Few bryologists have genuinely earned the accolade ‘a legend in his or her lifetime’ but Rudy Schuster was that in every possible way. His death in November 2012 was a major and truly sad event in the field of hepaticology as it brought to an end a remarkable, colourful and prodigiously productive career. He was one of the few really great hepaticologists of the twentieth century.

Rudolf M. Schuster was born on 8 April 1921 at Altmühlhof, near Munich in Bavaria, southern Germany. His father Mathias owned a small cabinet-making business, but because of the severe economic depression his father travelled to USA in 1929, arriving in New York on the day of the Wall Street crash on twenty-fourth October (Engel & Klekowski, 1988; Qiu et al., 2013). The family, including Rudy, followed the next year, and he became a US citizen in 1937. As a teenager he started work as a cabinet-maker’s assistant to his father and completed his schooling at Stuyvesant High School in New York in 1939. His university education was at Cornell University in Ithaca from 1942 to 1945 when he gained his Bachelor of Science degree, and continued a further year to gain his Masters degree (Qiu et al., 2013). During his Cornell days, he met his future wife Olga and they were married in 1943. Their daughters Erica and Hilde were born in 1948 and 1951, respectively. Olga was Rudy’s constant companion and assistant until her death in 2005, both in the field and in their summer and winter homes at Hadley, Massachusetts, and Green Valley, Arizona, acting as his herbarium curator and typing and editing his prolific books and papers. Rudy later got married again to Marlene who contributed much assistance on his later bryological works. He died at Stanwood, Washington, on 16 November 2012 (Qiu et al., 2013).

Since childhood in Germany, Rudy had had an interest in natural history, and at Cornell he took up the study of a genus of parasitic wasps – ‘Having written a research paper, as a sophomore at Cornell, on Ephuta (Mutillidae), I found that, on my arrival at the University of Minnesota in the summer of 1946, this would be acceptable as a Ph.D. dissertation after some relatively minor additional research’ (Schuster, 1953–1958). In Minnesota, zoology became a sideline and his main focus transferred to Hepaticae, which up to then had been his hobby. Thus, from 1946 to 1948 he focused on what was to become his first major liverwort flora – ‘Boreal Hepaticae. A manual of the liverworts of Minnesota and adjacent regions’ (Schuster, 1953–1958; Frenkel & Abbe, 1988). Although he cited a number of other collectors, it is clear from the specimen citations that he carried out most of the field work for this flora himself. Before it was published he had moved to the University of Mississippi as an Assistant Professor (1950–1953), not a happy match (Anderson, 1988), then he moved again to Duke University in North Carolina for three years, becoming a colleague of Lewis Anderson (b1912 – d2007) who provided a humorous and highly readable anecdote of this period (Anderson, 1988).

This period at Duke enabled him to focus on what was to become his biggest and most celebrated project: ‘The Hepaticae and Anthocerotae of North America, east of the hundredth meridian’ (Schuster, 1966–1992), which became colloquially known as ‘The Big Green Book’. As he explained in the Preface of the first volume: ‘The authorities of Duke University provided an appointment for three years involving minimal duties, thus encouraging the writing of this work [all 6 vols.]; nearly half of the writing of the initial draft was done there, and many of the illustrations prepared then’ (Schuster, 1966, page x). One person he acknowledged there was A. W. Evans, for whom Schuster had a very high regard because of the quality of his work. In fact, a great deal of ground work for Schuster’s flora had been laid by Evans in a long series of papers on North American liverworts published between 1892 and 1940, listed in Schuster’s comprehensive bibliography.
Obituary

(Schuster, 1966, Vol. 1, pp. 35–39), and frequently referred to in all six of Schuster’s volumes.

The dust wrapper of Volume 1 described the work as ‘a projected three-volume work’. However, of the six volumes and over 6000 pages eventually published, Volume 1 (1966) is arguably the most important as it contains a comprehensive bibliography running to 105 pages, and an extremely thorough treatise on the science of hepaticology, with a historical summary, treatment of morphology, cytology, reproductive biology, phytogeography, ecology, fungal symbiosis, evolutionary history and phylogeny and finally a summary of liverwort classification. The whole work is the most comprehensive liverwort flora ever published, with extremely detailed keys, descriptions and illustrations.

During this period at Duke he came into contact with some of the other leading lights in North American bryology such as Howard Crum, Jack Sharp and Wilf Schofield. These were muscologists who did not encroach into liverwort territory. Others who did, such as Johannes Proskauer and Margaret Fulford, were seen as competitors whose work was often criticised by Schuster, sometimes in footnotes which at times were particularly scathing. A typical example is in his monograph of Blepharostomataceae (Schuster, 1966–1967) where most of the work done by Fulford on this family is criticised. Ironically, some of Schuster’s work on this group contained errors, such as his ‘new’ genus Lophochaete invalidly published (and now sunk into Fulford’s genus Pseudolepicolea). This was pointed out by Proskauer (1967) in his review of Volume 1, which is full of praise for the work but not without criticisms, for example on nomenclature ‘Schuster seems to favour the kind of nomenclature which interprets a name in terms of what one worker thinks the man before him thought a name meant, and not the established type method.’

From his German origins he was completely bilingual and able to correspond freely in German with the foremost European hepaticologist of the time, Karl Müller of Freiburg im Breisgau, Germany, and later on Riclef Grolle of Jena. After a year in the University of Michigan in Ann Arbor, he moved in 1957 to the University of Massachusetts in Amherst, as an associate professor, and soon after full-time professor. This became his long-term home until he retired in 1983 (Qiu et al., 2013). Although his independent spirit and forthright views led to many conflicts with university bureaucracy, he gained a very high worldwide reputation for his scholarly and thorough research on liverwort taxonomy, evolution and biogeography. One can get a very good picture of this period of his career, particularly his teaching prowess, from the tribute by Barbara Thiers, Rudy’s only doctoral student (Thiers, 1988). At Amherst the Schuster house gradually became his herbarium and laboratory, and according to Lewis Anderson ‘he built much of the house himself’. Later, it became the summer residence when a house in Green Valley, Arizona, became the winter home to escape the New England winters. The prodigiously productive Amherst period and the long list of resulting books and papers are summarised by several authors in the Festschrift for Rudy ‘Bryological Contributions’ (Engel & Hattori, 1988).

With the help of Olga at the typewriter, Rudy never felt the need to move into the age of computers and never used one. However, his lab was furnished with high-quality microscopes and he used simple but remarkably effective technology in preparing his drawings of liverworts. Rudy’s pen and ink drawings were simply outstanding and grace all of his publications with their detail and superb quality – they are beautiful works of art as well as showing all the remarkable details of liverwort stems, leaves, oil bodies, gemmae and reproductive structures such as capsule wall thickenings, cross-sections of setae, spore ornamentation and so on. When the author visited their home in Hadley in October 1980 he was very warmly welcomed by Rudy and Olga who had invited him to stay for a few days, where Rudy demonstrated his drawing techniques using a vertically mounted old-fashioned micro-projector. Specimens (preferably living or preserved in fixative) were mounted on microscope slides and projected on to a sheet of paper below, where they could be traced at appropriate magnifications and later combined and inked to form the composite plates which are a hallmark of all his publications. On that visit they also generously and proudly took him on a tour of the New England forests in their colourful autumn splendour, and also to a classical music concert in Amherst. Long had first met Rudy in Scotland in 1978 when Rudy and Olga, along with Wilf and Peggy Schofield from Canada, had joined the annual meeting of the Nordic Bryological Society in Scotland, organised by Alan Crundwell at Ardornish Castle on the Morvern Peninsula (Figure 1). In a splendid week of sunshine, the author was able to show Rudy for the first time the rich Atlantic liverwort flora of western Scotland, including treasures such as Acroblus wilsonii, Plagiocilia carringtonii and to his particular delight, Cryptothallus mirabilis, and he enlivened the whole meeting with his humour and tales of his travels.

There is no doubt that a major factor in Rudy Schuster’s encyclopaedic knowledge of liverworts has been his worldwide field study of the group in many continents and countries. His numerous
collecting trips from 1946 to 1988 are summarised by Engel & Klekowski (1988), notable being his extensive work in the Arctic, from Ellesmere Island in 1955 (Schuster et al., 1959), to Greenland in 1960, 1966, 1970 and 1982 (Schuster & Damsholt, 1974; Damsholt, 1988), many parts of South and Central America, major trips in New Caledonia, Australia, Tasmania and New Zealand, shorter visits to Japan and numerous visits to Europe and Scandinavia, not to mention extensive work in many parts of USA. Only a few of these can be mentioned, but most have contributed significantly to his major publications, discussed below, in terms of acquiring high-quality herbarium specimens. His very sound approach was careful searching in the field for fertile plants and reproductive structures, and often microscopic observation of oil bodies in fresh material in field laboratories such as the Biological Station on Disko Island in West Greenland where he worked with his long-standing collaborator Kell Damsholt. He also habitually preserved reproductive structures in fixative in the field to facilitate more accurate illustration back in Amherst. He could also spot even tiny species in the field without a hand-lens because of his being extremely short-sighted (Rob Gradstein, pers. comm.).

Although his herbarium collections from these expeditions numbered over 60,000 in total, he was surprisingly reluctant to lend material to other workers (Gradstein, 1999), perhaps as he wished to keep them for his own studies, particularly his planned (for over 40 years) monographic treatment of the families and genera of liverworts for a comprehensive update of Schiffner’s world treatment of the liverworts in Engler & Prantl’s ‘Naturlichen Pflanzenfamilien’ (Schiffer, 1893). For unknown reasons (Rob Gradstein, pers. comm.) no part of this has been published. However, most of his published taxonomic papers on exotic liverworts after he moved to Amherst were in fact precursors for this work. In one case where he did lend collections to another researcher – in the case of his New Guinea collections which were sent to Riclef Grolle in Jena (Grolle was actively researching New Guinea liverworts at the time), Schuster told the author that he regretted lending these collections, because the material was subdivided and only part returned to him in Amherst. Grolle clearly planned a series of papers ‘Novae Guineae Hepaticae Schusteranae’ but in the end only one was ever published under this title (Grolle, 1969) which included a new species Colura schusteri Grolle. Although this series was halted, Grolle continued to use the collections in a series of 17 papers ‘Lebermoos aus Neuguinea’ up to 1979 (see Gradstein, 1999). This series included further new species such as Acromastigum longirete Grolle, based on Schuster material. Schuster’s own herbarium, including hundreds of type specimens, is now in the Field Museum in Chicago, Illinois, and specimens are at last available for study by other workers (Qu et al., 2013).

On one of the author’s visits to Jena to work with Grolle on Asterella, Riclef told him of one of his greatest disappointments, was not being allowed by the East German authorities to leave the country to take up an invitation to visit and work with Rudy Schuster in USA. In fact they never met until June 1980, in Poznan in Poland, at an international bryological conference, where they were introduced to each other by Professor Jerzy Szweykowski as described in a rather moving account (Greene, 1980). Riclef, because of his great physical disability (Zündorf et al., 2005), was unable to do any fieldwork and was forced to study only herbarium material loaned and gifted to him by many colleagues and institutes. On top of this he had a very sound grasp of botanical nomenclature and saw it as a priority to put to rights many unfinished or erroneous nomenclatural tangles. Rudy, on the other hand, was the complete field bryologist, working with his own material gathered using his critical eye and always of optimal quality. He had little desire to study old collections including types and was reluctant to get involved with nomenclatural matters and indeed was contemptuous of those who showed ‘an over-concern for nomenclature’ (Schuster, 1967, 1988; Gradstein, 1999). For example, he stuck to traditions at odds with the Code of Nomenclature, such as continuing to use the name Aspiromitus for what almost everyone else correctly called Anthoceros. Unfortunately, neglecting to study types sometimes caused serious misapplications of names, for which he was criticised concerning his treatment of Riccia (Jovet-Ast, 1994). Perhaps, had Rudy and Riclef been able to collaborate, they could have made a good complementary team.

The scientific achievements of a lifetime’s study of liverworts in the case of R. M. Schuster are enormous in scale and depth. They can be grouped into a number of themes: taxonomy and floristics of North American and Arctic liverworts; worldwide monographic studies on Lejeuneaceae, Lophoziaceae, Blepharostoma, Schistochilaceae, Treubiacceae, Takakia, and other groups; studies on austral Hepaticae from Latin America and Australasia; liverwort classification and phylogeny and finally liverwort biogeography. Frequently, these themes overlapped and merged with each other, but all culminated in major seminal works and in the description of numerous new families, genera, species, subspecies and varieties.
The numerous field trips, particularly to the southern hemisphere, helped him to gain a very detailed knowledge of Hepaticae on a global scale, never equalled by any other worker except Riclef Grolle. This led to a shift of focus to another major projected multi-volume work ‘Austral Hepaticae’ of which only two volumes were published (Schuster, 2000, 2002) – essentially a synoptic monograph of southern hemisphere liverworts but including many from the northern hemisphere. For example, most family treatments include keys to genera worldwide and treatments of austral species and often boreal species too. The lack of a rigid geographical circumscriptio to the work undoubtedly meant it could never be completed, but does make it an exceptionally useful work for those groups favoured. His field trips also enabled major monographs of large and difficult genera to be taken on, e.g. New Zealand and Tasmanian Plagiochilaceae with Hiroshi Inoue (Inoue & Schuster, 1971), Australasian Schistochilaceae with John Engel (Schuster & Engel, 1985) and Antipodal Gymnomitriaceae (Schuster, 1996). In total, 101 new genera were published by R. M. Schuster, and 76 of these are still recognised (Crandall-Stotler et al., 2009). Of those no longer accepted, most have become synonyms following more recent monographic or molecular work, and only a few were shown to be superfluous synonyms of previously existing genera such as Anomonomarsupella (=Eremonotus) and Dianthelia (=Gymnomitrion).

His accumulated encyclopaedic knowledge of liverworts allowed him to formulate and develop sophisticated ideas on liverwort phylogeny and biogeography, which became major preoccupations and resulted in several major publications in the 1980s, such as ‘Palaeoecology, origin, distribution through time, and evolution of Hepaticae and Anthocerotae’ (Schuster, 1981), ‘Generic and familial endemism in the hepatic flora of Gondwanaland: origins and causes’ (Schuster, 1982) and ‘Reproductive biology, dispersal mechanisms, and distribution patterns in Hepaticae and Anthocerotae’ (Schuster, 1983). These were followed by the ‘New Manual of Bryology’ (Schuster, 1983, 1984), edited solely by him with the help of Olga (as explained in the dedication), and of the 1295 published pages, well over a third (519) were contributed by him, and gave him the opportunity to develop and expand at length on the treatise in Volume 1 of ‘The Hepaticae and Anthocerotae of North America’. These chapters included Phytochorography of Bryophyta, Comparative anatomy and morphology of Hepaticae, Evolution, phylogeny and classification of Hepaticae, Morphology, phylogeny and classification of Anthocerotae and finally Palaeozoic and Mesozoic fossils (co-authored with V. A. Krassilov).

In the case of his liverwort classifications, that of 1984 shows many refinements from the 1966 one, for example in that Hornworts were removed from the Hepaticae, but Takakia remained deeply embedded in the liverworts within the order Calobryales of the subclass Jungermanniidae. Much later, in Volume 1 of Austral Hepaticae (Schuster, 2000) his classification of liverworts was further refined, for example by the removal of Takakia from the liverworts into its own class Takakiopsida – neither a moss nor a liverwort (see Schuster, 1997), in spite of increasing evidence that it was a moss (Murray, 1988; Smith & Davison, 1993), a position now generally accepted (Goffinet et al., 2009). Schuster (1997) argued that the mix of liverwort and moss features in Takakia supported the monophyly of the Bryophytes. In the case of the southern hemisphere thalloid genus Monoclea, he consistently stuck to his view that ‘it must be placed very low in any evolutionary scheme’, treating it as a separate order Monocleales, dismissing Proskauer’s (1951) assessment that it showed affinities with the Marchantialean genus Dumortiera as ‘unwar- ranted speculation’. In fact, Proskauer has now been vindicated by molecular evidence (in contrast to contradictory morphological evidence), placing in a highly derived position within order Marchantiales (Forrest et al., 2006).
These developments in understanding liverwort morphology, due in a large part to Schuster’s thorough study and interpretation of the whole spectrum of the liverworts, beg the question: What would have happened if Schuster’s lifetime’s work had overlapped or coincided with the molecular era? With the hindsight offered by the ever-increasing plethora of molecular phylogenetic studies on liverworts now available, it is easy to find places where his classification requires modification, as in the case of Monoclea. However, his work has provided us both with a superabundance of precise morphological data on all the liverworts and a whole range of well-constructed hypotheses which can now be tested using modern molecular tools. Many of these await critical re-appraisal in the face of new molecular data, and it is likely that many of his ideas will gain new support. Thus, the ‘Schuster Era’ of hepatocology is far from over and will continue to inspire researchers for many generations to come.

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