

BBS Annual Meeting and Conference

6-9 September 2013

Jeff Duckett reports on last year's Autumn Meeting held at the Natural History Museum, London



The 2013 Autumn Meeting at the Natural History Museum, London completed the capital ring after Edinburgh, Cardiff and Dublin. Council, Publications and Conservation Committee meetings were held on the Friday afternoon and evening in the Natural History Museum. 40 participants (a slightly lower number than at the last London Annual Meeting (Duckett, 2011)) attended the main programme of talks followed by the AGM on the Saturday. They were treated to an exceptionally eclectic range of presentations, including two from overseas speakers, as listed below:

Shoring up the foundations: preserving the critical features of moss type specimens for posterity Len Ellis, Natural History Museum London

Hornwort biology and evolution: structural innovations for life on land Juan Carlos Villarreal, University of Munich and Botanische Staatssammlung München, Germany

The island syndrome in bryophytes Jairo Patiño, University of Liège, Belgium

Bryophytes of Ascension Island Silvia Pressel, Natural History Museum London

Cryptic species and taxonomic practice in bryophytes Harald Schneider, Natural History Museum London

Mount Washington: snowbeds and climate change Jeff Duckett, Natural History Museum London

Epiphytic bryophyte diversity in orchard habitats Mari Whitelaw, University of Hertfordshire

The Society would like to thank all the staff at the Museum for contributing to the success of the meeting. The meeting rooms and food were excellent and all participants found their way around sundry dinosaurs and other dead large animals to the correct venue.

Excursion to Wimbledon Common

On Sunday 12 people joined the excursion to Wimbledon Common where over 40 taxa were seen. Though far less varied than Hampstead Heath (Duckett & Pressel, 2009), the Common still boasts a range of interesting taxa with pride of place going to *Pallavicinia lyellii* in a long known locality on one of the bogs that also harbours 5 species of *Sphagnum* (Gardiner, 1981).



△Above left: Smiles all round after Peter Howarth located *Pallavicinia*. J. Duckett. △Above right: *Pallavicinia lyellii*; note the female inflorescences. J. Duckett

Peter Howarth, with unerring accuracy, led us straight to the first colony growing around moribund *Molinia* tussocks with *Campylopus flexuosus*, *Calypogeia fissa* and *Cephalozia connivens*. Several further colonies were found and the species appears to be thriving. We do however, recommend periodic lopping of the tussocks to maintain the *Pallavicinia* niche. In contrast to quantities of male only *Pellia neesiana* growing nearby, all the *Pallavicinia* plants were female thus explaining the absence of sporophytes in both species.

The epiphytes on the Common closely mirror those on Hampstead Heath (Duckett & Pressel, 2009) and attest to the positive effects of the Clean Air Acts both north and south of the Thames. Ken Adams demonstrated the difference between *Orthotrichum tenellum* and *O. affine* growing on the same oak tree whilst other trees harboured *O. lyellii*, *O. pulchellum*, *Cryphaea heteromalla*, *Ulotia crispa* and *Frullania dilatata*. In contrast to their decline in Ted Wallace's lifetime of bryology in Surrey (Duckett, 2008; Wallace, 1955) all these species are now increasingly common in London.

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Braithwaitea sulcata (Hook.) A.Jaeger & Sauerb.



△Figure 1. On the left, the type of *Braithwaitea sulcata* (Hook.) A.Jaeger & Sauerb. attached to an herbarium sheet, the left hand shoot is the lectotype. On the right of the figure is Hooker's original illustration of the type shoot.

Shoring up the foundations: preserving the critical features of moss type specimens for posterity

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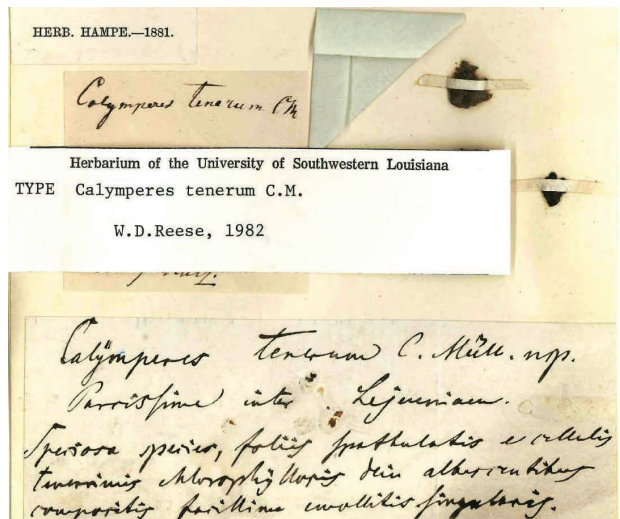
Original specimens of a vast proportion of moss taxa have survived in herbaria for two centuries or more; they may be obscurely labelled and difficult to relate to a deficient protologue. Careful lectotypification may also be required. However, even when typification has been resolved (spiritual), the venerable, taxon-underpinning type specimen (corporeal) is frequently not in the best physical shape or in sufficient quantity to survive further centuries of taxonomic investigation.

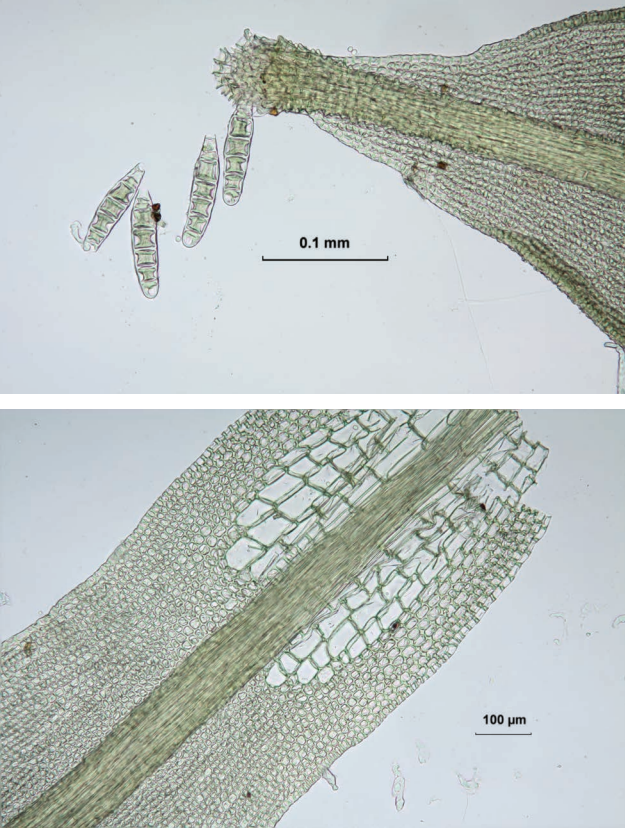
The bryophyte collections held in The Natural History Museum, London are rich in type specimens, mostly collected in the 19th Century and earlier. For example, the original material of *Braithwaitea sulcata* was collected over 200 years ago by Robert Brown in Australia, and described by W.J. Hooker in 1819. The exact shoot illustrated by Hooker to accompany his original description of the species is recognisable, mounted on a sheet in Hooker's herbarium (BM) (Fig. 1). This single ancient shoot on the left of the specimen serves as the lectotype for *B.*

sulcata.

It is in the nature of moss specimens to be small and fragile, and yet they will be vulnerable to the wear and tear of repeated invasive, potentially destructive examination in the cause of scientific enquiry. To reduce the need for potentially destructive investigation of the museum's moss type specimens, a programme has been piloted to obtain digital images of their critical microscopic features. The images are retained with their specimen record in the museum's collections database, and ultimately, will be made available

▽Figure 2. The type specimen of *Calymperes tenerum* Müll. Hal., no salient features of the plant are visible.





△Figure 3, top. Leaf apex from the type of *C. tenerum*, showing an excurrent costa and some associated gemmae. Elisa Cane. Figure 4, bottom. Leaf from the type of *C. tenerum*, showing hyaline lamina with bands of short, broad marginal cells. Elisa Cane

on the internet.

Our project has begun with a study of the pantropical moss family, Calymperaceae. Macroscopic images of our type specimens, such as that of *Calymperes tenerum* Müll.Hal. (Fig. 2), are already available to researchers on the internet, but as can be seen from the figure, only peripheral data associated with the specimen is visible. For the sake of longevity of this vital material, making available its critical microscopic features, such as the form of the leaf apex (Fig. 3) and leaf base (Fig. 4) is essential.

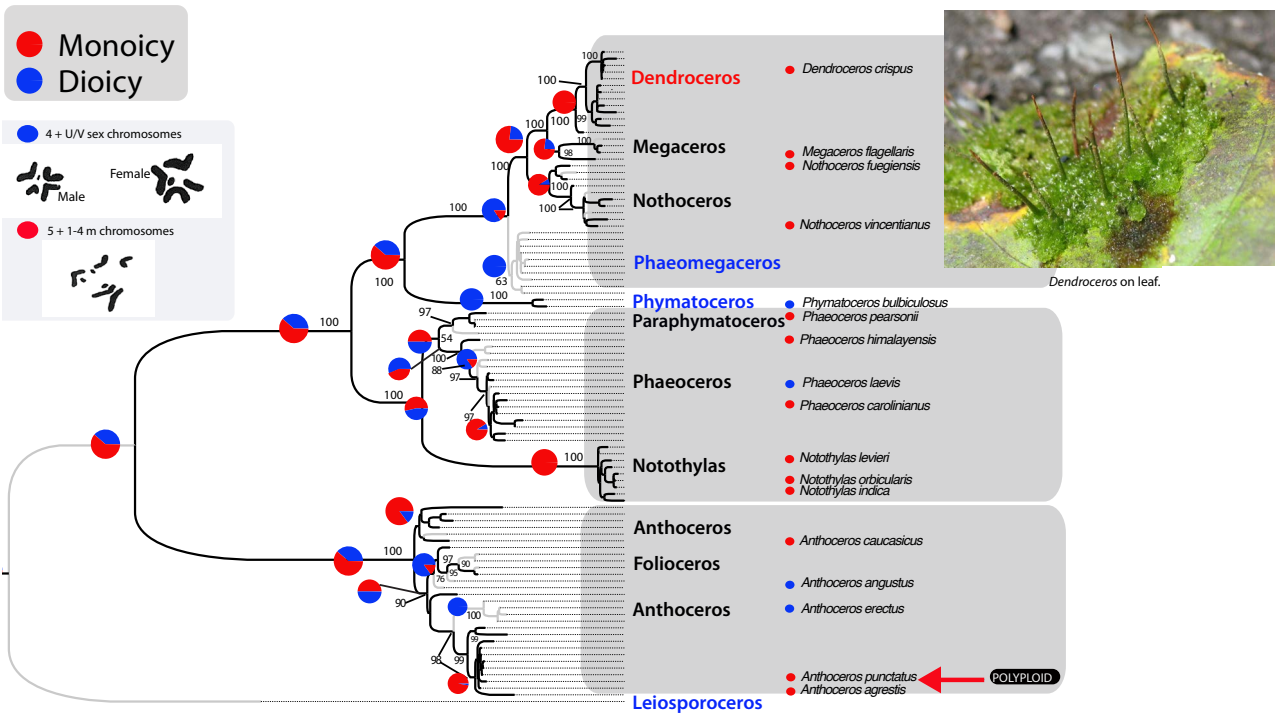
New insights on early land plant diversification: pyrenoid evolution and sexual system of hornworts

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Among bryophytes, the hornworts have the

most perplexing combination of features (e.g. solitary chloroplasts with pyrenoids, sporophytic basal meristem, stomata, asynchronized meiosis). Their unique and consistent morphology along with the small number of extant species would lead one to believe that the biology of the group has been well characterized, leaving little left to do. Recent studies have shown the opposite (Sayou *et al.*, 2014; Desirò *et al.*, 2013; Cox *et al.*, 2014; Li *et al.*, 2014; Liu *et al.*, 2014; Pressel *et al.*, 2014). A complete review of hornwort biology is being prepared by myself and Karen Renzaglia for *Journal of Bryology*. I focused on two topical studies: evolution of hornwort pyrenoid and sexual systems in hornworts.

Hornworts are thought to have diverged from their sister group, the vascular plants, in the Silurian, but no within-hornwort dating has been attempted. During the BBS meeting, I presented a plastid/mitochondrial tree that includes 36% of the c. 200 species representing 12 genera and calibrated strict or relaxed clocks, using average substitution rates or fossil calibrations with broad priors (Villarreal & Renner 2012). I reconstructed the evolution of the hornwort pyrenoid, the physical aggregation of the enzyme RuBisCO inside of the plastid and the site of a biophysical carbon concentrating mechanism in algae. The DNA clocks date the hornwort crown group to 308 mya, their split from the vascular plants to 460 mya (Silurian), and most genus-level crown groups to <60 mya; most species are but a few million years old. Pyrenoids evolved 5-6 times, fitting with their different morphologies, and were lost at least 10 times. The independent and relatively recent gains and losses of hornwort pyrenoids suggest that a pyrenoid-based CO₂-concentrating mechanism may be an adaptation to wet habitats, rather than low atmospheric gas levels. Experimental studies are needed to elucidate how pyrenoids may function in



△Figure 1. Chromosome number and evolution of sexual systems in hornworts, modified from Villarreal & Renner (2013, Fig. S1). Maximum likelihood tree for 98 species of hornworts (from Villarreal & Renner 2013) with ancestral reconstruction of sexual systems (mapped as proportional likelihoods in pie diagrams above nodes). States for each terminal node are given for the following traits: sexual system (monoicous (red) or dioicous (blue)). Chromosome counts are mapped onto the tree for monoicous species (red circles) and dioicous species (blue circles). Entire monoicous or dioicous genera are colour-coded and the main families are included inside of grey boxes. *Anthoceros punctatus* has the karyotype of a monoicous species and is a natural polyploid. Inset: The karyotypes of the dioicous *Phymatoceros bulbiculosus* from Portugal and of the monoicous *Nothoceros vincentianus* from Peru (listed as *Megaceros* sp. in the original paper, later identified by Proskauer as *Megaceros vincentianus*). Dioicous species typically have four chromosomes and one U/V sex chromosomes (the U chromosome slightly larger). Monoicous species typically have 5 large chromosomes with numerous (1-5) “m” or accessory chromosomes that can vary within a single gametophyte (modified from Proskauer 1957). Photo by S. Pressel and J.G. Duckett

thylakoid membrane formation and concentrate carbon under different environmental conditions. Another understudied aspect of hornwort biology is the evolution of sexual systems. A recent study (McDaniel *et al.*, 2013) evaluating the distribution of separate and combined sexes in mosses on a sparsely sampled genus-level phylogeny found a higher transition rate from monoicy to dioicy. I presented a phylogeny for 98 of the 200 species of hornworts, representing roughly equal proportions of all monoicous and dioicous species, to test whether a similar trend exists in the sister group to the vascular plants (Villarreal & Renner, 2013). We further tested whether a correlation between small spores and

dioicy found in mosses holds in hornworts. A trait correlation analysis on 5000 Bayesian trees weakly supported such a correlation, as did simulations; a contingency test then revealed that, while sexual system depends on spore size, the opposite is not the case. Selection for numerous spores in dioicous species may explain this finding, although we found no evidence for increased antheridium-per-chamber numbers in dioicous species. Differently from mosses, the transition rate from dioicy to monoicy in hornworts exceeds that in the opposite direction. An analysis of character state associated diversification shows that monoicous lineages tend to have a higher extinction rate than dioicous

lineages. Another correlation important in mosses, that between monoicy and polyploidy, apparently plays a small role in hornworts; of 20 species with chromosome counts, only one is polyploid, the monoicous *Anthoceros punctatus*. The recently published studies of hornworts have opened new avenues to explore and have pointed to the importance of exploring hornwort diversity at a global scale. The hornworts play a crucial role in evolutionary studies and their basic biology and taxonomy are still crudely known, particularly in Neotropical areas.

I thank Silvia Pressel and Jo Wilbraham for the invitation to the BBS meeting. Thank you to Karen Renzaglia and Jeff Duckett for fruitful discussions on hornwort biology.

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The island syndrome in bryophytes

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Island biotas exhibit a variety of biological, ecological and physiological traits that are commonly known as island syndromes. These phenomena result from the unique particularities of insular systems such as the high geographical isolation and low levels of interspecific competition in comparison with continental regions. Despite experimental support for this prediction being equivocal, island biogeography

theory predicts that insular organisms typically lose their dispersal power (Whittaker & Fernández-Palacios 2007). One of the potential explanations is that dispersal over water masses from isolated islands might *a priori* represent an unnecessary energetic cost with low chances of colonization success for organisms that are well adapted to the often climatically buffered insular environments.

A group of researchers, including Jairo Patiño, Alain Vanderpoorten, Irene Bisang, Lars Hedenäs, Gerard Dirkse, Agust H. Bjarnason



△Left. Sporophyte and specialized vegetative diaspores of *Leucodon sciuroides*. L. Hedenäs. Right. *Leucobryum glaucum* and the Macaronesian endemic *Plagiochila maderensis*, for which sexual reproduction is unknown in the Canary Islands. M.A. Peña

and Claudine Ah-Peng, recently published a study to determine whether typical reproductive island syndromes apply to bryophytes. They performed an extensive literature survey, which was combined with actual observations of populations, to compare life-history traits across continental, continental island, and oceanic island floras. The main aim was to investigate if Baker's law applies to bryophytes, being that there is a higher number of bisexual species on islands than on continents owing to the severe constraints imposed on fertilization after long-distance dispersal events. The study also examined if there is a tendency towards increased asexual reproduction and decreased sexual reproduction on islands.

Information on mating systems, production of sporophytes and specialized asexual diaspores were collected in three data sets. The first data set resulted from the scoring of life-history traits for island and continental floras worldwide. In total, sixty-three moss and liverwort floras

were selected on the basis of the availability of recent and updated information on species lists and reproductive traits. For the second data set, life-history traits in pairs of conspecific populations between islands and the nearest continent were scored. In the last data set, four unisexual moss species broadly distributed in Madeira, the Canary Islands and the Iberian Peninsula were selected to contrast their life-history traits on islands and on continents based on actual specimen observations. We selected two species known to produce sporophytes but not specialized asexual diaspores (*Isoetecium myosuroides* and *Leptodon smithii*) and two species capable of producing both sporophytes and specialized asexual diaspores (*Leucodon sciuroides* and *Orthotrichum lyellii*).

The life-history traits observed in oceanic island floras were significantly different from those observed on continents. In contrast, life-history traits of continental and continental island floras were quite similar, pointing to



differences in migration intensity between continents, continental islands and oceanic islands. Interestingly, the proportion of bisexual species in the floras examined was higher on oceanic islands than on continents. A significant proportion of species that are unisexual or bisexual on continents shifted towards exclusive bisexuality on oceanic islands, suggesting that Baker's law could apply to bryophytes. However, the underlying mechanisms are probably driven by environmental filters rather than by *in situ* selection for selfing.

The proportion of species producing specialized asexual diaspores, which are assumed to play a role in short-distance dispersal, was higher on oceanic islands than on continents. On the other hand, the proportion of species producing spores, which are involved in long-distance dispersal, exhibited the opposite tendency, suggesting a shift in the prevalent reproductive strategy to favour short-distance dispersal on oceanic islands. Approximately 50% of the species, however, maintained the ability to produce sporophytes on oceanic islands, and the relative frequency of fertile shoots within collections of four model species (*I. myosuroides*,

L. smithii, *L. sciuroides*, *O. lyellii*) was even higher on the Macaronesian islands than on European continental landmasses.

This study concluded that bryophytes exhibit typical island syndromes, demonstrating that migration rates between oceanic islands and continents are not sufficient to prevent the effects of genetic drift and therefore contradicting the view that the sea does not impede migration in bryophytes. Indeed, significant shifts in particular life-history traits towards increased production of specialized asexual diaspores and decreased sporophyte production on oceanic islands point to a 'global' loss of long-distance dispersal ability. The maintenance of sporophyte traits typically involved in long-distance dispersal in a large number of species has, however, important consequences for the understanding of island bryophyte evolution and the role of oceanic islands as possible sources of biodiversity for continental floras of bryophytes. I wish to thank Silvia Pressel and Jo Wilbraham for the invitation to attend the BBS meeting, and the colleagues that collaborated in the present study.

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Cryptic species and taxonomic practice in bryophytes

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For more than 200 years, plant taxonomy relied on the assumption that the origin of species coincides with the establishment of morphological variation, which provides the information required to distinguish species using morphological diagnostic characters.

This assumption is arguably the most critical component in the widely employed “morphological-typological species concept” (MTS). However, this crucial assumption has never been tested although empirical evidence suggests that the assumption is misleading at least in some cases. Among the different cases rejecting this assumption, cryptic species provide arguably the strongest evidence because the origin of cryptic species illustrates the independence of the assembly of species diversity and morphological disparity (Schneider, 2013). As a consequence, alternative concepts to the application of integrative taxonomy have been promoted (Dayrat, 2005; Schneider, 2013).

With the recognition of cryptic species in the hornwort genus *Megaceros* (Cargill *et al.*, 2013), cryptic species have now been recorded for all three lineages of bryophytes. Cryptic liverwort species were recorded for about 15 genera including representatives of each major lineage, whereas cryptic moss species were recognized for about 15 genera belonging mainly to derived lineages (e.g., Shaw 2002; Heinrichs *et al.*, 2009a, b). However, several studies showed that some of these reported cryptic species may actually represent semi-cryptic species because they may be recognized by using micro-morphological evidence or by the application of phenetic methods allowing the recognition of less visible unique character combinations (e.g., Vanderpoorten & Shaw, 2010; Renner *et al.*, 2013). Thus, the issue of cryptic species may be at least partly resolved by replacing a rather simplified application of the MTS (using easily observable morphological features) with a more comprehensive analysis based on a much greater detailed description of the plant body than is regularly done in traditional plant taxonomy.

Only a few studies have addressed this issue using a different approach. So far, we neither

know the frequency of cryptic species nor their distribution in the phylogeny of bryophytes. Based on theoretical arguments, divergence between the assembly of species diversity and morphological disparity may be linked to two main factors (Schneider, 2013). Firstly, speciation in extreme habitats may increase the probability of cryptic species because trait selection may reduce the morphological variation allowing the survival of the newly formed species. Secondly, limitations of the development program may reduce the morphological variation among closely related species. Recent studies focusing on the mainly epiphyllic liverwort genus *Cololejeunea* provided some evidence supporting the hypothesis that the establishment of cryptic species may be more frequent in bryophytes colonizing extreme habitats (Yu *et al.*, 2013a, b, 2014). However, the existing evidence is insufficient and exhaustive studies exploring evidence for cryptic species across the phylogeny of all three lineages of bryophytes are urgently required. Only such studies will enable us to obtain the resources necessary to replace a bryophyte taxonomy using mainly MTS with more comprehensive approaches such as integrative taxonomy, as for example applied to the *Radula buccinifera* complex (Renner *et al.*, 2013).

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△Top. The Slack team recording snowpatch vegetation surrounded by Krumholz. J. Duckett

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Alpine Bryophytes of Mount Washington, New Hampshire, USA

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In the summer of 2012 I was privileged to join Nancy Slack and her research team who were mapping the vegetation of the snow beds on Mt Washington, New Hampshire (Slack & Bell, 2013). My principal roles were liverwort identification and to search for *Haplomitrium hookeri*.



△Top. The Ice Gulch. J. Duckett

Mt Washington, in the Presidential Range stretching across Maine, New Hampshire and Maine is the highest peak in the Northeastern United States at 6,288 ft (1,917 m). For many years the summit held claim to the highest wind gust directly measured at the Earth's surface at 231 mph, on the afternoon of April 12, 1934; at which point the equipment broke. Indeed, it is an inhospitable place with winds exceeding 100mph every month and temperatures ranging between 9 degrees in July to minus 15 in January. The mountain is granite pluton (New Hampshire is the aptly named "Granite State" and even more forbidding is the state motto, "Live Free or Die") and, save for occasional base-rich dykes, is exceedingly acid. Above 600m the fragile alpine zone supports a myriad of flowers including *Linnaea borealis*, over 15 members of the Ericaceae and magnificent Krumholz of balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) where continual exposure to the fierce freezing wind causes the trees to become stunted and deformed (Slack & Bell, 2013).

Unlike the rich and varied bryophyte flora

of the Scottish mountains Mt Washington is somewhat species poor and bryologists hoping to see an array of *Grimmias* and *Andreaeas*, apart from *G. donniana* and *A. rupestris*, given the acid substrate, will be greatly disappointed. Highlights of the snow patch areas include quantities of *Aulacomnium turgidum*, *Dicranum elongatum*, *Kiaeria starkei*, *Pseudocalliergon trifarium*, *Rhytidium rugosum*, *Ptilium crista-castrensis*, *Tetralophozia setiformis*, *Anastrophyllum minutum* and *A. saxicola*. Soil on the exposed ridges is covered by extensive white carpets of *Gymnomitrium concinnatum* and *G. coralloides* whilst rocky outcrops, dominated by *Racomitriums*, also support *Arctoa fulvella* and *Conostomum tetragonum*.

Perhaps the richest exciting bryophyte locality is the so-called Ice Gulch where the topography of a narrow boulder-filled ravine maintains low temperatures throughout the year and many of the species listed above also occur some 1000m below the summit surrounded by thick forest. Most notable perhaps are quantities of *Hylocomiastrum pyrenaicum* and *Kiaeria*

blyttii with *Anastrophyllum michauxii* and *A. hellerianum* (on rotten logs) in addition to the 2 species in the alpine zone.

Whereas British bryologists are very familiar with *Haplomitrium hookeri* growing in a variety of niches including below late snow patches (Atherton *et al.*, 2010; Hill *et al.*, 1991), it is inexplicably rare in Eastern North America despite many apparently suitable habitats (Worley, 1969). It was originally found by Evans (1917) in the Huntingdon Ravine on Mt Washington, and subsequently at the base of Mt Katahdin in Maine by Schuster (1966, 1967), in both places growing with *Pellia neesiana*. Verdoorn subsequently looked for the plant at Evans' locality but was unable to find it and Schuster spent the rest of his life searching in vain for new localities in New England. After nearly a week on Mt Washington I shared Schuster's frustration having crawled around just about every likely habitat across the alpine zone. Finally I thought to explore one of the major ravines, the Tuckerman. Half way down the headwall of this north facing corrie is a wide waterfall and here, on vertical dripping rocks, are scattered shoots of *Haplomitrium* growing with *Cephalozia bicuspidata*, *Scapania undulata* and *Solenostoma hyalinum* and the mosses *Blindia acuta*, *Philonotis fontana*, *Poblia nutans*, *Racomitrium fasciculare* and *R. heterostichum* (Duckett & Slack, 2013). Considering these mundane associates we might now look for *Haplomitrium* in similar places in Britain.

Apart from appealing to my hunter-gatherer instincts the quest for *Haplomitrium* also had a more scientific purpose, namely to collect a sample of the underground axes for analysis of its fungal endophyte (Pressel *et al.*, 2012). Subsequent sequencing by William Rimington and Martin Bidartondo has now revealed

that this fungus almost exactly matches the mucoromycote found in *Haplomitrium* in Britain, S E Asia and New Zealand (Bidartondo *et al.*, 2011). This finding supports the Ancient Pangean origins of the association over 400 millions of years ago whilst physiological studies, as part of an ongoing NERC research project shared between the Natural History Museum, Imperial College, Kew and Sheffield University, have now established it to be truly symbiotic with exchanges of carbon, nitrogen and phosphorous between the partners in a similar manner to the mucoromycote association in *Treubia* from New Zealand (Field *et al.*, 2014), the sister genus to *Haplomitrium*, at the foot of the land plant tree of life (Crandall-Stotler *et al.*, 2009) dating back 470-480 millions of years ago.

Our symbiosis studies have revealed that mucoromycote fungi are widespread in thalloid liverworts and hornworts (Desirò *et al.*, 2013) and, most remarkably, also occur in Devonian fossils (Strullu-Derrien *et al.*, 2014) thus overturning the long held view that glomeromycotes were the first land plant fungal symbionts. Also growing on Mt Washington are numerous *Lycopodium* species: sequencing of their fungi (14 samples from 7 species) has now shown that these like hornworts and liverworts contain both mucoromycote and glomeromycote endophytes (Rimington *et al.*, 2014).

A final dimension to the Mount Washington expedition was collecting basidiomycete-containing leafy liverworts to see if the genetic diversity and species specificity in the endophytes mirrors that in Britain and the Alps (Bidartondo & Duckett, 2010). I was able to prepare 70 samples from 18 leafy liverwort species in the genera, *Barbilophozia*, *Leiocolea*, *Lophozia*, *Nardia*, *Scapania* and *Tritomaria*, common to Europe and North America. Unfortunately

Diplophyllum taxifolium, the only species in the genus found on Mt Washington, is fungus-free (Paton, 1999), unlike *D. albicans* and *D. obtusifolium*.

Acknowledgements

I thank Nancy Slack for inviting me to join her snowbed team supported by the 2012 award for alpine research on Mt Washington from the Waterman Fund. The fungal endophyte studies were made possible by an Emeritus Fellowship awarded to me by the Leverhulme Trust.

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▽ Below. The Tuckerman Ravine (actually a big corrie). J. Duckett



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Epiphytic bryophyte diversity in orchard habitats

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Orchard habitats have been described as biodiversity hotspots, home to a wide range of organisms. The diversity of epiphytic bryophytes in orchards lead, in part, to the creation of the UK Habitat Action Plan for traditional orchards. In this seminar I discussed the diversity of epiphytic bryophytes recorded in Hertfordshire orchards and some of the factors which may influence this diversity.

The data presented here showed that orchards represent variable but still valuable habitats for epiphytic bryophytes. A selected survey of Hertfordshire orchards recorded 38% of the known epiphytic bryoflora for the county. Factors which influence the diversity and distribution of bryophytes in orchards were investigated including tree and substrate variables. Within the same orchard, different apple varieties were found to have very different bryophyte cover and

this was accompanied by significant differences in bark pH. However, pH was found to be of low importance in explaining the distribution of epiphytic bryophytes on a single variety across orchards.

In-depth surveys of Bramley trees showed that across orchards, tree structure, as determined by management, explained about 10% of the observed variation in bryophyte cover. Trunk girth and distance to nearest neighbouring orchard trees were the most important factors. Site was found to be the strongest influence on epiphytic bryophyte distribution in the orchards.

Bryophytes of Ascension Island

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See 'Bryophytes Abroad' article on pp. 38-51 of this issue of *Field Bryology*.