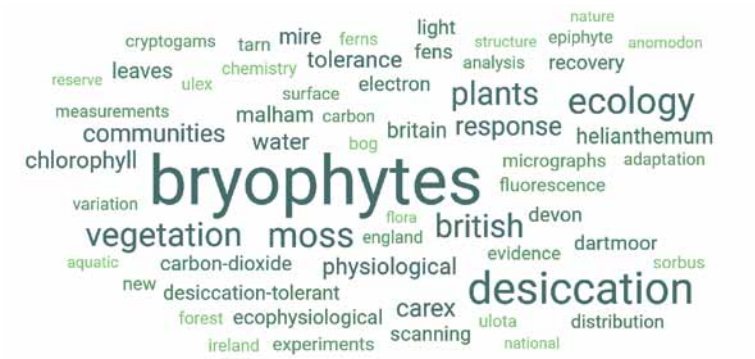
△ Figure 1. Michael at the BBS meeting in Torquay, 1997. *Ken Adams.*

Michael Proctor (1929–2017): a botanical polymath

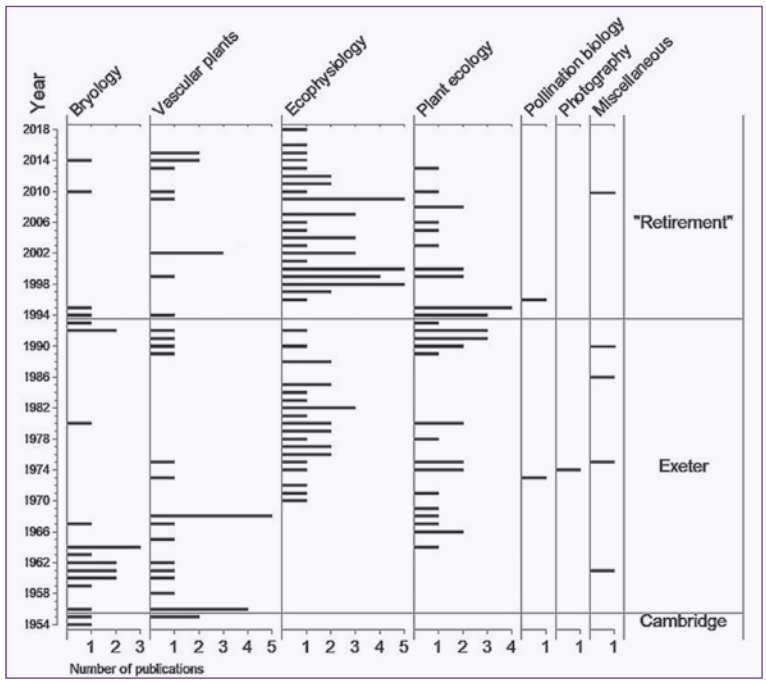
John and **Hilary Birks** outline Michael's life and his many achievements as a bryologist, plant taxonomist, ecologist, ecophysiologist, pollination biologist and photographer: a true polymath.

Michael Charles Faraday Proctor (21 January 1929–24 October 2017; Fig. 1) was a most remarkable botanical polymath with very many botanical interests and skills. He made major contributions to numerous topics. He was a very talented field biologist, bryologist, plant taxonomist, plant ecologist, experimental ecophysiologist, pollination biologist, photographer, teacher and mentor. He was one of the most outstanding, active and versatile botanists and ecologists in Britain between the mid-1950s and 2015. Everything he did was done to the highest possible standard. He loved fieldwork, devising challenging laboratory, greenhouse and field experiments, analysing data, working in herbaria, developing new ways of doing things and mastering analytical equipment, teaching (especially in the field), photographing a wide range of organisms and writing. He was a bit of a technical nerd, being fascinated by cameras, lenses and analytical equipment. He published six books, co-edited five more, and wrote over 170 papers and book chapters. Their scope is summarised in a Word Cloud (Fig. 2) constructed from the principal title words of his publications. The chronology of his research activities and hence his publications is summarised as a plot of the number of publications in each year between 1954 and 2018. His publications are grouped into seven major categories: bryology; vascular plants; ecophysiology; plant ecology; pollination biology; photography; and miscellaneous (Fig. 3). A bibliography of Michael's publications has been prepared and is available with the on-line version of this article on the BBS website.

This account draws on what has already been written by or about Michael (Bates, 2018; Birks, 2018; Birks & Birks, 2018, 2022; Marren, 1995,



◁ Figure 2. Word cloud based on the main title words of Michael Proctor's publications. The larger the size, the more frequent the word.



◁ Figure 3. Chronological plot of Michael's publications grouped into seven major categories. The plot is divided into three phases – Cambridge (and Bangor) (1954–56), Exeter (1956–94) and 'Retirement' (1994–2018). The category 'Ecophysiology' primarily includes publications on bryophyte physiology.

2005, 2016, 2017; Proctor, 2013b; Ross, 2018), on our own interactions and correspondence with Michael from 1963 to 2017, on memories shared with us from some of his colleagues, and on his many publications. We conclude by discussing what can be learnt today from Michael's approach to teaching, both in the lecture-room and the field, to inspiring students and colleagues, to encouraging and developing identification skills and to implementing novel and innovative scientific investigations.

Early life

Michael was born in Harrow on 21 January 1929, the son of Edith (a schoolteacher) and Roland Faraday Proctor (a scientist), a descendent of the self-taught Michael Faraday (1791–1867). Faraday was also a polymath,

having made contributions to physics, chemistry and environmental studies. With his younger brother Robin, Michael Proctor was educated locally. He was always interested in nature, both plants and animals. At an early age he avidly read his mother's copy of Bevis & Jeffery's wonderful book *British plants: their biology and ecology* (1911), one of the first books in Britain about plant ecology, plant associations and the links between ecology and plant form – topics which Michael studied throughout his career. Inspired by this book he explored the nearby 'commons' in Harrow and the Chilterns and, from his aunt's house in Woking, the then more extensive Surrey heaths. In 1946 the Proctor family moved to Hampshire and Michael was soon on his bicycle exploring the flora and fauna of the New Forest, the Isle of Purbeck and the Dorset coast.

Michael won a Natural Sciences Scholarship to Queens' College, Cambridge where he read Botany, Zoology, Organic Chemistry, and Biochemistry in Part I of the Natural Sciences Tripos (1948–50) and Botany in Part II (1950–51), gaining a First Class degree. Michael told us that he would also have liked to have studied Geology in Part I but the regulations did not allow an extra whole (2-year) subject. His direct contemporaries at Queens' included talented botanists Peter Yeo, also an entomologist (Proctor, 2010b), and Franklyn Perring, who went on in 1962 to produce with Max Walters the *Atlas of the British Flora* for the then Botanical Society of the British Isles (Preston & Oswald, 2006).

When he started as an undergraduate in 1948, Michael already had an excellent knowledge of southern British plants, common bryophytes and lichens, insects (especially Hymenoptera), snails, birds, mammals, fossils, etc. Max Walters, who lectured to Michael on plant taxonomy, told us of a 1949 excursion to Hayley Wood, an ancient woodland near Cambridge. On the walk into the wood, Michael was happily identifying all the plants, insects, snails, plus two veteran aeroplanes that flew over. At the end of the excursion and returning to the main road, a vintage-car rally drove past and Michael identified all the car models!

Bryology

In 1950, whilst a second-year undergraduate, Michael joined the British Bryological Society and organised and co-led with Harold Whitehouse a Cambridge Botany School bryophyte excursion of 19 people to the Lake District in March–April (Fig. 4). Members of the excursion included Pat Whitehouse and Franklyn Perring. Michael prepared for the excursion a key to British *Sphagnum* species that he subsequently published (Proctor, 1955a). He actively bryologised in Cambridgeshire (vc 29) between 1948 and 1954 and in 1956 he published the first detailed bryophyte flora of Cambridgeshire (Proctor, 1956a) in which he emphasised that it 'embodies the accumulation of Cambridgeshire bryophyte records begun by Prof. P.W. Richards in 1927'. Preston (2006) and Preston & Hill

◁ Figure 4. The Cambridge Botany School Bryology Excursion to the Lake District, March–April 1950. Michael is in the centre at the front and Harold Whitehouse is on the far left. *Pat Whitehouse*

△ Figure 5. A wet Michael examining *Zygodon gracilis* on a stone-wall near Pen-y-ghent (vc 64), April 2004. *Jeff Duckett*

△ Figure 6. Cronkley Fell, where the endemic *Helianthemum oelandicum* subsp. *laevigatum* has its sole occurrence on the 'sugar limestone'. *John Birks*

(2019) analyse who was responsible for the records cited in the 1956 flora. Paul Richards was responsible for more 20th-century records than anyone else (25%), followed by Michael (18%), Eustace Jones (11%), Harold Whitehouse (8%), Reg Parker (7%) and 'Heff' Warburg (5%). They note that the only large group for which Richards' contribution was clearly outnumbered by the records of another bryologist was Pottiaceae, a group for which Michael cited more than twice as many of his own records. Michael's flora laid the foundation (Preston, 2006) for subsequent careful and systematic recording, leading to Harold Whitehouse's (1964) flora and Chris Preston and Mark Hill's recent flora in 2019. The latter documents the remarkable dynamics and recent changes in the Cambridgeshire bryophyte flora. Michael appropriately wrote in his review of a new check-list for vc 29 'it seems to me that v.c. 29 is beginning to show us that we can never expect to know the flora of an area finally or completely, and probably we should rejoice that this is so' (Proctor, 1984a). Other important field bryological publications by Michael include thorough accounts of the bryophytes of Dartmoor (Proctor, 1962, 1964), the Malham area (Proctor, 1960a) (Fig. 5) and Slapton Ley (Bates *et al*., 1993); an innovative numerical classification of the distribution of British hepatics at the vice-county scale (Proctor, 1967c); and the first use of hemispherical photography in bryology using an ultra-wide-angle fish-eye lens to estimate the radiation climate of selected bryophytes (e.g. *Anomodon viticulosus, Polytrichastrum sexangulare, Hylocomiodelphus triquetrus, Colura calyptrifolia, Orthothecium rufescens, Herbertus hutchinsiae*) in different habitats (e.g. woodland, mountain, grassland, ravine, cliff, scree) (Proctor, 1980a). He occasionally attended BBS field meetings (see Fig. 1).

Vascular plants

Besides being an active field bryologist, for his Cambridge PhD Michael studied the taxonomy, cytology, ecology, biogeography and variation of the three species of *Helianthemum* (rock-roses) in Britain and Ireland under the supervision of Sir Harry Godwin (Griffiths & Proctor, 1956; Proctor, 1955b, c, 1956b, c, d, 1957, 1958; Proctor & Lambert, 1961). Michael showed that the population of *H. canum* growing on

the Cronkley Fell 'sugar limestone' in Upper Teesdale (Fig. 6) was different from other *H. canum* populations in Britain and Ireland. He described it as *H. canum* subsp. *laevigatum*. It is now called *H. oelandicum* subsp. *laevigatum*, an endemic taxon. He maintained his interest in the family Cistaceae, especially *Helianthemum* and the related *Tuberaria guttata* (Spotted Rock-rose) (Proctor, 1960b) and wrote the accounts for *Flora Europaea* of *Helianthemum* (31 species, 27 subspecies), *Halimium* (False Sun-rose; 9 species) (Proctor & Heywood, 1968) and *Tuberaria* (10 species) (Proctor, 1968).

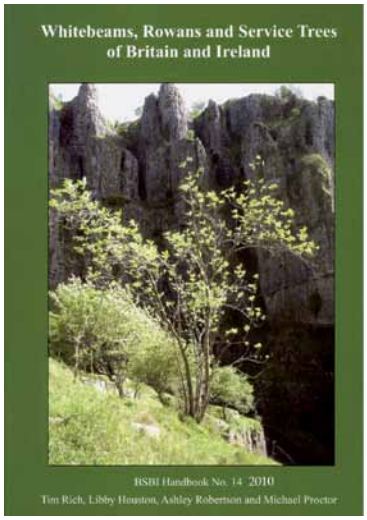
In 1955, after his Cambridge PhD (Proctor, 1955c), Michael was appointed a Scientific Officer in the newly formed Nature Conservancy (NC) and was based in Bangor, north Wales. He enjoyed exploring Snowdonia and photographing its flora. He met his future wife Jean Mobbs, daughter of the Professor of Forestry at the then University College of North Wales in Bangor. Jean and Michael married in 1957. Sadly, Jean died in 1983. Michael found NC work far too bureaucratic and in 1956 he moved to a lectureship at the then University College of the South-West, later the University of Exeter. He remained there until he retired as a Reader in 1994, although he took partial retirement in 1985. From 1994 he continued as an Honorary Research Fellow until his death.

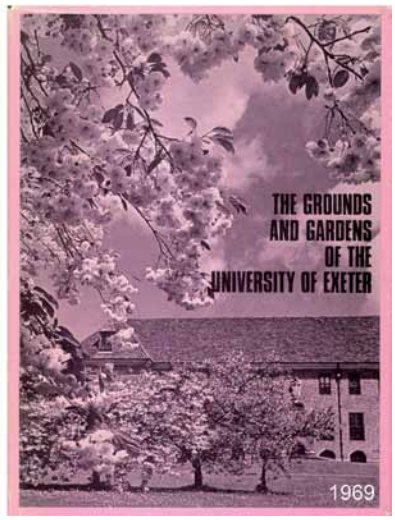
Michael was a long-standing member of the BSBI (now the Botanical Society of Britain and Ireland), joining in 1950. He maintained a strong interest in angiosperm taxonomy, for example of *Ulex* (Proctor, 1965, 1967a) and *Carex*.

As a student in 1950 he ventured to Abisko in Swedish Lapland with Keith Goodway and found and identified 96 species of *Carex* out of the 104 species known there. When Michael returned to Abisko with us in 1988 (Proctor, 1991), he remembered all 96 species and showed us several that were new to us. His last set of publications (Proctor & Bradshaw, 2013, 2014a, b, 2015a, b) is a series of five detailed and elegantly illustrated articles on the scanning electron microscopy of British *Carex* leaves.

Michael developed a strong interest in *Sorbus* taxonomy, particularly taxa growing in Devon and Somerset. *Sorbus* is a very critical genus of many species around the rowans *S. aucuparia* agg. and the whitebeams *S. aria* agg., *S. intermedia* agg. and *S. latifolia* agg. There are now at least 52 taxa described from Britain and Ireland: four described by Michael (Rich & Proctor, 2009). Besides 'classical' taxonomy and much fieldwork, often in challenging terrain (gorges, limestone cliffs, coastal cliffs, etc.), Michael used biochemical approaches, such as peroxidase isoenzymes, gel electrophoresis and plastid DNA, to help distinguish taxa (Proctor & Groenhof, 1992; Proctor *et al.*, 1989; Rich & Proctor, 2009). These approaches clarified 'Taxon D' (*sensu* Proctor *et al.*, 1989) as a new species, *Sorbus margaretae* M. Proctor. There are about 70 plants of this taxon along the north Devon and Somerset coast and it is named after Michael's second wife Margaret Proctor (née Bradshaw). In contrast, there is only one plant known of Proctor's Rowan *Sorbus* × *proctoriana* (= *S. aucuparia* × *S. scalaris*) growing in Leigh Woods by the Avon Gorge. Michael co-authored the BSBI Handbook on *Whitebeams, Rowans and Service Trees of Britain and Ireland* (Rich *et al.*, 2010) (Fig. 7).

As Michael developed his interests and expertise in the ecophysiology of bryophytes (see below), he also studied the ecophysiology of ferns (Proctor, 2003a, 2009a, 2012c) and *Helianthemum*, his PhD genus (Proctor, 2012a). In an elegant study, he compared the growth of the common *H. nummularium* (Common Rock-rose) and the grass *Koeleria macrantha*





◁ Figure 7. Covers from Michael's books on *Whitebeams, Rowans and Service Trees of Britain and Ireland* (2010) and *The grounds and gardens of the University of Exeter* (1969).

(Crested Hair-grass) with the rare *H. apenninum* (White Rock-rose) and *K. vallesiana* (Somerset Hair-grass) in replacement and water-treatment experiments. He showed that the two rare taxa grew best in dry and unshaded conditions and the physiological contrasts between the two rock-roses are related to leaf morphology, with *H. nummularium*'s leaf having simple hairs on the upper surface and stellate tomenta on the lower surface. In contrast, *H. apenninum* has stellate indumenta on both surfaces, characteristic of a semi-xerophytic plant. Presumably this favoured *H. apenninum* in the open, dry conditions typical of late-glacial environments (cf. Proctor, 1958). As a Cambridge student of Sir Harry Godwin, Michael retained an interest in pollen analysis, vegetation and floristic history and plant geography (e.g. Proctor, 1958, 1964, 1967c, 1973, 2012a; Proctor & Lambert, 1961). Michael's investigations on the ecophysiology of vascular plants, particularly ferns, centred on the comparative physiology of species pairs (e.g. Proctor, 2012a; see above), their responses to light, their water relations and their tolerance to desiccation. For a bryologist, an obvious species pair for ecophysiological studies is *Hymenophyllum tunbrigense* (Tunbridge Filmy-fern) and *H. wilsonii* (Wilson's Filmy-fern) (Proctor, 2003a). Michael concluded that 'Filmy ferns with their membranous leaves [also in *Leptoseris*] can be seen as a pteridophyte excursion into the typical adaptive strategy (poikilohydry) of bryophytes in habitats where that strategy is adaptively optimal' (Proctor, 2003a). He also investigated the light and desiccation response of filmy-ferns from Trinidad (4 species), Venezuela (3 species) and New Zealand (1 species) (Proctor, 2012c; see also Proctor, 2014). Michael viewed the 'Hymenophyllaceae as a rare example of an evolutionary shift of adaptive strategy from typical vascular plant adaptation to the poikilohydry of bryophytes' (Proctor, 2012c). In other words, filmy ferns are honorary bryophytes!

Michael (Proctor, 2009a) completed a fascinating study of the comparative desiccation tolerances of ten species of British ferns. He showed that *Asplenium ruta-muraria* (Wall-rue), *A. septentrionale* (Forked Spleenwort), *A. trichomanes* (Maidenhair Spleenwort), *A. ceterach* (Rustyback), *Polypodium cambricum* (Southern

Polypody) and *P. interjectum* (Intermediate Polypody) are all very tolerant, *A. adiantum-nigrum* (Black Spleenwort) and *A. obovatum* (Lanceolate Spleenwort) are moderately tolerant, whereas *Polystichum aculeatum* (Hard Shield-fern) and *P. setiferum* (Soft Shield-fern) are intolerant of desiccation. These results largely conform to general field observations.

Ferns are interesting in both ecological and evolutionary contexts (Proctor, 2007, 2014). There are two major strategies for terrestrial plant life – homoihydry which is the strategy of nearly all vascular plants and poikilohydry which is the strategy of desiccation-tolerant bryophytes. Another contrast is between the endohydry of vascular plants whose physiologically important free water is in the xylem and the water-repellent epidermis and the ectohydry of bryophytes whose physiologically important free water is in capillary spaces outside the plant. Many fern sporophytes can withstand some desiccation (partly poikilohydric) but all are endohydric, thanks to their vascular tissue. In contrast, fern gametophytes are unequivocally poikilohydric and ectohydric and are thus like bryophytes.

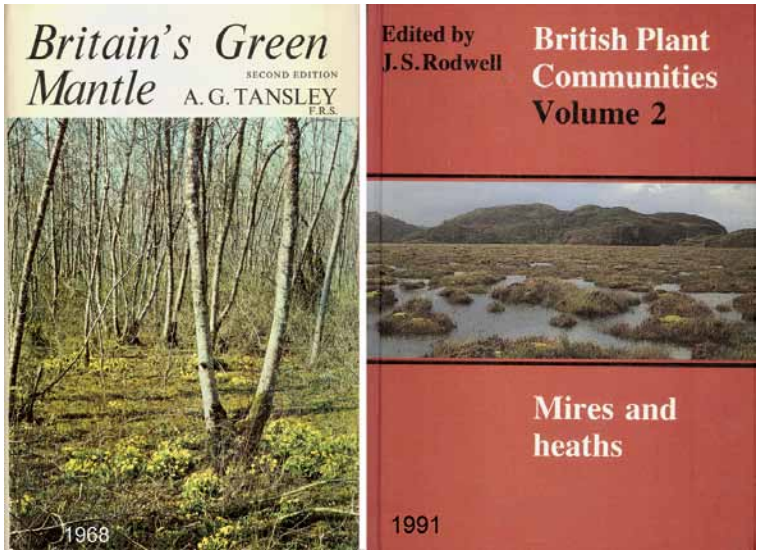
Michael was naturally also interested in resurrection plants. These are 'normal' vascular plants (e.g. *Selaginella lepidophyta, Polypodium polypodioides, Notholaena marantae, Haberlea rhodopensis*) that have a 'fall-back' option of remarkable desiccation tolerance (inherent in their spores or seeds) when water is not available. In ecological terms, resurrection plants occur in a realised ecological niche-space where several adaptive strategies converge but where none is really optimal (Proctor & Pence, 2002).

Although Michael joined the British Lichen Society on its foundation in 1958, he only published three papers solely on lichens, studying their growth in Devon (Fisher & Proctor, 1978; Proctor, 1977b) and Switzerland (Proctor, 1983). He also made comparisons of moss and lichen responses to desiccation (Tuba *et al.*, 1996) and of bryophyte and lichen growth in biological soil crusts (Green & Proctor, 2016). However, in his many ecological and plant sociological studies, lichens were always included.

Plant ecology and phytosociology

Michael combined his considerable taxonomic skills and wide field experience of vascular plants, bryophytes and lichens in many wide-ranging descriptive vegetational ecological studies. These included in-depth studies of several Devon habitats such as the Exe Estuary (Proctor, 1980b), the Otter Estuary (Brooks *et al.*, 1988), hedges at Chudleigh (Michelmore & Proctor, 1994); Dartmoor mires (Proctor, 1989), Aylesbeare Common (Ivimey-Cook *et al.*, 1975) and Dartmoor woodlands (Proctor, 1962; Proctor *et al.*, 1980). He also made detailed studies of the vegetation supporting *Helianthemum apeninnum*, *H. nummularium*, *H. oelandicum* and *Tuberaria guttata* (Griffiths & Proctor, 1956; Proctor, 1956b, c, 1960b).

In the summers of 1958 and 1959, Michael and his Exeter colleague Brian Ivimey-Cook, with support from the Burren Survey Committee of the British Ecological Society (BES) and the University of Exeter, conducted a very thorough plant-sociological study of the Burren in County Clare (Ivimey-Cook & Proctor, 1966b). Despite its famous floristic interest, Burren vegetation had largely been ignored, especially by the fathers of continental phytosociology, Josias Braun-Blanquet and Reinhold Tüxen, who visited the Burren on the Ninth International Phytogeographical Excursion to Ireland in 1949. After a few hours of recording relevés, they declared to the leaders David Webb and Frank Mitchell that 'there is something wrong here, we must go somewhere else'! David Webb politely

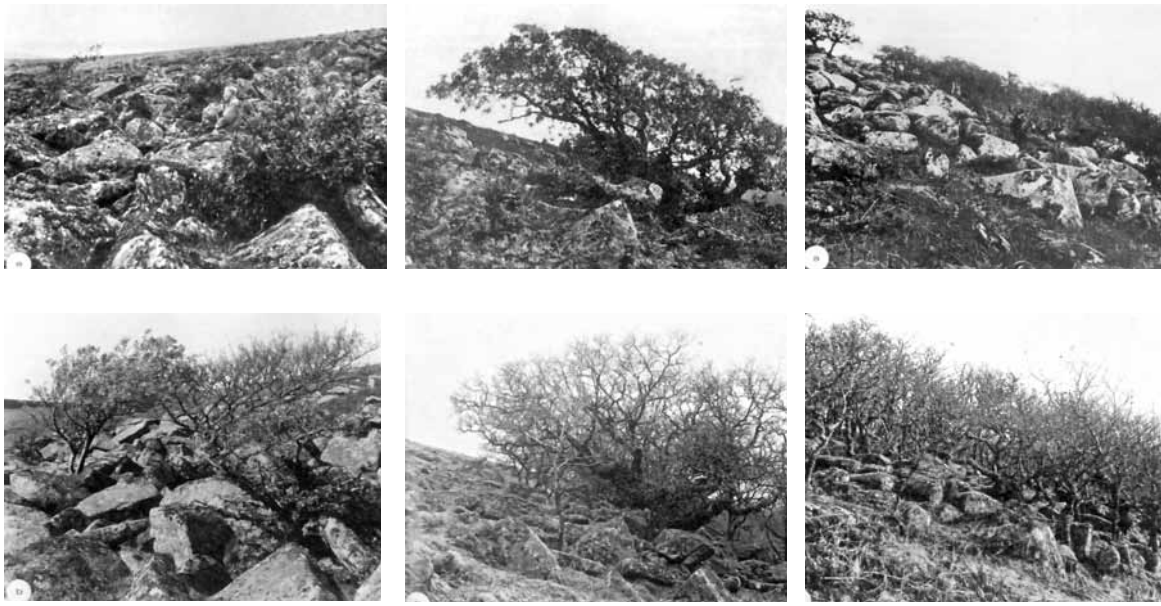


◁ Figure 8. Covers from Michael's books on *Britain's green mantle* (Tansley & Proctor, 1968) and *British plant communities* volume 2 (Rodwell *et al*., 1991b). Michael synthesized the data for this volume.

replied that they were there for a further two days. The Braun-Blanquet system did not allow for calcifuge plants such as *Antennaria dioica* (Mountain Everlasting), *Hypericum pulchrum* (Slender St John's-wort) and *Calluna vulgaris* (Heather) to grow together with the calcicole *Dryas octopetala* (Mountain Avens). Braun-Blanquet & Tüxen (1952) invented the taxa *Antennaria hibernica, Hypericum pulchrum* subsp. *hibericum* and an ecotype of *Calluna vulgaris* to save their system. Tüxen once replied to a query from Michael about continental phytosociology 'the proof of the pudding is to eat him'! Michael and Brian Ivimey-Cook regularly led Exeter undergraduate excursions to the Burren (Marren, 2016) and Michael studied in detail changes in the lakes, fens and turloughs of the Burren (Proctor, 2010a). He also took undergraduate excursions to Switzerland (Proctor, 1983) and the Channel Isles (Proctor, 1975).

After his work on the Burren, Michael used his strong interest and extensive knowledge of British and Irish vegetation to prepare a major revision of Sir Arthur Tansley's classic *Britain's green mantle* (Fig. 8) (Tansley & Proctor, 1968). This edition was substantially rewritten by Michael and extensively illustrated by many of his superb photographs of plants, their habitats and landscapes. Other ecological studies by Michael include the vegetation of Alderney (Proctor, 1975) and the Malham area (Cooper & Proctor, 1998; Proctor, 1974c), the vegetation and water chemistry of bogs and fens (Proctor, 1992a, 1993, 1994, 2003b, 2006, 2008; Proctor & Maltby, 1998; Proctor *et al.*, 2009; Wilson *et al.*, 1995) and impacts of severe fire on heathlands (Legg *et al.*, 1992; Maltby *et al.*, 1990; Thomas *et al.*, 1994). He also contributed thoughtful and critical reviews on various controversial topics in descriptive, quantitative and mire ecology (e.g. Clément & Proctor, 2009; Ivimey-Cook & Proctor, 1966a, 1967; Ivimey-Cook *et al.*, 1969; Proctor, 1967b, 1974a, 2013a; Wheeler & Proctor, 2000).

Of all Michael's ecological studies in Devon, perhaps the most notable is his analysis of changes in Wistman's Wood on Dartmoor using repeat photography (Proctor *et al.*, 1980).



△ Figure 9. Photographs of different parts of Wistman's Wood, Dartmoor, comparing old photographs (above) with more recent ones of the same location. Upper row left: 1932, *R. Lythgoe*; middle: 1904, *C.R. Rowe*; right: 1892, *R. Burnard*. Lower row left: 1973, middle: 1979, right: 1980, all *Michael Proctor* (from Proctor *et al.* 1980; Proctor 2013b).

Wistman's Wood is one of three remote high-elevation (380–435 m) woods of *Quercus robur* (Pedunculate Oak) on Dartmoor. Wistman's is the highest oakwood in Britain. It has attracted various legends over the last 100–150 years – a sacred grove of the Druids; the home of the kennels for the terrible 'Whist Hounds' of Dartmoor; an ancient Lych Way or 'way of the dead' to Lydford; a remnant of primeval forest. The last legend was put to rest by Bradshaw *et al.* (2015). Their 1200-year pollen record from a humus profile within the wood shows that oak only became dominant in the last 170 years and prior to that the area was more open and heavily grazed. The oaks today are about 5–7 m tall, show a tangled growth, and have fascinated visitors for the last 100 years. Michael did an extensive resurvey (Proctor *et al.*, 1980) and patiently relocated trees and areas where there were photographs from 1892, 1904 and 1932 (Fig. 9). The general trends are that tree growth is becoming more 'normal', the canopy is becoming more open, epiphytic cover is less abundant and trees are expanding.

Michael naturally became a key member of the National Vegetation Classification (NVC) project, financially supported by the then Nature Conservancy Council (1974–81). NVC members included Donald Pigott, Derek Ratcliffe, David Shimwell, Andrew Malloch, John Rodwell and others including ourselves. The end result was the five-volume *magnum opus* on *British plant communities* (Rodwell *et al.* 1991–2000). Michael played a major role in synthesising all the NVC data from mires and heaths (Fig. 8), as well as sharing his extensive knowledge of British flora and vegetation with the NVC team. NVC meetings were to us, as

◁ Figure 10. Covers from Michael's three New Naturalist volumes: *The pollination of flowers* (1973), *The natural history of pollination* (1996) and *Vegetation of Britain and Ireland* (2013).

young researchers at the time, a great learning experience as we listened to Donald, Derek and Michael discuss in detail critical aspects of British vegetation, based on their vast field knowledge and observations.

Michael joined the BES in 1951 and co-edited the BES's *Biological Flora of the British Isles* for over 20 years, always generously sharing his remarkable knowledge about the ecology, pollination biology or insect visitors of particular species. Soon after his death, the BES compiled a 'virtual issue in tribute to Michael Proctor' of the *Journal of Ecology* containing all 16 of Michael's papers that had been published in the journal (Ross, 2018). Tony Davy (Editor-in-Chief of *Biological Flora of the British Isles*) writes 'Contributions to the Biological Flora benefited from much more than Michael's expertise on pollination however. His insight into the composition, variation and distribution of plant communities was unrivalled and will be sorely missed. … Michael always lamented when authors merely summarised the [NVC] information therein and could not contribute original material, preferably from their own field work, or broader insight from the foreign literature. He, on the other hand, could usually do both, introducing information from his own foreign excursions or relevant material from the German- and French-language phytosociological traditions. He seemed blithely unaware that many contributors did not have his facility with languages. … Michael continued to review *Biological Flora* accounts with his customary wit and wisdom until the age of 87. I personally will greatly miss the humour and discursive anecdotes that nearly always featured in the emails that accompanied his reviews, although I rarely felt able to pass these on to authors.' (Davy in Ross, 2018)

In 2013, at the age of 84, Michael published his masterly 516-page book on the *Vegetation of Britain and Ireland* (Proctor, 2013b) in the New Naturalist series (Fig. 10). It distils his life's observations and studies and contains over 400 excellent colour photographs taken by Michael. Unfortunately, the colour reproduction by Collins did not always do justice to the images submitted by Michael. We were fortunate to receive a CD from Michael containing the photographs submitted to Collins along with another 200 images and two additional indexes that Michael wanted to include but Collins declined.

Bryophyte ecophysiology

It is perhaps surprising that Michael who was a very active and productive taxonomist, plant ecologist and sociologist and pollination biologist (see below) should have his largest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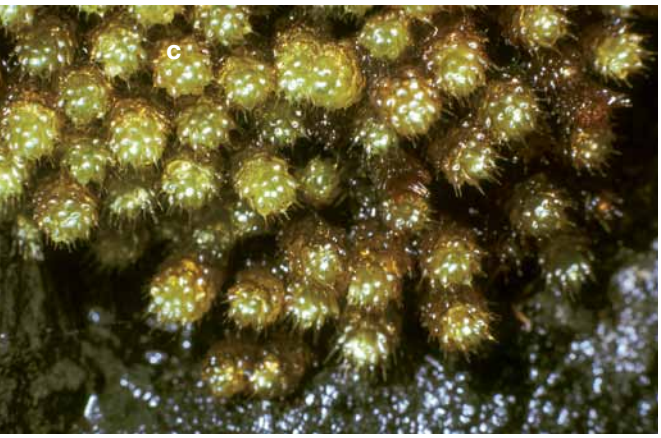
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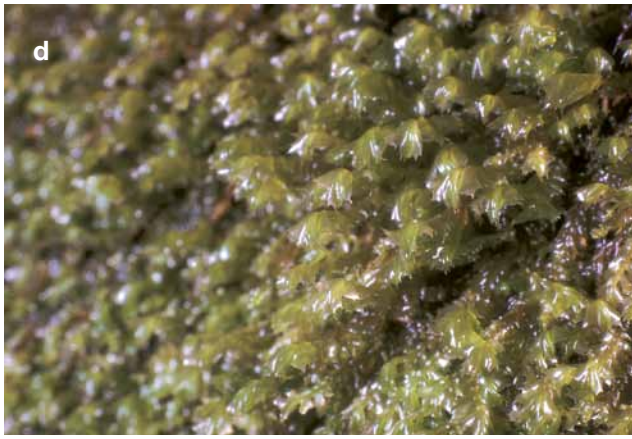
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◁ Figure 11. Some bryophytes that Michael used in his ecophysiological studies (Proctor 1979b; Dilks & Proctor 1975). (a) *Drepanocladus trifarius*, (b) *Orthothecium rufescens*, (c) *Myurium hochstetteri*, (d) *Plagiochila spinulosa*, (e) *Schistostega pennata*, (f) *Saelania glaucescens. All photographs John Birks*

scientific output (68 papers, book chapters and review articles) on ecophysiology and functional morphology (Fig. 3). This large output was mainly, but not exclusively, in the period 1985–2015, with 65% of this output being published after Michael retired in 1994. In fact, 50% of all Michael's publications (not only ecophysiology) were published after his so-called retirement in 1994.

Michael's interest in the functional morphology of bryophytes was a natural development to someone interested not only in bryophyte taxonomy and phytogeography but also in plant structure and function. His contributions on bryophyte functional morphology include Proctor & Smith (1995), Clayton-Greene *et al.* (1985) and Proctor (1979b, 1984b, 1992b, 2005, 2010d, 2014). He completed a fascinating study on the occurrence of surface wax on moss leaves such as *Saelania glaucescens* (Fig. 11), *Schistostega pennata* (Fig. 11), *Pohlia cruda, P. wahlenbergii, Bartramia pomiformis* and *Conostomum tetragonum* (Proctor, 1979b). Interestingly, all the species Michael examined with detectable leaf wax are endohydric in their adaptation to water use and movement.

The major research questions in bryophyte ecophysiology that Michael addressed were centred on how bryophytes grow and survive and what is their tolerance to desiccation and hence evasion of drought. There was always a slant towards comparisons and contrasts with vascular plants, especially ferns and resurrection plants.

Michael's studies on the ecophysiology of bryophytes primarily started with his post-doctoral fellow Tim Dilks. Their work centred on desiccation and subsequent rapid assimilation and respiration with most species withstanding drying to water contents of about 10% dry weight and recovering in a few hours or even days. There is naturally much variation in sensitivity between species, with *Racomitrium lanuginosum* being most resistant with a rapid recovery after 239 days at 12% relative humidity. In contrast, *Hookeria lucens* and *Plagiochila spinulosa* (Fig. 11) are some of the most sensitive of the twelve species examined by Dilks & Proctor (1974) and Hinshiri & Proctor (1971). Tim and Michael also studied the temperature responses of bryophytes in terms of their assimilation, respiration and freezing damage (Dilks & Proctor, 1975). They showed that for the 36 species they studied, there was considerable variation in the optimal temperature for net assimilation with *Drepanocladus trifarius* (Fig. 11) and *Orthothecium rufescens* (Fig. 11) having low optima. Surprisingly, several other northern and montane species (e.g. *Andreaea nivalis, Anthelia julacea*) did not differ substantially from the majority of lowland species in their response of net assimilation to temperature. Even more surprisingly, 'oceanic' species such as *Plagiochila spinulosa* and *Myurium hochstetteri* (Fig. 11) could withstand 1–2 weeks at –5°C. Tim and Michael also investigated the effects of intermittent desiccation on bryophytes (Dilks & Proctor, 1976a); seasonal variation in desiccation tolerance (Dilks & Proctor, 1976b); and the relationships between respiration, photosynthesis and water content in bryophytes (Dilks & Proctor, 1979).

These pioneering studies (also Proctor, 1972, 1977a; Proctor & Hinshiri, 1970) provided the basis for much of what Michael subsequently

developed in bryophyte ecophysiology. Important questions he addressed include

- how does photosynthesis interact with water availability (Tuba *et al.*, 1996);
- do aquatic bryophytes such as *Fontinalis antipyretica* show photosynthetic uptake of bicarbonate from water (Bain & Proctor, 1980);
- how long will dried-up bryophytes survive at low temperatures (Hearnshaw & Proctor, 1982; Proctor, 2004a);
- what biochemical changes occur with desiccation and recovery (Marschall *et al.*, 1998);
- are some bryophytes 'shade plants' (Marschall & Proctor, 2004);
- why are there so few salt-tolerant bryophytes (Bates *et al.*, 2009);
- what are the recovery of chlorophyll-fluorescence (photosynthetic function) parameters after desiccation (Proctor & Bates, 2018) and do bryophytes and pteridophytes differ in their recovery rates (Proctor, 2010c);
- why do Polytrichaceae have lamellae (Clayton-Greene *et al.*, 1985; Proctor, 1992b, 2005);
- how does the structure of bryophytes relate to their ecological adaptation and physiology function (Proctor, 1979a, 1984b, 2014);
- what is the physiological basis of bryophyte production (Proctor, 1990)?

Besides using British and Irish bryophytes in his ecophysiological work, Michael also used species from Hungary (Csintalan *et al.*, 1997, 1998, 1999, 2000; Tuba *et al.*, 1996, 1997, 1998, 1999), Uganda (Proctor, 2002), Australia and New Zealand (Proctor, 2004b) and Venezuela (León-Vargas *et al.*, 2006), as well as filmy-ferns from Trinidad, Venezuela and New Zealand (Proctor, 2012c).

With the publication of these and other primary research papers and from his thorough, wide-ranging and thoughtful reviews and lively commentaries (e.g. Proctor, 1981, 1982, 1984b, 2000a, c, 2007, 2009b, 2011, 2012b, 2013a, 2014; Proctor & Tuba, 2002; Proctor *et al.*, 2007), Michael was widely recognised as one of the world's leading bryophyte ecophysiologists. He had opened up several new research avenues (e.g. Pressel *et al.*, 2009; Proctor *et al.*, 1998, 2007), had developed and adapted analytical techniques and procedures more commonly used in vascular-plant physiology and biochemistry (Proctor, 2010c; Proctor & Bates, 2018; Proctor & Smirnoff, 2000, 2011, 2015; Proctor *et al.*, 1992), had addressed many key questions in our understanding of the growth and survival of bryophytes (Proctor *et al.*, 2007) and had provided many new insights into the structure, function, growth and physiology of bryophytes (Proctor, 2014). His last publication (Proctor & Bates, 2018) used chlorophyll-fluorescence measurements for 37 species to show three main types of light-curve responses (photoinhibition, photoreduction and photosynthesis) in bryophytes.

During his ecophysiological research, Michael returned to his life-long question of how bryophytes and vascular plants have adapted to the uneven and erratic supply of water in many parts of the globe – what he termed 'the bryophyte paradox' (Proctor, 2000a). He also considered 'poikilohydry and homoihydry: antithesis or spectrum of possibilities?' (Proctor & Tuba, 2002). He emphasised (Proctor, 2000a, b, 2014) that the vast majority of terrestrial vascular plants have only one strategy for adaptation to an erratic water supply. Desiccation-tolerant bryophytes, however, have an alternative strategy: photosynthesise and grow when water is available and suspend metabolism when it is not. The major contrasts between vascular plants and bryophytes are summarised

Table 1. Ecophysiological and structural differences between terrestrial vascular plants and bryophytes

Vascular plants	Bryophytes
Endohydric; a few are ectohydric	Ectohydric; a few are endohydric
C3 or C4 or CAM metabolism	C3 metabolism
High carbohydrate content	Low carbohydrate content (as in seeds)

in Table 1. The ability to tolerate desiccation avoids the problems of drought. Desiccation-tolerant bryophytes are more similar to mesic desert ephemerals or temperate winter annuals (with desiccation-tolerant tissue substituting for desiccation-tolerant seeds) than to drought-tolerant xerophytic vascular plants (Proctor, 2000a, b; Proctor & Tuba, 2002). Proctor (2000b) emphasises that 'Bryophytes are not simply potential vascular plants that have not yet got round to evolving stomata; they represent a radically different way of doing things'. He also suggested that 'Bryophytes … may be seen as the mobile phones, notebook computers and diverse other rechargeable battery-powered devices of the plant world – not direct competitors for their mains-based equivalents, but a lively and sophisticated complement to them'. Bryophytes can survive long periods without water, they are ectohydric and benefit from drying and wetting cycles, some can survive without nutrients (*Sphagnum*) and some can survive in extreme hazardous environments (e.g. fire-prone systems) (Proctor, 2000b). Michael concluded that 'Bryophytes have much to offer plant science research. Apart from being fascinating plants in their own right (and sometimes a source of surprises), they can provide us with simpler systems to work with than vascular plants (avoiding such complications as stomata and diploidy) – though that simplicity may need to be approached with a certain critical caution. As a stimulus to lateral thinking they can lead us to question facile assumptions we may make from long familiarity with vascular plants, and get us back to thinking physiological problems through from first principles.' Michael's many contributions to bryology illustrate not only how fascinating bryophytes are but also how they represent 'a radically different way of doing things'. His last reviews (Proctor, 2011, 2014) exemplify the points discussed above, namely bryophytes and vascular plants are different and should both be studied in detail. In his last commentary article (Proctor, 2012b), he argues that 'Lichens and bryophytes are sophisticated photo-autotrophs in their own right, not in any way "primitive" or "lower" in the sense of "haven't made the grade". They … should be approached from cell-biological and physical first principles. The label "lower" plants is like "black". As simple adjectives they are both harmless, but in plant science as in society it is the cluster of associations they arouse in many people that do the damage.'

Pollination biology

Another area where Michael made important contributions is pollination biology. Michael was a very keen and knowledgeable entomologist and was fascinated by pollination biology. He shared these interests with his Queens' contemporary Peter Yeo (Proctor, 2010b). As undergraduates, they frequently went plant-hunting and Hymenoptera-collecting, especially searching for early species of *Andrena* and *Halictus*. In about 1960, Peter and Michael were asked by John Gilmour, an editor of the New Naturalist book series, if they would write about pollination. They agreed and Michael took on the challenge of photographing pollinating insects. He initially used a home-made flash bar to support his Mecablitz flash-gun on his Praktica or


△ Figure 13. Michael in characteristic position photographing *Cinclidium stygium* on Malham Tarn Fen in 1965 and the actual patch he was photographing (right). *John Birks*

Pentax 35 mm single-lens reflex cameras fitted with extension tubes. He subsequently used a Minicam ring-flash along with a 55 mm macro-lens to produce shadow-free images of insects collecting pollen. He used Ilford Pan F or Kodachrome 25 colour film. As Michael notes (Proctor in Proctor *et al.*, 1996) 'Overall, perhaps 50% of exposures yielded reasonably framed and acceptably sharp negatives, but the really worthwhile pictures probably averaged only two or three on a 36-image film'. The 200 stunning photographs in *The pollination of flowers* (Proctor & Yeo, 1973) (Fig. 10) took up much of Michael's spare time over two years. 'In effect, they were my research project … I got through quite a lot of film. In those days, black-and-white film was reasonably cheap if you bought in bulk and reloaded the cassettes yourself' (Proctor in Marren, 1995, 2005). The book quickly became a classic and Michael, Peter and Andrew Lack (a former PhD student of Peter's who had worked on the pollination of the two native species of *Centaurea* (Knapweed) on the Devil's Dyke near Newmarket) combined forces to produce a new and extensively revised book *The natural history of pollination* (Proctor *et al.*, 1996) (Fig. 10). Andrew Lack recalls (in Marren, 2005) that this revision 'took a long time, but towards the end when Michael in particular was in full steam, he took to ringing me up at 10:30 in the evening and discussing a few arcane points for an hour. … I think at least once I picked up the phone and said "Hello Michael" before he said anything!' The resulting book, with over 250 stunning black-and-white and 30 colour images by Michael, was a great success.

Photography

In addition to being an outstanding botanical polymath, Michael was also a most talented photographer, not only of all types of plants and their habitats, but also of vegetation, landscapes and insects (see above). He had a wonderful eye for what would make a good photograph, and the gift to recognise what would result in an 'acceptable', 'pleasing', or 'very pleasing' image. As an undergraduate he acquired an old German plate camera, held together by tape and wire, which he loaded with ex-RAF government surplus sheet film, which he cut up in a darkroom into 2½ × 3½ inch sections. As Marren (1995, 2005) notes, 'these large-format plates produced prints of superb technical quality, with all the characteristic sharpness and depth of Proctor's photographs'. Some of these outstanding pictures are reproduced in the New Naturalist volumes *Wild flowers* (Gilmour & Walters, 1954) and *Mountain flowers* (Raven & Walters, 1956).

Michael progressed from his old and well-used plate camera to single-lens reflex cameras, initially an East German Praktica (Fig. 13) and then a Pentax (Fig. 14) and colour film as it became readily available. His first colour pictures to be published are in *Mountain flowers* (Raven & Walters, 1956) He later migrated to Olympus equipment, and he rapidly embraced digital photography as it developed in the early 1990s. He published many outstanding pictures, probably over 1000 images, of vascular plants (e.g. Pigott & Walters, 1954; Proctor, 1991, 2013b; Tansley & Proctor, 1968), trees and shrubs (Caldwell & Proctor, 1969; Proctor *et al.*, 1980) (Figs 7, 14), bryophytes (Proctor, 1964, 2013b), vegetation and landscapes (Pigott & Walters, 1954; Proctor, 1958, 1967b, 2013a, b; Proctor *et al.*, 1980; Tansley & Proctor, 1968) and insects (Proctor & Yeo, 1973; Proctor *et al.*, 1996). He wrote an invaluable and highly informative chapter about plant photography (Proctor, 1974b) in Turner Ettlinger's (1974) book on *Natural history photography*. Michael became a Fellow of the Royal Photographic Society in 1973, an honour that gave him very much pleasure.

△ Figure 14. Michael photographing trees in the grounds of the University of Exeter *c*. 1970. *Peter Marren*

When it came to photography or his final-year exams, Michael had his own priorities. His Cambridge colleague Donald P1igott recalls 'a particular memory of those early years, which says something about Michael's priorities, was meeting him one morning [1951] during his Tripos exams at the entrance of the Botany School. He was clearly going out with camera

and bicycle and, on asking if he had no exams, he replied "not until later" but as there was no wind, conditions were ideal for photographing *Linum anglicum* on the Gog and Magog Hills.' (Pigott in Ross, 2018)

Teacher and mentor

As one might expect from Michael's wide range of interests and expertise, he was a very stimulating teacher, especially in the field. He taught a wide range of courses – plant ecology, plant anatomy, history of the British flora, lower plants, plant taxonomy, bryophytes, etc., plus field courses in Britain, Ireland, Channel Islands and Switzerland (see Proctor [1967b] for how he taught plant ecology in the lecture room and the field). Michael greatly enjoyed teaching as it provided, as he once told us, 'a good excuse to keep up-to-date'. As a student at Exeter, Peter Marren (1995, 2005) commented 'as a classroom teacher, he perhaps took an over-optimistic view of the intelligence of his students' and also wrote that 'his students will remember his illustrated lectures, full of slides of dazzling quality' (Marren, 2017). His teaching in the field was always a great learning experience, as he was knowledgeable about almost every organism, from seaweeds and flies to birds, bryophytes and trees. He generously shared his vast knowledge of these subjects, and his many non-biological interests, with anyone who was interested.

Personality

Michael was an erudite but very modest, self-effacing person who never sought the limelight. Besides his family of one daughter (deceased) and two sons, to whom he was devoted, he lived for botany and, of course, photography. He joined the BBS in 1950, was its President in 1984–85, helped edit *Journal of Bryology* in 1980–82 and was elected an Honorary Member in 1992. He also joined the BSBI in 1950, edited its journal *Watsonia* from 1959–71 and was elected an Honorary Member in 1971. It is a rare distinction to be an Honorary Member of both the BSBI and BBS. He was a trustee of Paignton Zoo (1969–81, 1991–96), which specialised in the conservation of rare species, and was a founder of the Devon Wildlife Trust. He was elected a Foreign Member of the Norwegian Academy of Science and Letters in 1997 and an Honorary Member of the Hungarian Society for Plant Physiology in 2000, as well as being a Fellow of the Royal Photographic Society in 1973.

Michael was not really a person for administration, bureaucracy or committees; he was a person for action (Pigott in Ross, 2018). He generously served as External Examiner for many doctoral theses in Britain, Ireland, Sweden and Norway. His examinations were always fair, performed in a friendly and understanding way, and often with some rather Michael-type jokes that did not always work well with our Norwegian candidates. He was well travelled, ranging from Iceland to Uganda and Australia, but most of all in the Alps, Scandinavia and eastern Europe. With his genuinely inquisitive mind and prodigious memory, he was interested in almost everything – plants, animals, landscapes, history, folk-traditions, geology, fossils, languages, aeroplanes, vintage cars, locomotives, steam engines, Tom Lehrer and music, especially choral music and the music of Beethoven and Schubert. He enjoyed singing and in his retirement he joined Exeter Cathedral Choir. With his remarkable memory, he could cite long passages from A.A. Milne, Hilaire Belloc, Gilbert and Sullivan, Flanders and Swann, Beyond the Fringe and even Virgil (in Latin of course!). He had a stock of funny limericks, mostly botanical. He had a dry, rather academic sense of humour, rather in the style of

the Cambridge Botany School's students spoof journal *The Tea Phytologist*. All the articles are anonymous, but we wonder if Michael was the author of 'A contribution to the speculative phytogeography of discontinuous distributions' in the March 1954 Vol. 0.002127 issue of *The Tea Phytologist*. This article is written by someone with an erudite and academic humour, and knowledge of botany, *Helianthemum oelandicum, Veronica spicata, Hypochaeris maculata,* phytogeography, physics, diffusion theory and mathematics: Michael is certainly a potential candidate! Michael loved making puns and jokes, often in different languages such as Welsh, German, Russian, Japanese, or Latin. Sadly, few could really understand the jokes as the vast majority of us are linguistic ignoramuses.

We were beneficiaries of Michael's generosity in sharing his vast knowledge with anyone who was interested. For example, while we were students, we attended his Field Studies Council course on Mosses and Liverworts at Malham Tarn Field Centre in the early 1960s where he showed us 395 species in six days. At the end of the course, Michael gave us a test to identify 20 specimens. One of us (John) got one very wrong by calling it *Nardus stricta* (Mat Grass) when the specimen was *Nardia scalaris* – a sure sign of memory overload! His Malham course stimulated our life-long interest in bryophytes. He also initiated and encouraged our photographic activities. Michael suggested key areas in the Alps for us to explore on our first botanical trip there in 1969. He joined us in Abisko (Swedish Lapland) in 1988, visited us in Cambridge and Bergen many times and botanised with us in Devon, the Lake District, Yorkshire and Cambridgeshire.

Lessons from Michael's life

Besides reading and learning from his many published contributions as a scientist and as a photographer, what can one learn from Michael's life and achievements about teaching, research, inspiring students, developing identification skills, and transferring knowledge in today's academic environment? First, always be inquisitive and try to develop a good memory and language skills. Second, teach yourself identification skills using floras and monographs, not illustrated field guides or apps. Third, be self-motivated, ask interesting and novel questions and try to find answers for oneself. Fourth, realise the importance of sound taxonomy as it is the basis of plant sociology, ecology and comparative ecophysiology. Although describing vegetation in terms of species is considered by some to be old-fashioned, it provides a tremendous training in field discipline, plant identifications, careful recording and an appreciation of location and vegetation type in the landscape. Fifth, realise that everything is interesting if you study it in enough detail! And sixth, realise that there are at least two approaches to doing research – hypothesis-testing and the inductive–deductive approaches. Both are valuable and science proceeds not only by hypothesis-testing but also by assembling systematic bodies of data that invite further study (Proctor, 2010d).

Michael Proctor was a truly great botanist, bryologist, plant ecologist, ecophysiologist, photographer, author, teacher, mentor and friend. As Peter Marren (2016) writes about Michael, 'his wizardry in the field was matched by technical know-how in the lab. I began to think I had met my first "genius"'. We totally agree with Peter's thought. Michael was a really great botanical polymath.

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