It is with great sadness that we note the passing of Richard M. Elliott of the MRC-University of Glasgow Centre for Virus Research.

Richard brought bunyaviruses, which today are recognized as a clear threat to public health and agriculture and one of the largest RNA virus families, to the attention of a broader scientific audience. Richard’s career began with a PhD in virology in the laboratory of the late David Kelly at the University of Oxford, followed by a post-doctoral stay with Peter Palese at Mount Sinai Medical School in New York. He then moved back to the UK in 1981, joining initially what was at the time known as the MRC Virology Unit located in Glasgow. He moved to the University of Glasgow Department of Virology as Senior MRC Fellow in 1986 before becoming Professor of Molecular Pathogenesis in 1995 and joint Head of Division of Virology in 1998. He continued to work at the University of Glasgow until 2005 when he moved to the University of St Andrews and became Professor of Virology. In 2013, he returned to Glasgow to join the newly established MRC-University of Glasgow Centre for Virus Research where he held the Bill Jarrett Chair of Infectious Diseases.

Richard’s contributions to the understanding of bunyavirus molecular biology were world leading. Most bunyaviruses are transmitted by arthropod vectors such as mosquitoes, ticks, sandflies and midges. Until a couple of decades ago, most of the viruses transmitted by arthropods (‘arboviruses’) were confined to tropical and subtropical areas of the world. However, the exponential increase in travel and commercial exchanges, as well as ecological and climate change have led to a geographical expansion of many arboviruses, including bunyaviruses. Thus, although studies on ‘emerging viruses’ have become trendy among virologists, Richard was one of the pioneers in this field. Richard was an exquisite molecular virologist. Over the last three decades he unveiled many of the properties of bunyaviruses, from the intricate secrets of their replication cycle to how they counteract the immune responses of the cells and organisms they infect. His interest, however, was not just limited to the arthropod-borne bunyaviruses, but also extended to the related hantaviruses, which are rodent-borne. Molecular biology was only just developing when his research was to manipulate viral genomes to understand their structure and function, which for the segmented, negative-sense bunyaviruses meant a real challenge. Undeterred, he tried every possible method to achieve this aim and eventually managed to generate a Bunyamwera virus entirely from cloned cDNA (Bridgen & Elliott, 1996). This was the first ‘rescue’ of a negative-strand RNA virus with a segmented genome from plasmid DNA and paved the way for all the others that followed, including influenza virus. The system was optimized in such a manner that eventually just three plasmids encoding the viral antigenome sequences were sufficient to rescue virus (Fig. 1) (Lowen et al., 2004). Bunyamwera virus rescue from cDNA is without doubt one of the most important contributions to bunyavirus molecular biology and the key achievement of Richard’s career. In the subsequent years, Richard himself contributed major findings on viral virulence factors, gene regulation, promoter function, intracellular replication and particle assembly, and found ways to attenuate the viruses into safe and efficient vaccine candidates (Brennan et al., 2011b; Bridgen et al., 2001; Kohl et al., 2004, 2006; Lowen et al., 2005; Rezelj et al., 2015; Shi et al., 2007; Tilston-Lunel et al., 2015; van Knippenberg & Elliott, 2015). He published >130 papers, with many in the last few years and a considerable number in preparation at the time of his passing. Recently, his group created a Rift Valley fever virus with an altered S segment, providing valuable insight into the roles of the S segment-derived proteins in the arthropod vector. Together with collaborators in Brazil, he corrected the published genome sequence of Oropouche virus and identified novel reassortant viruses. His group established reverse genetics systems for newly emerging viruses such as Schmallenberg virus, severe fever with thrombocytopenia syndrome virus, as well as Uukuniemi virus. For the development of Schmallenberg virus reverse genetics, Richard returned to the bench and took the lead in carrying out experiments. Other avenues of recent research included looking at how bunyavirus polymerases evolve to deal with deletions in their genomes. His group also pushed the flexibility of the viral genomes to the limit by creating a recombinant Bunyamwera virus that had an ambisense coding strategy more akin to the phleboviruses. Richard had many
Richard was a member of the International Committee on Taxonomy of Viruses Bunyavirus Study Group, an important service to the community. He was also strongly involved in the organization of the European Meetings on Viral Zoonoses since 2001, which have played a major role in bringing researchers in this field together. Richard was also a major contributor to UK virology: from 1999–2002 he served on the council of the Society for General Microbiology and was Editor-in-Chief of the Journal of General Virology from 2008 to 2012. He oversaw a considerable rise in the journal’s impact factor and cemented its position as a leading journal in the field at a time when competition from new online and open-access journals began to increase.

It was characteristic of his passion and determination that he worked on manuscripts and was in touch with the laboratory and colleagues until the very last days. His sense of humour was infectious and he had many friends both through his work and his passion for fly fishing for trout. Richard was an excellent mentor, he was always enthusiastic and made time to discuss science with his post-docs and students, despite a very busy schedule. He leaves a legacy of students and post-docs with exceptional training in molecular virology, many of whom went on to become principal investigators in their own right. His passion and enthusiasm for virology influenced more than just those individuals that were fortunate enough to work with him, Richard has had an important influence in the careers of many virologists both in the UK and further afield. Whilst we mourn one of the greatest virologists of his generation, we are proud of the legacy he leaves behind, and to have been friends, colleagues and members of his group.


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**Fig. 1.** Rescue of Bunyamwera virus using the three-plasmid system. This is carried out in cells constitutively expressing T7 RNA polymerase by transfection of plasmid encoding the Bunyamwera virus L, M and S full-length antigenomes. The transcribed L, M and S antigenome RNAs are sufficient to initiate protein synthesis and virus replication, resulting in production of infectious virus.
segments of Batai, Cache Valley, Guaroa, Kairi, Lumbo, Main Drain and contributes to viral pathogenesis.

bunyavirus nonstructural protein NSs is a nonessential gene product that recombines Rift Valley fever virus with a two-segmented genome. RNA-dependent RNA polymerase.

of a recombinant Rift Valley fever virus expressing a V5 epitope-tagged Pasteur, 25 rue du Dr Roux, 75724 Paris cedex 15, France

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REFERENCES


