Article

Harold Whitehouse (1917–2000): His Life and Legacy

△Fig 1. Harold Whitehouse.

Jeff Duckett sets the life of a distinguished bryologist in the context of the academic world of his time

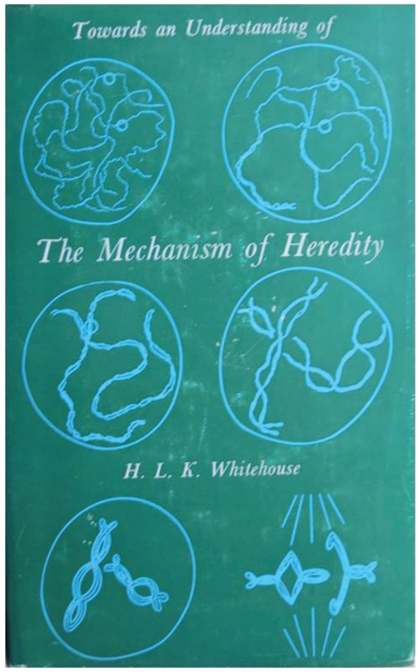
'There's some corner of an arable field that is forever England'

Apart from some remarks, from a personal perspective, about Harold Whitehouse's scientific activities in the 1960s and their effects on my subsequent botanical career, rather than repeat in this account what has previously been written about Harold (Fincham, 2000; Hill & Preston, 1997; Hill, 2000; Lawley, 2018; Preston, 2001, 2002; Proctor, 1984) I have focused here on contextualising his life and wider achievements in terms of university life from his student years in the 1930s to the end of the twentieth century and also publish images that have not appeared in previous accounts of Harold's life. In addition to a few personal anecdotes, this account is also a vignette of what academic life in Britain used to be like. In retrospect, it is now very clear that Harold's career spanned a period of remarkable stability in British universities and this undoubtedly shaped what he did. Had he started out 20 years later things might have been very different.

On Saturday 7 October 2017 my drive from London to the BBS AGM and Paper Reading meeting in Cambridge took me past Therfield (Royston) Heath and the village of Gransden. Both names were especially poignant to two facets of the presentation I was about to deliver on the Life and Legacy of Harold Whitehouse. When Harold's bryophyte excursions strayed beyond Cambridgeshire, Therfield was a delightful chalk grassland site in nearby Hertfordshire. As I recall, from the 1960s, it was particularly good for *Didymodon acutus* which Harold had taught participants in his excursions to separate in the field, even from just one or two stems, from other *Didymodon* species and *Dicranella varia*. Gransden Wood, Huntingdonshire must now be amongst the most cited bryophyte localities in the world: it was here in 1962 that Harold collected *Physcomitrella patens* (Fig. 2) and established cultures from a single spore. The culture he then gave to David Cove became the 'Gransden strain' of the model moss subsequently used worldwide and now cited in over 20,000 publications. Recent papers on cold tolerance (Tan *et al.*, 2017) photoreceptors (Soriano *et al.*, 2017) polyketide synthase (Li *et al.*, 2017) and MADs-box genes (Barker & Ashton, 2016) underline the current eclectic use of this strain.

Back in 1962 *Arabidopsis thaliana* was the only other axenically cultured land plant used extensively for genetics research and there were not very many other widely used model organisms. These included two unicellular algae, *Chlorella* and *Chlamydomonas*, yeast (*Saccharomyces cerevisiae*), fruit fly (*Drosophila melanogaster*), western clawed frog (*Xenopus tropicalis*) and mouse (*Mus musculus*). The development of the zebrafish (*Danio rerio*) and nematode worm (*Caenorhabditis elegans*) from the 1960s more or less paralleled that of *Physcomitrella* which was chosen initially almost solely on the basis of its very short life cycle of 10–12 weeks from spore to spore. David Cove and his colleagues, particularly Neil Ashton, soon found out that it was easy to produce mutants in *Physcomitrella* and that it was simple to transform and to carry out somatic hybridisation using protoplasts (Ashton & Cove, 1977; Ashton *et al.*, 1979a, b; Featherstone *et al.*, 1990; Grimsley *et al.*, 1977a, b). The subsequent discovery that targeted gene-knockouts can be made efficiently in the laboratory facilitated the development of reverse-genetics (Hohe *et al.*, 2004; Martin *et al.*, 2009; Mittmann *et al.*, 2004). It should also be noted, however, that there is an extensive list of drawbacks from using *Physcomitrella*; it is monoicous, making controlled crossing problematic, it has a large genome and is polyploid, asexual propagules have never been

▽Fig. 2. A sward of *Physcomitrella patens.* J. G. Duckett.



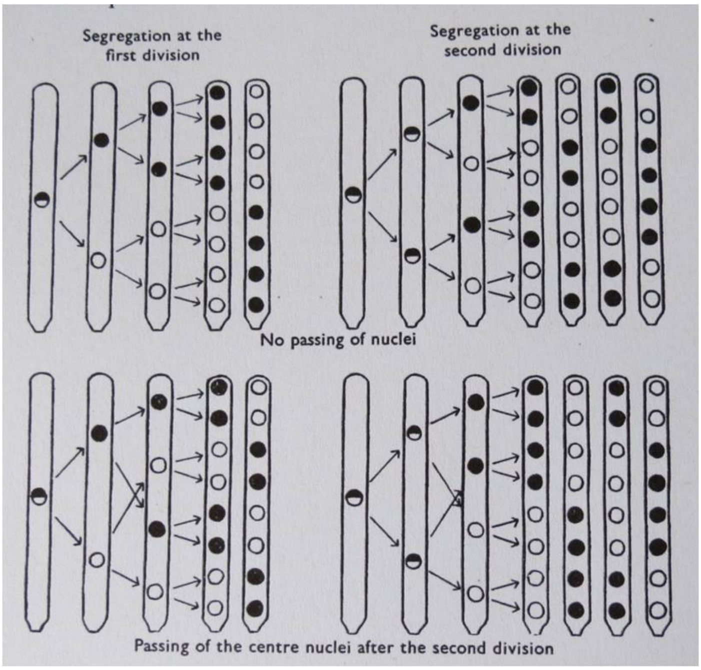
▷Fig. 3. Harold's book *Towards an Understanding of the Mechanism of Heredity* ran to 3 editions (cover, left; illustrations in text, right). All the illustrations had to be meticulously drawn by hand.

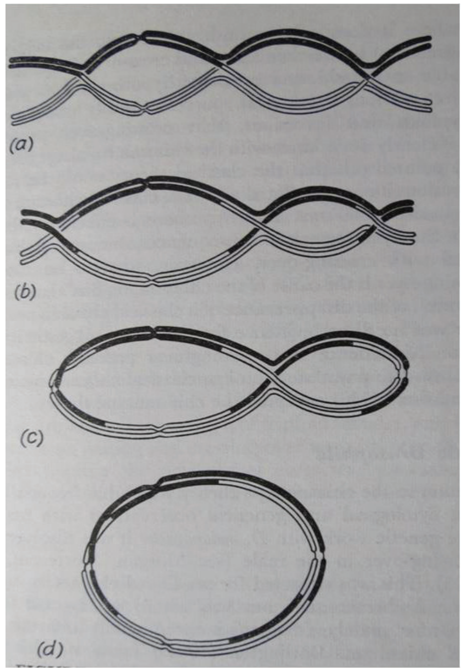
seen, it is not desiccation tolerant, the very reduced cleistocarpous sporophytes lack many typical moss features like lids and peristomes and the stomata are unusual in having only one guard cell. Finally physcomitrologists are normally not field bryologists so tend to hang on to using strains of ancient origin like that from Gransden rather than seeking out new stocks from nature. They likewise stick with a name generally regarded as outdated instead of *Aphanorrhegma patens.* Despite these snags it is more than likely that, were we looking for a model moss today, the choice would be the same.

Harold went up to Queen's College Cambridge in 1936 to read Natural Sciences. His PhD (1939–1946), *The Genetics of Ascomycetes* (Whitehouse, 1948), long delayed by the war years when he served in the RAF photographic interpretation unit at Medmenham, Bucks., with E.F. Warburg, was supervised by the fungal geneticist D.G. Catcheside who in retirement wrote the *Bryophyte Flora of South Australia* (Catcheside, 1980). Harold also attended the first Cambridge Bryophyte excursions in 1938 and in 1939 joined forces with Paul Richards on botanical expeditions to Ireland and Scotland. Unlike today, with bryology virtually extinct as a paid academic pursuit, the immediate post-WWII years were a time when several British universities and research institutes had bryologists or people with strong bryological research interests on their staff. In addition to Richards and Catcheside at Cambridge and Warburg (Oxford), these included Eric Watson (Reading), Alan Crundwell (Glasgow), Charles Gimingham (Aberdeen), Kathryn Benson-Evans (Cardiff), Eustace Jones (Oxford) and Peter Wanstall (Queen Mary).

David Catcheside was the first geneticist employed by the Botany School, Cambridge where he firmly established fungal genetics (Grubb, 2004). Harold very much followed in Catcheside's footsteps, first becoming a Demonstrator in Botany followed by a lectureship in 1952 when Catcheside left to take up a chair in Adelaide, South Australia. Promotion to a readership in 1959 followed by the award of a DSc, Cantab., in 1968, were much deserved rewards for his work on recombination. Formal recognition of his outstanding contributions to the BBS and Bryology had to wait until his election as an Honorary Member of the Society in 1988 (Anon., 1989).

The results of an extensive search, to compile the first full list of Harold's publications and to analyse their authorship and readership, gave me and I suspect bryologists in general, some major surprises. His almost 200 publications comprise not only around 82 bryological papers but also 64 on genetics (mainly fungal) plus one book on botany for beginners (Whitehouse, 1952), two major textbooks (Whitehouse, 1965, 1969, 1973, 1982), one of which went to three editions (Fig. 3), five about people, 39





book reviews, two major works on the wren (Armstrong & Whitehouse, 1977; Whitehouse & Armstrong, 1953) but only one on flowering plants (Preston & Whitehouse, 1986). With its remarkably understated title Harold's *Towards an Understanding of the Mechanism of Heredity* is a beacon of good scientific writing as it explains how we know what we know rather than simply blurting out facts with no context. The record shows that between 1947 and 1980 Harold was a rather prolific reviewer not just of books but also symposia and other multi-author works. He also wrote some anonymous articles for the *British Medical Journal*, commissioned by 'Dougal' Swinscow, an editor of that journal as well as a distinguished bryologist. Whereas 18 of his genetics works were co-authored mainly by Harold's research students, the co-authors of the majority of 44 of his co-authored bryological papers were bryologists well established in their own right.

Looking at his writings chronologically, almost two decades elapsed between Harold's first genetics publication in 1942 and his first on bryophytes, although the records of the Cambridge Bryophyte excursions clearly show his passion for these since the late 1930s. By the time Harold was awarded his DSc in 1968, his work on bryophytes had hardly got off, or strictly speaking, out of the ground; his bryophyte publications amounted to seven on Cambridgeshire records (Whitehouse, 1958, 1959, 1960, 1961b, 1962, 1966b) including one account updating Proctor's earlier county flora (Proctor, 1956; Whitehouse, 1964), reviewed by Jones (1965), three on *Hennediella stanfordensis* (Whitehouse & Coombe, 1960; Whitehouse 1961a; Whitehouse & Paton 1963), just two on tubers (Whitehouse, 1963, 1966a) and an important account (Whitehouse & Smith, 1963) heralding the BBS mapping scheme.

What seems to have really set Harold alight was the discovery of *Hennediella stanfordensis* on the Lizard in 1958 during one of his magical spring excursions based on Coverack (Whitehouse & Coombe, 1960). Harold published no fewer than seven papers on this moss and also visited its *locus classicus* on the campus of Stanford University, California where it thrives to the present day (JGD, personal observation). It was undoubtedly Harold's dual obsessions with tubers and culturing that led to our current understanding of the allied species *H. macrophylla*, first found by Alan Crundwell on the banks of the River Mole at the foot of Box Hill, Surrey.

◁Fig. 4. The young Harold Whitehouse in the field. Campsite at Múlafjall. Iceland 1949.

Eight of Harold's genetics works have over one hundred citations, compared to just over 80 and 30 citations respectively for his top bryological works on tubers in European mosses (Whitehouse, 1966a) and the *Bryum bicolor* complex (Smith & Whitehouse, 1978). In the context of the present metrics-obsessed academic world driven by citation numbers in journals ranked according to their impact factors Harold's 16 papers in *Nature* look very good indeed. In contrast, his bryological works would be ruled insignificant and most research-led universities would not be happy with him. However, putting this into its proper context not only makes a mockery of modern metrics but also underlines the immense value of Harold's 'potato bryology' (Hill & Preston, 1997). Whereas papers on new methods may result in literally hundreds of citations, identification guides crucial to ecological studies and distribution maps are hardly ever listed. Had Harold's original descriptions been referenced for just about every occurrence of tuberous *Bryum* species, not to mention *Dicranella staphylina*, we would be looking at tens if not hundreds of thousands of citations. Harold gets similarly scant credit for fathering Physcomitrology by supplying the Gransden culture. Curiously one of Harold's least well known works (Wearmouth *et al.*, 1984) has now turned out to be highly prophetic. Consequent on a search of the literature following discovery of an extensive colony of *Syntrichia papillosa* on a house wall in Slapton, Devon, this paper was probably the first to bring together scattered suggestions that this moss might be nitrophilous. The growing number of present day records of this moss as an epiphyte along major roads is closely in line with NOX pollution from car exhausts.

Whereas Harold had no research students who worked on bryophytes, he was very successful at recruiting those who wished to study fungal genetics, several of whom went on to become distinguished academics in their own right. Two early 1960s students who worked with *Neurospora* included Fred Cooke, who went on to become a world authority on avian ecology

▽Fig. 5. Summit of Selfjall, Iceland 1949.

in Canada, and Phil Hastings, who also went to Canada (University of British Colombia) and remained true to genetics. When they joined the laboratory, Harold was already well known for having been the first person to work out how to analyse recombination events from ascospore tetrad analysis and they persuaded him to focus on understanding recombination rather than moss taxonomy. Harold then switched his attentions to another ascomycete, *Sordaria fimicola*, which has autonomous spore colour determination, so that conversion and post-meiotic segregation can be scored by eye. He published extensively with research students and came up with mismatch repair in heteroduplex DNA as the mechanism for gene conversion. There were some problems with his models and the correct version, the 'Holliday Junction', is now generally credited to Robin Holliday (for a full account and explanations see Haber, 2008). In retrospect, Harold has almost certainly not received the credit he deserved for his ground breaking work on recombination.

In the 1960s Harold's scientific contacts with undergraduate students were decidedly bipolar. As Reader in Genetic Recombination he lectured and ran practicals in the Botany School, Cambridge on Genetics to Part 1 (second year) and Part 2 students reading Botany as part of the Natural Sciences Tripos. His teaching load was 20–30 lectures plus a handful of practicals, the latter mainly devoted to analysing spore segregation in asci and variously coloured maize ears. Degrees were decided solely from examinations and there was no coursework to mark. Harold's lectures were a model of logical thinking and our notes were ideal for revision – providing that you could write very quickly so you didn't miss out vital steps in his arguments, since Harold produced very few class handouts. Seven A4 pages were around the norm for each

△Fig. 6. Whaling station, Hvalfjördur Iceland 1949.

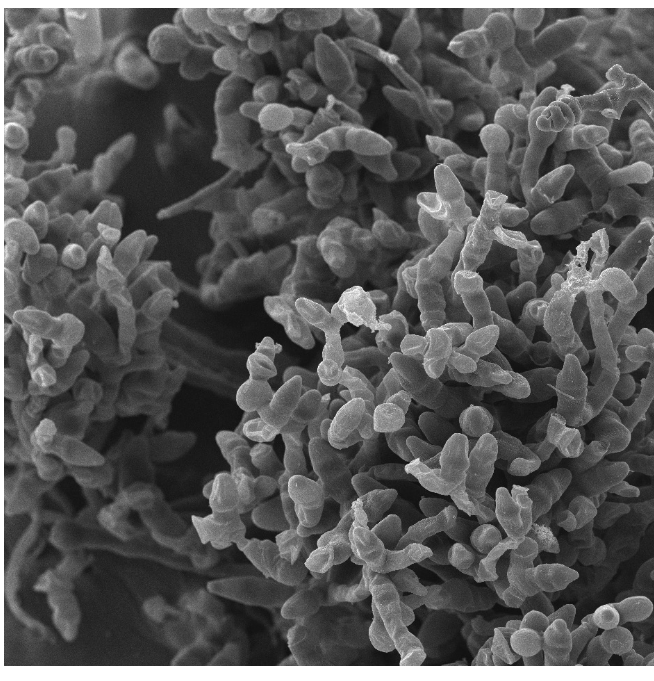
lecture.

I do not recall a single mention of bryophytes; they were reserved for the Saturday afternoon field excursions which, at that time, and very different from today, were attended by large numbers of undergraduates (Richards & Whitehouse, 1988). There are several reasons for the 1960s student bryophilia. There were lectures on Saturday mornings so students didn't hive off for the weekend and, not being short of money because of grants and no fees, they didn't have to work. There were few other distractions apart from sports and IT hadn't been invented. Bryophytes are the right size to make good, easily housed collections. Most biology students had a good working knowledge of the British vascular plant flora and wanted a new hunter/gatherer challenge – and challenge it certainly was. Cambridgeshire was one of the worst places in Britain to encourage bryology, particularly if you like big pleurocarps, leafy liverworts and epiphytes. The last group was pretty miserable; indeed, I recall special detours to see scraps of non-fruiting *Cryphaea*. As a result we became acrocarpophiles and got very excited when we saw *Ephemerum minutissimum* at Gamlingay Wood and *E. recurvifolium* in chalky fields, not to mention diverse Pottiaceae with *Weissia sterilis* on the Devil's Dyke and *Tortula vahliana* at Cherry Hinton being particular jewels. Liverwort highlights for me were *Ricciocarpos natans* and *Riccia fluitans* at Wicken Fen, fossicking for *Aneura mirabilis* at Flitwick Moor, the special day in November 1966 when John Birks found *Lophozia perssonii* at Cherry Hinton chalk pit (Paton & Birks, 1968) and *Lophozia excisa* along the disused railway line at Hayley Wood in 1968, my only new record for v.c. 29 on Harold's excursions.

We learned a great deal more than just species identifications and ecology from the excursions. Explanations for the origins of disjunct distributions are never forgotten when you've seen iconic species like *Pleurochaete squarrosa, Ptilium crista-castrensis* and *Rhytidium rugosum* in the field. Exploring the Godwin plots, established in 1927 at Wicken Fen and which are now one of the world's longest running ecological experiments, makes an indelible impression today just as they did when they supported populations of Sphagna nearly 50 years ago.

The Lizard excursions with David Coombe are less well chronicled than those in Cambridgeshire. Highlights included *Cololejeunea minutissima* and *Ulota phyllantha*, two bryophytes which now exemplify distribution changes during and after Harold's lifetime that can best be attributed to climate change and which since 2011 and 1986 respectively have been found in Cambridgeshire. We admired *Colura* growing on old gorse bushes, and considering the spread of this liverwort in recent years, it may only be a matter of time before it is also found in Cambridgeshire. Obligatory on these excursions was crawling along the cliff paths at Polbream Cove and Housel Bay to measure just how far *Hennediella stanfordensis* had spread since the last visit (Whitehouse, 1975) and recording a then undescribed and totally underwhelming '*Dicranella pusilla*' with tubers in just about every arable field. It is singularly appropriate that this was later described and named by Harold as *D. staphylina* (Whitehouse, 1969). We also learned, but absolutely not from Harold, how to catch adders with a forked stick: in those days Health and Safety rules were an almost complete unknown.

In addition to honing my identification skills, a further influence from Harold was that, during my PhD on sex determination in *Equisetum*, I also began to grow bryophytes axenically. This reinforced my acrocarpophilia and pleurocarpophobia; acrocarps have diverse protonemal morphology and, as Harold found, many readily produce gemmae and tubers in culture with the vast majority conforming to the Whitehouse rule: propagules produced in



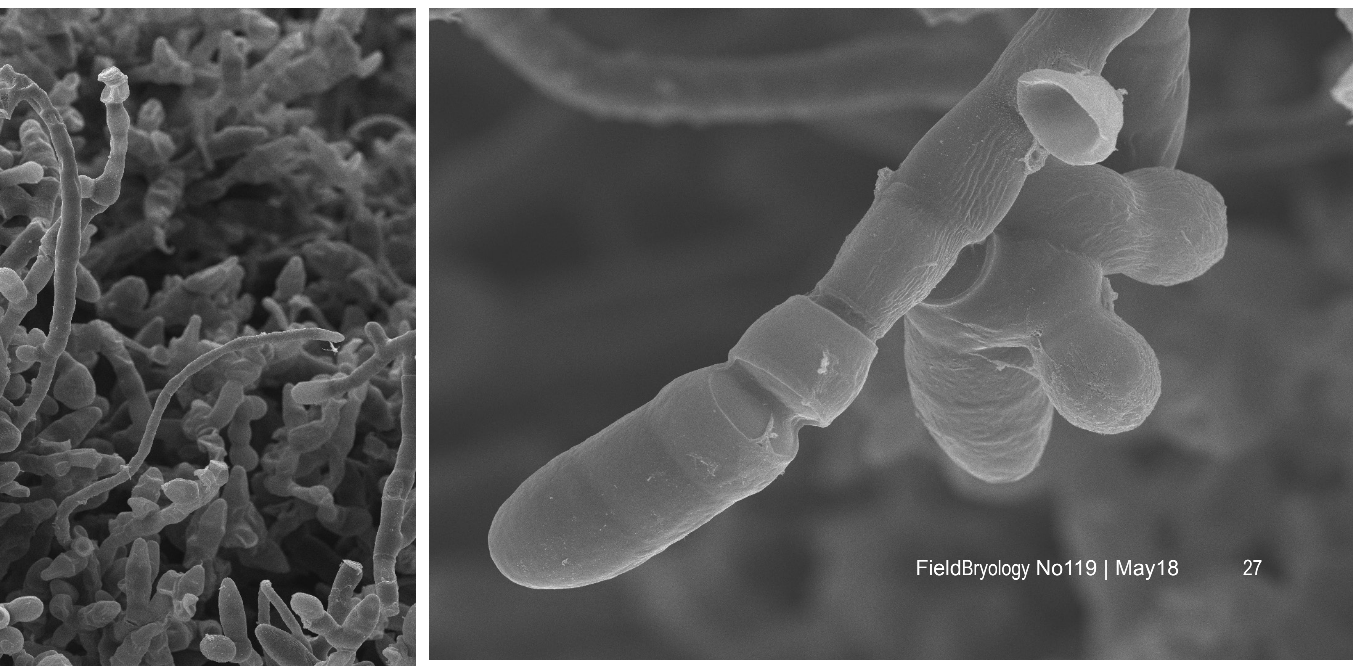
culture can generally be found with the same plants in nature (Whitehouse, 1987a; Duckett *et al.*, 2001). The most notable exception is *Zygodon gracilis*; unlike all other *Zygodon* species its protonemal gemmae in culture have yet to be found in nature (Fig. 7). Harold also found propagules on plants growing in the most bizarre habitats like dimly lit caves (Whitehouse, 1980).

Given that bryologists generally thought of Harold as very much a practical scientist, always keen to collect and examine new specimens, it may come as a surprise to learn that after his PhD and initial fungal studies on recombination in *Neurospora* he did very little hands-on experimental genetics and bryological research. Most experiments were performed by his technician Graham 'Nobby' Clarke and research students who mainly learned from one another about techniques and tricks of the trade. Similarly Nobby made up Harold's culture media and was more than willing to continue with this for several years after Harold lost his research laboratory on retirement in 1985. The usual modus operandi was for Harold to initiate the cultures in Petri dishes and then select the promising shoots which Nobby transferred to test tubes which were maintained in racks in his office sheltered from direct sunlight by tea towels. For most of Harold's career Nobby helped with final inking of Harold's drawings. Those involving models of recombination were particularly demanding as they required very skilful manipulation of flexicurves (Fig. 3).

Axenic culturing back in the 1960s was much less straightforward than it is today. Laminar flow cabinets were not available and their progenitors were hand-made hoods where the air was sterilised with an alcohol mist from a pump action flyspray. Everyone also used glasswear rather than plastic disposable containers and we were very glad that Harold's lab employed two washers up. A testimony to the effectiveness of our methods and our careful work, despite the primitive equipment, was that contaminated cultures were rarely if ever a problem.

It is also rather puzzling that, given his wife Pat's flair for photography and her development

▽Fig. 7. *Zygodon gracilis* produces gemmiferous protonemata (shown in these SEM images) in culture but not in nature. J. G. Duckett & S. Pressel.

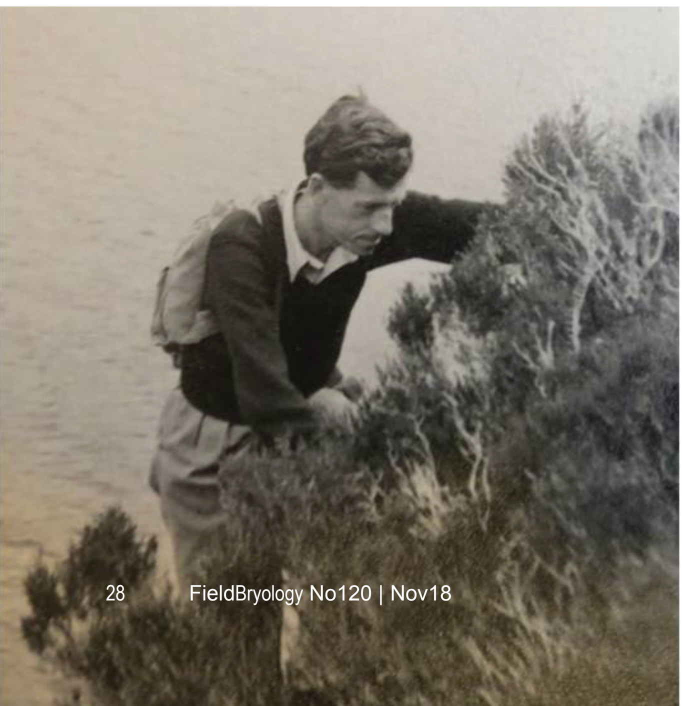


△Fig. 9. Investigating a wren's nest, Loch Assynt Scotland, 1950.

of stereo imaging (Walters, 1990) with Harold taking on this mantle after her death in 1988, he scarcely ventured into the practicalities of light and electron microscope imaging. The only scanning images he ever published of his beloved tubers were with a co-author and were the result of a student project (Hart & Whitehouse, 1978) though the stereo image collection is now specially housed and curated in the National Museum of Wales, Cardiff (Proctor, 1990; Tangney, 2007; Walters, 1990; Walton, 2001a, b, 2002).

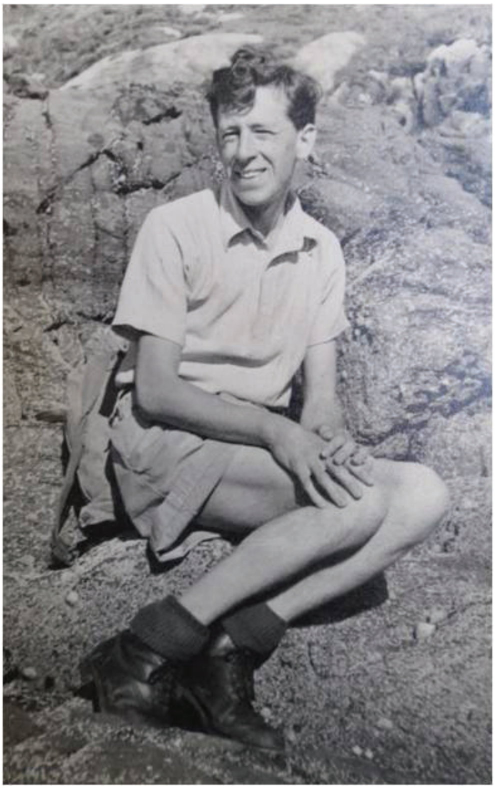
It is a pleasure to record that Harold's laboratory was a very happy place and a venue where several members of the Botany School staff came for coffee, lunch and tea despite being surrounded by an array of highly toxic chemicals. These included Peter Grubb, who first described the subterranean 'root' systems in *Haplomitrium* and *Takakia* (Grubb, 1970) and David Briggs who discovered lead-resistant genotypes of *Marchantia* in pavement cracks in Glasgow (Briggs, 1972). When Harold was away, the students played cricket with a rolled newspaper as bat and a ball made of parafilm. Exhaustive testing over several years conclusively demonstrated that such balls, whatever their velocity, do not dislodge bottles containing toxic chemicals from open shelves. On inadvertently disturbing this anarchic activity, Harold's favourite, or rather only, expletive was 'crumbs'.

▽Fig. 8. Climbing a sea cliff, Lochinver, Scotland, 1950.



Perhaps the biggest downside of Harold's laboratory was that his chosen fungus, *Sordaria fimicola*, grows best at 36 degrees and that the culture room doubled for our darkroom. Consequently most of us perfected our printing skills wearing little or no clothing. The favourite trick was to set off the fire alarm when distinguished visitors were having tea or coffee. Thus, David Catcheside, on a visit from Adelaide, must have left Harold's lab with the strange impression that the research dress code had become semi-nude.

It is probably true to say that all those who knew Harold personally were immediately struck by his quiet and self-effacing manner. It may therefore come as something of a surprise that Harold's immediate student following in the



△Fig. 10. Continental tour, 1953.

1960s nicknamed him Flash. This deserves an explanation as this is both relevant yet singularly inappropriate. Harold's wartime service took him to Italy and botanical excursions took him there again after WWII. Indeed, Harold enjoyed many family excursions to Scotland and a notable early visit to Iceland (Fig. 4). From the 1940s to the 1960s 'Harold in Italy' by Berlioz was one of the favourite pieces of conductor Malcolm Sargent who was also known as Flash – which was appropriate.

Given his well circumscribed teaching duties during the working week, the very short terms at Cambridge, no major college commitments like undergraduate supervisions even after he became a fellow of Darwin College and no major administrative tasks like Research Selectivity Frameworks, Teaching Quality Assessments, Student Satisfaction Surveys, an ever pressing need to get grants, and job insecurity following the abolition of tenure in the 1988 Education Reform Act that bedevil academic life today, Harold had a lot of time and space for research and original thinking underpinned with excellent facilities and technical support. He was also fortunate at being able to continue his bryophyte research after retirement from a base in the herbarium and was not turfed out like many retiree academics today.

I therefore conclude by asking how Harold's career path might have been different in the present academic world with all its added pressures. One thing is almost certain; he would not have had the time for the Saturday bryophyte excursions, neither would he have taken on major editing and reviewing activities and his much acclaimed book would almost certainly not have seen the light of day. Today Physcomitrology is a bryological goldmine, attracting large grants and employing research teams engaging in molecular research across the world. In this environment, knowing perhaps more than anyone else about growing bryophytes combined with genetics, Harold might well have become the director of the world's first centre of excellence for molecular work on bryophytes. Personally I am sad that he was not added posthumously to the 70 authors of the full genome sequence of *Physcomitrella* (Rensing *et al.*, 2008).

Acknowledgements

My sincere thanks to Anne Whitehouse for permission to use previously unpublished photographs of Harold from the family albums and to Phil Hastings and Neil Ashton for background information about Harold's work on recombination and the uses of *Physcomitrella* as a model organism. Chris Preston added to the anecdotage and kindly checked the bibliography for errors and omissions. Phil Stanley's index was absolutely invaluable for checking Harold's publications, as were some of Harold's files in Cambridge University Library (MS Add.10210).

References - for references, see the **Other references,** p. 35