchymatous protonemata.

At the infrageneric level, our current comparative studies of twelve species of the genus *Weissia* offer another good example of the taxonomic potential of culturing studies (Duckett, Pressel & Ligrone, in press). The protonemata of this genus have a highly distinctive morphology with undulating caulonemal main axes,

acuminate, water-repellent chloronemata, and absence of diaspores. Against this common ground plan there are distinct differences between taxa. Most striking is the presence in *W. controversa* var. *densifolia* of very deeply pigmented and extremely thick-walled caulonemata with a prominent cuticle. In contrast, the caulonemata of *W. controversa* var. *controversa* is much less heavily pigmented, like those of other *Weissias*. These substantial differences in protonemal morphology suggest that var. *densifolia* could well merit elevation to specific status. In order to confirm this the morphology of intermediate forms from Cornish mining sites is being investigated.

Protonemal morphology has also been used to clarify the uncertain taxonomic position of *Discelium nudum*, which has been variously classified in the Funariales or Catoscopiaceae (Duckett & Pressel, 2003). The chloronema of *Discelium* closely resembles that of all other members of the Funariales we have grown in culture, except that in *Discelium* even the oldest rhizoids are non-pigmented. The only other family that appears to have such strikingly colourless rhizoids is the Gigaspermaceae (Magill, 1987). We hypothesise that *Discelium* could be closely related to the Gigaspermaceae; molecular studies are now needed to test this hypothesis.

Rhizoidal tubers in *Discelium*

Taxonomic considerations aside, we were initially quite baffled by the protonemal morphology of *Discelium*, in particular by the presence of colourless rhizoidal tubers approximately 1 cm below the ground that are filled with starch grains (typically found in short-lived propagules), rather than lipids and proteins (the dominant storage materials of longer-lived propagules). A visit to *Discelium* sites in autumn and spring helped to shed light on these observations. The top 1 cm of the unstable clay banks on which this species grows exfoliates regularly in spring following winter frost, thus exposing the starch-filled tubers. Upon exposure the tubers germinate within 48 hours and rapidly produce a mat of chloronemal filaments (also seen in *in vitro* cultures). Thus the tubers in *Discelium* behave as short-lived diaspores, being filled with starch, germinating rapidly, and quickly losing their viability. This is a most striking contrast with tubers of all other species analysed to date, which are longer-lived, desiccation-tolerant, slowly germinating (e.g. those of *Ditrichum cylindricum* take 7-14 days to germinate), and filled with lipids/proteins. We conclude that the exposure of rapidly germinating tubers in the spring gives *Discelium* a distinct advantage in colonising unstable clay banks, and enables it to persist in this habitat ahead of more vigorous competitors.

Desiccation studies

Cytological studies of the effects of desiccation and rehydration in moss protonemata have so far proved most promising. Moss caulonemata and rhizoids contain highly polarised cells with a distinctive cellular organisation whereby a system of longitudinally-aligned endoplasmic microtubules (MTs) is associated with a spindle-shaped nucleus, elongate plastids and mitochondria, endoplasmic reticulum, and membrane-bounded vesicles and tubules (a cellular organisation also typical of moss food-conducting cells (Duckett, Schmid & Ligrone, 1998)). In the dehydrated state this cellular organisation is severely disrupted: longitudinal organelle alignment is lost, chloroplasts become rounded, the endoplasmic MTs disappear, and the cytoplasm becomes filled with large vesicles and aggregates of free ribosomes. Following rehydration, over a period of several hours, the cytoplasmic vesicles disappear, the ribosomes disperse, and chloroplasts and mitochondria regain their original shapes and longitudinal orientation along endoplasmic MTs. The nucleus, which in the dehydrated state appears rounded with condensed chromatin, regains its spindle-like shape and the chromatin redisperses. Based on these preliminary studies we suggest that desiccation tolerance/injury in bryophytes is intrinsically linked to the disruption of the microtubule cytoskeleton and its ability/inability to reassemble upon rehydration. Thus it is envisaged that MTs play a fundamental role in the desiccation responses of moss caulonemata (and most likely bryophyte cells in general), and that their reassembly is a crucial event in recovery following desiccation. It follows that resumption of normal metabolic activities after dehydration may well depend on how quickly bryophyte cells can reassemble their cytoskeleton.

Based on the hypothesis that dehydration and freezing affect cells in a similar manner, we hope that these desiccation studies will also help us to elucidate the ultrastructural consequences of cryopreservation and the cellular events associated with regeneration following cryotreatment. Ultrastructural studies of cryopreserved and regenerating material should allow us to determine the integrity of stored samples, to assess whether regeneration is direct, and to identify the regions of cellular survival.

We have also started analysing the effects of desiccation on a range of other bryophytes. A series of desiccation experiments has been conducted on *Southbya tophacea*, a liverwort that is able to dry out for months in the Mediterranean summer climate and then fully recover. Cells that have been in a prolonged dehydrated state (for approximately three months) appear collapsed, but oil

bodies are still present and, compared to those of rehydrated cells, seem hardly changed in shape and size. Electron microscopic observations confirm this finding; indeed, the oil bodies appear largely unaffected by desiccation, contrary to statements that desiccation causes loss of oil bodies.

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The model moss

Neil Ashton, Stacey Singer & Bevin Akister (University of Regina, Canada)

Background

Many important aspects of plant development, including specification of the temporal and spatial patterns of organ formation in both vegetative and reproductive apical meristems in flowering plants, are genetically programmed predominantly by members of two multigene families: *MADS-box* genes and *KNOX* genes. *MADS-box* genes are best known for their roles in regulating the transition of shoot apical meristems (SAMs) into inflorescence and floral meristems and in the determination of floral organ (sepal, petal, stamen and carpel) identities. They have recently been discovered in non-flowering plants, including conifers, *Gnetum*, ferns, a clubmoss and a moss (Henschel *et al.*, 2002; Krogan & Ashton, 2000, and references therein). *KNOX* genes are required for the generation and/or maintenance of SAMs in flowering plants. Recently, they too have been found in non-flowering plants, including spruce and a moss (Champagne & Ashton, 2001, and references therein). In a few cases, it has been shown that specific non-flowering plant *MADS-box* or *KNOX* genes display similar expression patterns to those of distinct subsets of flowering plant *MADS-box* or *KNOX* genes respectively. Discovery of these non-flowering plant genes has fuelled a resurgence of interest in plant 'evo-devo' (the close relationship between evolution and development), and in particular has raised the intriguing possibility that mechanisms governing the differentiation of reproductive structures and of SAMs in higher and at least some lower plants are fundamentally similar and evolutionarily conserved.

The discovery of putative orthologs of some angiosperm floral *MADS-box* genes in conifers, and most recently of floral organ identity *B*- and *C*-function orthologs in *Gnetum* (Winter *et al.*, 1999; Becker *et al.*, 2000), lends strong support to this idea, at least so far as seed plant groups are concerned. Furthermore, phylogenetic analyses show that at least seven clades of *MADS-box* genes contain representatives from both gymnosperms and angiosperms (Becker *et al.*, 2000); thus a significant proportion of the *MADS-box* gene diversity apparent in extant flowering plants was generated prior to separation of the two main seed plant lineages about 300 million years ago. Conversely, phylogenetic reconstructions and expression studies including fern, clubmoss and moss sequences indicate that structural and functional diversification into the gene subfamilies recognisable in extant angiosperms and other seed plants occurred after the cryptogam and spermatophyte lineages diverged (Münster *et al.*, 1997; Hasebe *et al.*, 1998; Krogan & Ashton, 2000; Svensson, Johannesson & Engström, 2000; Henschel *et al.*, 2002). Nevertheless, it remains an open question whether some of the cryptogam *MADS-box* genes are orthologous to recognised subsets of spermatophyte *MADS-box* genes. Interestingly, *MADS-box* genes of clubmosses and mosses have been resolved phylogenetically into two clades: *MIKC*^{c}-type (classic *MIKC*-type) and the

structurally deviant *MIKC**-type that appears to be absent from all other plant groups examined (Svensson *et al.*, 2000; Henschel *et al.*, 2002; Svensson & Engström, 2002). The most likely explanation of this last observation is that the most recent common ancestor of mosses and vascular plants, which probably existed about 450 million years ago, already possessed a *MIKC* and a *MIKC** gene. Given the failure to discover a *MIKC** gene in *Arabidopsis* despite the availability of its complete genome sequence, it seems that this class of *MADS-box* genes was lost in the lineage that led to extant ferns (*sensu lato*) and seed plants. This raises the intriguing question as to what functions *MIKC** genes had and have, which led to this gene type being conserved for about 450 million years in mosses and clubmosses but becoming dispensable in 'higher' vascular plants.

Angiosperm *KNOX* genes can be resolved into two groups based on gene sequence, architecture and expression patterns. Class 1 genes are expressed in vegetative and reproductive SAMs, and also in internodal intercalary meristems (IMs), and appear to be needed for the maintenance of cells comprising distinct spatial domains in an undifferentiated, undetermined state. Class 2 genes are expressed more globally and their function is unknown. The discovery of a putative class 1 ortholog in spruce (Sundås-Larsson *et al.*, 1998) with similar expression patterns and functions to angiosperm class 1 genes indicates that these genes acquired a regulatory role in the maintenance of SAMs prior to the divergence of angiosperms and gymnosperms. The recent identification of both class 1 and 2 putative orthologs in *Physcomitrella* (*Aphanorhegma*) *patens* (Champagne & Ashton, 2001) suggests that the duplication and diversification of ancestral *KNOX* genes may have been essential steps in the evolution of terrestrial plant SAMs.

To obtain clues about the ancestral functions of genes that are now involved in regulating specialised developmental processes, such as the generation of flowers and SAMs, we are conducting experiments to determine the roles and expression patterns of *MADS-box* and *KNOX* genes of the 'model moss': *Physcomitrella patens*. This plant model system offers unique opportunities for these kinds of study because of its amenability to sophisticated genetic analysis. The results obtained, when combined with information about these gene families in other plants, should provide a more profound comprehension of the evolution of a) the *MADS-box* and *KNOX* multigene families and their functions, and b) the various major land plant groups, and structures, such as angiosperm floral organs, that define each of them.

Summary of results to date from functional genetic studies with the model moss

Transformed strains of *Physcomitrella*, in which individual *MADS-box* or *KNOX* genes have been targeted and disrupted, have been generated for three *MADS-box* (*PPM* [*Physcomitrella patens MADS-box*]) genes, two class 1 *KNOX* (*MKN* [*Moss KNOX*]) genes and one class 2 *KNOX* (*MKN*) gene. In all cases, we have verified disruption of the targeted gene by both PCR and Southern analyses. Most of these strains exhibit a normal or nearly normal phenotype, probably because of functional redundancy within each gene family.

Southern probing of *Physcomitrella* total genomic DNA using a conserved *MADS-box* or *KNOX* sequence and low stringency conditions suggests that there are between eight and 12 *PPM*-like genes and several additional *MKN* genes in the *Physcomitrella* genome. This finding increases the likelihood of functional redundancy within these gene families. We are endeavouring to solve this problem by constructing multiple gene knock-out strains for each gene family or subfamily, and alternatively by employing RNA antisense and RNA interference methods to knock out expression of all members of a chosen gene family, including those we have yet to identify.

Preliminary results have been obtained in which strains transformed with an antisense *PPM* gene (and shown by RT-PCR to make the antisense message abundantly) display an altered phenotype with delayed and abnormal sporophytes. While most strains in which single *PPM* genes have been knocked out develop normally, one example has been obtained with an altered phenotype very similar to that of transformed strains expressing the antisense gene. We suggest that in addition to the targeted gene (which we have confirmed by molecular analysis is disrupted), one or several other closely-related, functionally-redundant gene(s) has/have been knocked out fortuitously in this strain. At present we do not know whether sporophyte development in these mutant strains has been affected directly or indirectly, for instance, through delayed production of antheridia and/or archegonia. If it transpires that antheridia formation alone is affected, then we would be able to infer a function for the moss *PPM* genes consistent with the fundamental role proposed for higher plant *B*-function *MADS-box* genes, namely that these genes are required to differentiate male reproductive structures (with B expression on) from female reproductive organs (with B expression off) (Winter *et al.*, 1999). If, however, both antheridia and archegonia production are affected, we would infer a function for the moss *PPM* genes consistent with the fundamental role proposed for

higher plant *C*-function genes, namely that they are needed to differentiate reproductive organs (with C expression on) from non-reproductive organs (with C expression off) (Winter *et al.*, 1999).

Results using a *KNOX* (*MKN*) promoter-*GUS* reporter gene fusion cassette targeted to the corresponding chromosomal *MKN* gene reveal that the expression cassette has been integrated at the correct site, and that the reporter gene is differentially expressed in the transformed moss plant, expression being absent or at an undetectable level in protonemal (filamentous) stages and conversely very pronounced in gametophore buds developing into multicellular apical meristems. This preliminary finding is exciting given the documented role of class 1 *KNOX* genes in the maintenance of SAMs in seed plants, and indicates that this function may have been conserved in plants for at least 450 million years.

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Schistidium maritimum revisited: salt tolerance and survival

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Background

Schistidium maritimum is one of the few truly halophytic mosses found in Britain and Ireland. Its blackish-green cushions are a familiar feature growing among lichens in the wave-splash zone of rocky shores. The speaker initiated studies into the ecology and physiology of this moss more than 30 years earlier as part of his PhD studies with Dr D.H. Brown at the University of Bristol (Bates, 1975). In the 1970s the emphasis had been on understanding the mechanism of salt tolerance in *S. maritimum* (then known as *Grimmia maritima*) and some other seashore mosses, such as *Tortella flavovirens* and *Ulota phyllantha*. The aims of the present paper are to present some new data that provide a fuller picture of how *S. maritimum* survives on rocky shores and to highlight factors that may limit its distribution.

Distribution and ecology of *Schistidium maritimum*

The distribution pattern of *S. maritimum* in Europe is reasonably well known. In the British Isles it is entirely coastal and strongly associated with areas that have relatively hard, non-calcareous lithology, predominantly in the west and the north. Ratcliffe (1968) classified *S. maritimum* in his 'Sub-Atlantic' category of oceanic bryophytes, and noted that its distribution corresponded with areas receiving 120-140 'wet days' per annum – an important observation. Outside the British Isles, it is common on the shores of the north Atlantic in both Europe and North America, but it also extends around the northern Pacific and is currently known from the American west coast, the Aleutian Islands, Japan and China. In Europe it is most plentiful in the north and extends into the Baltic (as var. *piliferum*). Its most southerly recorded European locality is on Ile d'Yeu

(Vendée) in western France (Boudier, 1987). It becomes increasingly rare southwards – this is not very apparent from dot distribution maps but quite clear from more local studies in different regions. In the highly exposed Shetland archipelago *S. maritimum* occurs everywhere on boulders and drystone walls, even several miles from the sea. In the Outer Hebrides, on the exposed west coast of Barra, Watson (1939) recorded it growing to an altitude of 100 ft (30 m), but noted that it was much more restricted on the sheltered east coast. Over much of the west coast of Ireland and Britain it occupies a rather narrow zone above high-water mark. In south-west England it occurs mostly in more shaded sites, or where the rock is particularly rough (especially on schists), or where there is very slight freshwater seepage. In the Channel Islands *S. maritimum* is quite noticeably restricted to such sites. Further south, in Brittany, it is even more localised. For example, on the large breton island of Belle Ile (Morbihan) it was found in only two shaded sites on pitted schist (Bates, 1989), despite an abundance of apparently suitable rocky shore habitat.

The geographical distribution pattern is mirrored within single sites in respect of aspect preference. Data (collected with Dr M.C.F. Proctor) from a raised beach platform at Start Point, south Devon, show that *S. maritimum* only occupies steeper rock surfaces when facing northwards. This aversion for sunny habitats and scarcity in southern localities is curious for a lowland species of Grimmiales, many of which occupy extremely sunny surfaces and extend much further southwards.

On the seashore *S. maritimum* occupies a distinct zone in the supralittoral, usually above mean high-water level. The height to which it reaches, as for many other shore organisms, depends on wave action: the band rises and widens where there is greater wave action. In most localities the direct physical stresses of wave impact prevent the moss from extending lower down shores, although in a few very sheltered sea lochs and saltmarshes (usually on stones) the plant is immersed by the highest tides. In all its habitats *S. maritimum* must often become saturated with seawater, and available analytical data make it clear that its cushions are rarely, if ever, free of sea-salt.

Salt-tolerance mechanisms in *Schistidium maritimum*

Salt-tolerance mechanisms in plants are now relatively well understood. Vascular species ameliorate absorbed salt by transporting it to the cell vacuoles as well as by actively pumping out salt ions. Organic acids, such as proline, are produced in the cytoplasm to balance the low solute potential of the cell vacuole and external solution so that continued water uptake is possible. A simpler mechanism seems to operate in *S. maritimum*. This involves the possession of cell membranes that maintain a high degree of impermeability to external solutes when confronted with seawater, a feature lacking in non-halophytic bryophytes (Bates, 2000). However, exclusion of salt puts the moss at risk of 'physiological drought', i.e. osmotic water loss to the external solution.

Earlier observations of rates of metabolism in *S. maritimum* during immersion in seawater (Bates & Brown, 1975) are corroborated by recent observations of photosynthetic integrity (measured by chlorophyll fluorescence using the ratio: variable fluorescence/ maximum fluorescence [F_v/F_m]). These observations show that, although desiccated *S. maritimum* can rehydrate and metabolise in seawater, the rates of metabolism achieved are far below the optimum rates obtained in salt-free conditions. Consequently, the ability to tolerate desiccation is as important a component of the halophytic physiology of *S. maritimum* as its ability to exclude salt ions. In nature, during 'hydrated' periods, its photosynthetic productivity is likely to be almost continuously challenged by osmotic stress. Thus increased inputs of freshwater from rain or seepage would be beneficial as they would raise solute potential (lowering osmotic pressure), whereas increased external salt concentrations (i.e. lower solute potential) as a result of rapid evaporation would be disadvantageous. The latter factor is probably mainly responsible for the absence of *S. maritimum* from warm and dry southern districts.

The above hypothesis is indirectly supported by observations of the colony dynamics of *S. maritimum* at St Anthony Head in Cornwall. Photographs of the same 20 x 20 cm plot in nine consecutive years show that in most instances moss colonies existing in 1995 were still present and of unchanged dimensions in 2003. Little or no *de novo* colonisation of the extensive bare rock areas was observed. These observations suggest that productivity is extremely low in *S. maritimum*, and that the successful establishment of the existing colonies was linked to the presence of rock crevices that are now fully occupied.

Summary

S. maritimum dominates the usually sparse bryoflora of salty coastal rocks by virtue of an intrinsically high impermeability to salt ions coupled with a high tolerance of desiccation. Owing to osmotic stress its net photosynthetic productivity is probably marginal for most of the time. However, few other bryophytes can withstand sea-salt, and the main associates of *S. maritimum* are seashore lichens that probably endure a similar 'subsistence' lifestyle.

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Bryophytes in a peat core from South Georgia – an ecological and climatological interpretation

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Background

There is only a restricted number of species of vascular plant in the sub-Antarctic region (26 on South Georgia), and most of these were already present directly after the deglaciation. Because of this, palynological data yield only limited palaeoecological and palaeoclimatological information. On the contrary, there are many more bryophyte species (175 mosses and 85 liverworts on South Georgia), and bryophytes are a major component of the present-day vegetation (Longton, 1988). Furthermore, many bryophytes occupy restricted ecological niches, many are sensitive to ecological and climatic change, and many extant species can be recognised in fossil deposits. Fossil bryophytes can, therefore, be extremely useful indicators for environmental reconstruction (Jonsgard & Birks, 1995).

In this account we present a summary of the bryological aspects of a study of fossil bryophytes, seeds and fruits from a continuous peat sequence near Tønsberg Point on South Georgia. The full results are presented in Van der Putten *et al.* (in press).

The island of South Georgia is situated in the South Atlantic Ocean, approximately 1,300 km east-south-east of the Falkland Islands. The northern coast is indented by deep fjords, which were formed during the Pleistocene. The climate is cold, wet and cloudy with strong winds; it is subject to rapid changes but lacks great seasonal variation (Headland, 1984). The mean annual temperature in the coldest month (August) is +2.0 °C, and in the warmest month (February) it is -1.2 °C. Mean annual precipitation is 1600 mm. Extensive peat cover has developed at lower altitudes, varying in thickness between 1 and 5 m (Smith, 1981).

Methods

In the austral summer of 1992-1993, C. Verbruggen (Ghent) and L. Beyens (Antwerp) made a geomorphological survey of the Husdal area and the peninsula near Tønsberg Point on the south side of Stromness Bay. They also located Holocene peat sequences suitable for palaeobotanical research. At 50 m altitude, they found a shallow depression, 40 m long and 25 m wide, filled with peat to a depth of 320 cm. It was separated from a nearby lake basin by a low ridge of moraine, covered by approximately 70 cm of peat. The threshold was thus *ca* 250 cm above the bottom of the depression. The sample point is only 15 m from the upper margin of the depression, close to the hillside.

The core was sampled by drilling an 11-cm diameter PVC tube into the peat. ^{14}C-analysis showed a difference in the age:sediment-thickness ratio throughout the sequence. The lowermost 140 cm represent almost 7,000 radiocarbon years, and the upper 180 cm represent the last 2,600 years. Therefore, samples for macrofossil analysis (15-20 cm^3) were taken every 20 cm from the top of the sequence (surface) to a depth of 180 cm, and every 10 cm below that. The samples were heated for 5 minutes in a 5% KOH solution and washed gently through a 250-µm mesh sieve.

The peaty sediment of the Tønsberg sequence is well preserved, and is dominated by bryophyte remains. Material was systematically examined using a stereomicroscope, and fragments of interest were picked out. Leaves and branches were counted separately. In the counts, branches were given a weighting of five and leaves a weight of one.

To summarise floristic similarities between the samples, a TWINSPAN classification (Hill, 1979) was constructed and used as a starting point to define zones in the sequence. Only small adjustments were necessary to obtain continuous and ecologically well-defined zones.

Results

Thirty-one bryophyte taxa were found in the samples. It was possible to identify many of these to species level, but some remains were too degraded and identification was possible only to genus (e.g. *Bryum* sp., *Polytrichum* sp. and *Syntrichia* sp.). *Sanionia uncinata* and *S. georgio-uncinata* could not be distinguished because the alar cells were not preserved in the fossil leaves. Interesting species include *Cephaloziella varians*, rhizoids of *Marchantia* cf *berteroana*, *Sphagnum fimbriatum* and *Tayloria dubyi*.

The TWINSPAN clusters are largely ordered according to the depth of the samples. There is one exception: at the first division the two lowest samples cluster together with the highest ones. Indeed, *Sanionia uncinata s.l.*, *Warnstorfia fontinaliopsis* and *W. sarmentosa*, three pleurocarps that dominate the species-poor samples in the upper layers, are also prominent at the base of the sequence. Based on the analysis, four clear-cut zones can be distinguished, with a transitional zone between zones 2 and 3. The four zones are based on analysis of all macrofossils, including vascular plant seeds.

Zone 1 (315-295 cm) contains three main species groups found in laminated sediments: a) species of (very) wet habitats (*Sanionia uncinata s.l.*, *Warnstorfia fontinaliopsis* and *W. sarmentosa*), b) species of eutrophic mire vegetation (*Syntrichia* sp. and possible fragments of *S. robusta*), and c) species of fellfield communities and mineral soil (*Andreaea* cf *regularis*, *Bryum orbiculatifolium*, *Kiaeria pumila* and *Racomitrium sudeticum*). This suggests that after the retreat of the ice (10,000 BP), the depression became a small pond (bordered) with a floating mat of *Warnstorfia* and *Sanionia* species, and with *Acaena-Juncus scheuchzerioides-Syntrichia* mire vegetation on the marginal slopes of the depression, surrounded by fellfield. Plant remains are presumably derived from fragments washed into the pond.

Zone 2 (295-245 cm) is characterised by *Syntrichia robusta* (and *Syntrichia* sp.). Constant species, but optimal in the transition to the next zone, are *Bartramia* cf *patens*, *Chorisodontium aciphylum*, *Conostomum pentastichum* and *Philonotis polymorpha*. This zone begins with the strongly disturbed upper part of the laminated sediments, which indicate that the pond dried up. The dry period may have lasted no more than 1,000 ^{14}C years. After this dry period a marked peak of *Pediastrum boryanum* var. *longicorne* suggests that the depression quickly became filled with water again, and became a pool serving as an overflow basin for the catchment, with species of mire peat vegetation and eutrophic seepage mire.

The transitional zone between zones 2 and 3 (245-205 cm) is characterised by *Marchantia berteroana* (rhizoids), *Bryum* cf *pseudotriquetrum*, *Ceratodon purpureus*, *Polytrichastrum alpinum* and *Tayloria dubyi*, and by the reappearance of *Sanionia uncinata s.l.*, *Warnstorfia fontinaliopsis* and *W. sarmentosa*. This suggests a mosaic of *Polytrichum-Chorisodontium* banks with drainage runnels containing *Philonotis polymorpha* and some open ground (*Marchantia*, *Bryum pseudotriquetrum*, *Ceratodon purpureus* and *Tayloria dubyi*).

Zone 3 (205-130 cm) is characterised by high values of *Polytrichum strictum*, *Sanionia uncinata s.l.*, *Warnstorfia fontinaliopsis* and *W. sarmentosa*. Species from flushes and mossbanks are no longer deposited. The sediment consists of peat with a higher organic content than the lower zones. The vegetation core was presumably part of a central floating bog, probably surrounded by mire peat vegetation. The occurrence of *Sphagnum fimbriatum* between 179 and 156 cm could indicate wetter conditions. The zone ends with a decomposed greyish layer at 156-130 cm, in which macrofossils and pollen are very fragmented and corroded. This suggests a dry period with some slope erosion (*Dicranoweisia antarctica* and *Racomitrium sudeticum*).

Zone 4 (130-0 cm) consists of the most recent deposits of a wet *Warnstorfia sarmentosa-Sanionia uncinata* bog with impoverished floristic composition. *W. fontinaliopsis* is predominant in some of the lower samples.

The deposits thus form a nice hydrosere, driven by local successional vegetation processes. The early deposits in the core reflect the species composition of the vegetation mosaic in and around the pool. Later, the vegetation at the sample point rose above the water-level, and the macrofossil composition reflects the vegetation at this point rather than the surrounding vegetation.

Correlation with climatic changes

Several events seem to be correlated with climate. The start of the sequence is associated with the disappearance of the ice cover (*ca* 9,520 BP) in a warming but unstable climate, which caused the laminated sediments. Then there is a dry period, roughly between 8,200 and 7,100 BP, followed by the increased wetness of the glacial depression after 7,000 BP; this is interpreted as a rise in precipitation. In the following period, the core shows a species-rich flora, which probably resulted from the inwash of fragments from a

complex vegetation mosaic, but may point to a climatic optimum. Finally, there is a much wetter period after 2,600 BP with an interruption at *ca* 2,250 BP.

These events are in agreement with the palaeoclimatic interpretations of Clapperton *et al.* (1989) and Rosqvist, Rietti-Shati & Shemesh (1999). The 2,600-2,250 BP event is the most striking. It concurs with the evidence summarised by Van Geel, Buurman & Waterbolk (1996) and Van Geel *et al.* (2000) for a worldwide climate change around 2,700 BP. Maley (2001) depicts the dramatic influence of this climatic event on the central African rain forests.

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Ex situ conservation of bryophytes

Jane Burch & Margaret Ramsay (Royal Botanic Gardens, Kew)

A pilot study for the *ex situ* conservation of bryophytes is being undertaken by the Royal Botanic Gardens, Kew. Funded by English Nature, Scottish Natural Heritage (SNH) and the Countryside Council for Wales (CCW), the main aim of the project is to develop techniques for the collection, propagation and basal storage of threatened UK bryophytes. The first phase is complete. Despite increasing pressure on financial resources, English Nature, SNH and CCW have agreed to fund the project for a further three years.

Three collection protocols have been produced that ensure that genetic variation is represented and that there are no detrimental effects on *in situ* populations.

Media trials using *Ditrichum cornubicum* established that ½-strength Murashige and Skoog medium solidified with Gelrite with no additional sucrose was optimal for growth. Aseptic culture is essential to reduce the possibility of contamination of liquid nitrogen when samples are in cryostorage. Novel methods for the elimination of contaminants have been developed and sterilisation protocols produced for gemmae, gametophytes and protonemata. Removal of fungi can be problematic and further research is required. Eleven Biodiversity Action Plan (BAP) species are in culture, ten in aseptic culture.

Storage in liquid nitrogen (at -196 °C) secures conservation collections on a long-term basis as the suspension of cellular metabolic activities minimises genetic drift. Cryopreservation trials established that pre-treatment with 5% sucrose and 10 μM ABA resulted in high recovery rates in the majority of bryophyte species tested. Five BAP species are now in cryostorage.

Joint NERC studies with Queen Mary College will look at the effect of these processes on the cytoskeleton and organelle organisation. Herbarium specimens are prepared at every stage during the sterilisation, cryopreservation and recovery procedures. Material of *Ditrichum cornubicum* has been shipped to Kings Park and Botanic Gardens, Western Australia as part of a cryo-exchange project investigating techniques for the establishment of duplicate gene-banks.

Initial trials have been undertaken into the 'weaning' of bryophytes out of culture and onto their natural substrate. Four species have been successfully transferred and a provisional protocol produced.

The aims of the next phase of the project will be a) to increase the number of priority species in the *ex situ* collection, b) to evaluate and extend the methods already developed, and c) to investigate methods for re-establishment (following IUCN guidelines) using material propagated and stored in the laboratory. The launch of the Francis Rose Reserve for cryptogams at Wakehurst Place, besides raising awareness of bryophyte conservation, will provide opportunities to trial reintroduction techniques for species such as *Orthodontium gracile*.

Conversazione

Following the AGM and dinner, delegates strolled back to the School of Biological Sciences. Here durian-flavoured crisps added a 'je ne sais quoi' to the general atmosphere, and were devoured with alacrity, as was a large collection of reprints kindly donated to members by Jennifer Ide. Other exhibits included a presentation on William Wilson's letters to Thomas Lyle by Mark Lawley (see abstract below), a selection of original illustrations for Eustace Jones' African Hepatic Flora brought along by Herman Stieperaere, and a poster entitled 'Reinstatement of *Plagiochila maderensis*, a liverwort endemic to Madeira, based on phytochemical, phylogenetic and morphological evidence' by David Rycroft, H. Groth and J. Henricks (Glasgow and Göttingen).

A particular treat was a tour of the largest concentration anywhere in Britain of rare and endangered bryophytes: the cultures in the Queen Mary/Kew *ex situ* programme. Silvia Pressel was literally rushed off her feet as everyone wanted to see protonemal gemmae in *Didymodon glaucus*, *D. tomaculosus*, *Ditrichum plumbicola*, *Seligeria carniolica* and *Zygodon gracilis*.

William Wilson's letters to Thomas Lyle

Mark Lawley (Ludlow)

A request recently appeared on the website 'Bryonet' for information about William Wilson (1799-1871), author of *Bryologia Britannica* (1855) – 'the prince of bryological books'. This request came from Nancy Hoffmann in New Zealand, who is descended from Thomas Lyle (1791-1859). As an amateur bryologist, Lyle corresponded with Wilson during the 1840s and 1850s. Nancy possesses Wilson's hand-written letters to Lyle, which are hand-bound into two volumes, and she has kindly scanned and sent images of many of these letters to me (compact disc available).

According to Desmond's *Dictionary of British and Irish botanists and horticulturalists* (2nd ed., 1994), Lyle's letters to Wilson are at the Natural History Museum here in London. It would be advantageous for historians of bryology to have the text of Wilson's letters accessible for examination alongside Lyle's, as otherwise it is rather like reading a book with only the text on the left-hand pages visible.

In return for information about Wilson, Nancy also sent me details of Lyle's background and life, which add considerably to the sketchy information previously available. Lyle was probably born on 16 August 1791 in Kilmacolm, near Paisley, Renfrewshire, the son of Robert (*ca* 1764-1793), who was a farmer, and Mary (*née* Cochrane, 1765-1797) of Paisley. Thus, Thomas (along with his elder brother John and younger sister Anne) lost both parents in young childhood. John served in the 91st Argylls, was almost certainly at Waterloo, escorted Napoleon to exile in Elba, and died of yellow fever in Jamaica in 1822.

Nothing further is known of Thomas's childhood. Perhaps he was brought up by relatives in Kilmacolm, Paisley or Glasgow. He qualified as a surgeon in 1816, after studying at Glasgow. In 1821 he married his first cousin, Margaret Cochrane (1796-1854), by whom he had eight children between 1822 and 1835. He practised at Airth in Stirlingshire for at least a decade after 1830,

as well as in Glasgow, where 'in 1856 he pursued his vocation in High Street, a little below the Bell o' the Brae'.

Lyle was also a poet and lyricist, now remembered for the beautiful song 'Let us haste to Kelvin Grove, bonnie lassie, O', which was first published anonymously in the *Harp of Renfrewshire* in 1820, with an amended version included in *Ancient ballads and songs* (1827), a volume which Lyle himself edited.

Lyle died on 19 April 1859. No will has yet been found. Desmond (1994) states that his mosses and letters are in the Wilson correspondence at the Natural History Museum, and 'plants at Paisley Museum'. Nancy Hoffmann also has an 'exquisite book full of watercolours of mosses, meticulously catalogued … a work of art in itself'. The compact disc also carries details of Lyle's 'Illustrated lichens of Airth district, 1842'.

Field excursion to Mereworth Woods and the Medway Valley Walk, 7 September 2003

A mini-bus journey of less than an hour through the Blackwall Tunnel and passing the infamous Millennium Dome saw members in deepest Wealden countryside (West Kent, v.-c. 16) for the day's two venues. The field trip was led by Roy Hurr and Jeff Duckett.

The morning excursion was to Mereworth Woods, an extensive area of ancient woodland, *Castanea* coppice and plantation on Kentish ragstone. Although, consequent on the long summer drought, nothing of note was found in the stubble fields en route to the woods, arabological frustration turned to delight when damp rides and banks within the woods revealed *Fossombronia pusilla*, *Jungermannia hyalina*, *Scapania irrigua*, *Archidium alternifolium*, *Cratoneuron filicinum*, *Dicranella schreberiana*, *D. staphylina*, *Ephemerum serratum* var. *minutissimum*, *Hypnum lindbergii*, *Pohlia annotina*, *P. wahlenbergii* and *Scleropodium tourettii*. David Long produced an impromptu masterclass on separating *Riccia glauca*, *R. sorocarpa* and *R. subbifurca**.

The bryophyte flora of the old sweet chestnut coppice stools mirrored that of hornbeam woodlands in Hertfordshire, with all three British *Orthodicranum* species (*D. montanum*, *D. tauricum* and *D. flagellare*); the last species was seen for the first time by many members. Herman Stieperaere demonstrated protonemal plates on *Tetraphis pellucida c.fr.* Epiphytes on the bases of ash included *Anomodon viticulosus* and *Homalia trichomanoides*, and Tom Blockeel found *Heterocladium heteropterum* var. *flaccidum* and *Plagiothecium latebricola* on pieces of ragstone protruding through the woodland floor.

After lunch, in pleasant early autumn sunshine, the party explored the environs of the River Medway from East Peckham. As we strolled along the river bank, mutterings that 'this is just the place for *Hennediella macrophylla** but it isn't known for West Kent' changed to more animated cries: 'it is now!'. Bare mud in old pits was completely overgrown by willow and alder and yielded only *Leptodictyum riparium*, while *Cinclidotus fontinaloides*, *Dialytrichia mucronata*, *Leskea polycarpa*, *Scleropodium cespitans* and *Syntrichia latifolia* grew on stonework and trees by the river. A battle through two-metre nettles to explore old elders added *Bryum laevifilum*, *Cryphaea heteromalla*, *Orthotrichum lyellii*, *Ulota bruchii*, *U. crispa*, *U. phyllantha* and *Zygodon viridissimus* var. *viridissimus* to the card, but in striking contrast to apparently similar elders seen on the Norfolk/Suffolk meeting in the spring of 2003, there was not a single tuft of *Orthotrichum pulchellum*.

The mini-bus group was transported back to London to catch their trains after a most enjoyable weekend. It was generally felt that Queen Mary would be an excellent venue when next the Society seeks a London location.