Atlas of Plant Viruses

Volume I

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PREFACE

Electron microscopy has played an important role in the development of virology, contributing significantly to an understanding of the molecular biology and pathology of viruses and to the development of virus taxonomy and diagnostics. Nevertheless, our impression is that, while electron microscopes and their attendant techniques are generally capable of producing micrographs of high quality, the micrographs presented to journals (and accepted by them) or published in books, vary in quality from excellent to poor. No publication exists that assembles a comprehensive collection of plant virus electron micrographs of good quality, offers a consistent treatment, and backs the visual data with a consistent and comprehensive text.

It was with these considerations in mind that we decided to embark on preparing an atlas of plant viruses. Our aim has been to bring together, in a systematic way, the available information about the morphology and cytopathology of plant viruses in all the taxonomic groups recognized by the International Committee on Taxonomy of Viruses (ICTV). We have also tried to consider some viruses that are quite well known but still unclassified.

The project might arguably have been better tackled by an editor marshalling a group of authors to write chapters on viruses with which they were especially familiar. By this procedure each group of viruses would have been treated in the most authoritative way. In practice, however, such an approach has its pitfalls. Uniformity and coherence are difficult to attain in such a book, and the near-impossibility of extracting manuscripts from all the authors on time can mean that certain chapters (written by the promptest authors) are painfully out of date at the time of publication. Believing that uniformity and coherence are important in an atlas, we chose the rather ambitious task of preparing the book ourselves. In striving to be authoritative we have relied heavily on many colleagues for information and material.

Although this book is primarily about the structure of virus particles and infected cells, we see little virtue in studying structure without function. Hence we have referred to the results of biochemical experiments where relevant, so that the virus particles described appear as part of a replicating complex. Similarly, we have tried to portray infected cells as active rather than static structures.

In Chapter 1 a brief account is given of the development of studies on virus structure, nucleic acids, cytopathology and taxonomy from their beginnings. We hope that this will provide a useful background to the chapters that follow. The two authoritative guides to the taxonomy of plant viruses used are the Reports of the ICTV and the Commonwealth Mycological Institute and Association of Applied Biologists' *CMI/AAB Descriptions of Plant Viruses*, edited by B. D. Harrison and A. F. Murant. It seems important to standardize on a list of virus abbreviations or sigla that will come to be used unambiguously by all plant virologists. We have used the list of van Regenmortel published in his book *Serology and Immunochemistry of Plant Viruses* (Academic Press, 1982) where possible, and have extended it.

We have tried to present not only the current state of knowledge about the viruses discussed, but also the current state of uncertainty (or sheer ignorance) in particular areas. In several of the chapters, data are included on unclassified viruses with possible affinities to the group under discussion; in doing this, we hope to stimulate investigations that will clarify the positions of such viruses.

The bibliographies at the end of each chapter are not exhaustive, but they include references that we consider the most relevant, and sufficient for the reader who wishes to explore further.

Many of the electron micrographs in this book concern viruses investigated as a part of a research project supported by a Commonwealth Special Research Grant from the Australian Department of Primary Industry on the "Characterization of Plant Viruses in Australia".

Many others were prepared in the Italian National Research Council Plant Virus Institute in Turin, Italy (the Istituto di Fitovirologia Applicata del CNR). Other photographs, or virus preparations from which we prepared photographs, were kindly supplied by colleagues. For easier comparison, we have presented the particles of at least one example of each virus group negatively stained in the same material (uranyl acetate) and magnified a nominal (i.e., not always accurately calibrated) 300,000 times. This is not to deny the usefulness of other negative stains or preparative techniques. In selecting the micrographs of virus-infected cells, we have included large areas of the cells where possible, so as to give a better idea of the ultrastructural context.

The treatment of some virus groups is more comprehensive than that of others. This is, we hope, mostly a reflection of the current unevenness of the available data. Perhaps the *chiaroscuro* may encourage some readers to do experiments that would help a future atlas to be more comprehensive.

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AUTHORS

R. I. B. Francki is a Reader in Plant Pathology at the Waite Agricultural Research Institute of The University of Adelaide, South Australia.

Dr. Francki received his B.Sc., M.Sc., and Ph.D. degrees in Botany from the University of Auckland in 1955, 1958, and 1961, respectively.

He has published over 100 research papers and a number of reviews in the field of plant virology. He was Chairman of the Plant Virus Subcommittee of the International Committee on Taxonomy of Viruses from 1975 to 1981. He is also presently Secretary of the Virology Division of the International Union of Microbiological Societies.

Dr. Francki is an Associate Editor of the journal, *Virology,* and of the *Journal of General Virology* and is on the Advisory Boards of *Current Topics in Vector Research* and *Microbiological Sciences*. He has also served as an Associate Editor of *Intervirology* (from 1976 to 1981).

Dr. Francki is a member of a number of national and international scientific societies, including the Society for General Microbiology, the Association of Applied Biologists, the New York Academy of Science, the International Society for Plant Molecular Biology, American Society for Virology, and the American Phytopathological Society. In 1983 he was elected a Fellow of the American Phytopathological Society.

Dr. Francki has worked as a visiting researcher in a number of laboratories including the Department of Plant Biochemistry, University of California at Los Angeles in 1964 to 1965. He was a Fulbright Scholar at the Department of Agricultural Biochemistry, University of Arizona, in 1970 and a State Agricultural University Senior Research Fellow in the Department of Virology, Agricultural University, Wageningen, The Netherlands.

R. G. Milne, Ph.D., is a senior researcher with the Italian National Research Council, Institute of Applied Plant Virology, Turin.

He received his B.A. from Trinity College, Cambridge, in 1956, and his Ph.D. from Wye College, University of London, in 1960. From 1960 to 1964 he taught virology at the Botany School, Oxford University, and from 1964 to 1966 did postdoctoral research in electron microscopy at the Molecular Biology and Virus Laboratory, University of California, Berkeley. Here he was lucky to have contact with Wendell Stanley, Robley Williams, Heinz Fraenkel-Conrat, Arthur Knight, and "Geheimrat" Kleinschmidt. Returning to England, he joined the Plant Pathology Department, Rothamsted Experimental Station, Harpenden, from 1966 to 1970, and then did a year of medical electron microscopy at the Clinical Research Centre, Northwick Park, Harrow. In 1972 and again from 1974 to 1977 he was Visiting Fellow of the Italian National Research Council in the Institute of Applied Plant Virology in Turin. From 1972 to 1974 he was Associate Professor at the Institute of Molecular and Cell Biology of the University of Strasbourg. He assumed his present position in 1977.

Dr. Milne was born in Tanganyika, and when very small acquired the nickname *Bwana Madudu* ("He of the Creepy-Crawlies") due to his interest in large scorpions. As he grew bigger, the bugs that claimed his attention grew smaller. He is now author or co-author of about 80 research papers and reviews dealing mainly with thin sectioning, negative staining, and immunoelectron microscopy of plant viruses. The plant reo-like viruses have been a major interest, and lately a side-interest in virus taxonomy and nomenclature has grown uncomfortably large. He has served on the editorial board of the *Journal of General Virology* and is currently a member of the Plant Virus Subcommittee of the International Committee on Taxonomy of Viruses.

T. Hatta, Ph.D., is a head of the Plant Pathology Division, Aburahi Laboratories, of Shionogi & Co., Ltd., Shiga, Japan.

Dr. Hatta received his B.Ag.Sc. (1968) and M.Ag.Sc. (1970) from the University of Osaka Prefecture, Japan, and the Ph.D. (1975) from the University of Auckland, Auckland, New Zealand, where he studied with S. Bullivant and R. E. F. Matthews.

He was Postdoctoral Fellow in the Department of Plant Pathology at the University of Adelaide from 1975 until he assumed his present position.

He is the author of a number of research and review papers, particularly in the field of electron microscopy of plant viruses.

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TABLE OF CONTENTS

Volume I

Volume II

Chapter 1

INTRODUCTION

Who first "discovered" viruses or developed the concept "virus" as we understand it today is perhaps an idle question, as the idea took form over a number of decades.[1,2] Flower-breaking in tulips was familiar in the middle of the 16th century, and by 1719 it was well established, at least in some circles, that flower-breaking in jasmine could be graft-transmitted.[3] In 1883, Mayer[1] made a significant contribution when he found that tobacco mosaic virus (TMV) was sap-transmissible, and Ivanovski[1] in 1892 made another with his discovery that TMV was small enough to pass a Chamberland filter candle that prevented passage of ordinary bacteria. Although this discovery was important, Ivanovski did not appear to realize it, for he at first favored a bacterial toxin as the disease agent, and later suggested that it was a bacterium.[2] It was left to Beijerinck[4] at the turn of the century to develop the concept that viruses differ basically from bacteria. Nevertheless, his choice of the term *contagium vivum fluidum,* or living infectious liquid, was unfortunate and probably hindered his ideas being taken seriously for some time.

In the mid 1930s research activity on viruses gained impetus when TMV was purified more or less independently in the U.S., Britain, and Australia[5-9] and was found to be a nucleoprotein.[6] Various physical and chemical methods were used to investigate the size and shape of TMV particles. (Particles by now had superseded fluid, but for a long time arguments, that we now see as empty, continued about whether or not viruses were "living.") Even before TMV was purified, it was concluded from rather ingenious stream double refraction experiments that the particles were rod-shaped.[10] Subsequently, using crystalline purified virus preparations, X-ray diffraction studies confirmed that TMV particles were rod-shaped and that they were made up of regularly arranged, uniform subunits.[6] Furthermore, it was concluded that the particles were about 18 nm in diameter and at least ten times as long.[6] However, it was not until 1939 that the blindfold was finally removed from the eyes of researchers when a virus was examined in the electron microscope. TMV again had the distinction of being the first virus to be studied by this technique.[11]

Although of obvious potential, electron microscopy was initially slow to contribute to virology. In the early days, the cost of the tricky and capricious instrument represented a disproportionate amount of the modest budgets of virus laboratories. Suitable specimen preparation methods had also to be developed before full advantage of the electron microscope could be taken. Today, most virologists, whether researchers or diagnosticians, would consider an electron microscope as one of the most basic instruments in their laboratories. Without it, they would feel inadequate to detect, identify, or characterize the viruses they work with as well as the impurities and contaminants they hope to avoid.

I. VIRUS PARTICLE STRUCTURE

Early electron micrographs of isolated virus particles were not very informative because of the low contrast between particle and background. This is because neither proteins nor nucleic acids are opaque to the electron beam. However, even without any enhancement of image contrast, some valuable work was done. Kausche and his colleagues[11] confirmed the shape of the TMV particle and later Stanley and Anderson[12] obtained accurate size distributions of rods in purified virus preparations. Viruses with isometric particles were also examined, but the resolution was rather poor and little was achieved other than dispelling the then-prevailing view based on hydrodynamic data that particles of all viruses were anisometric.[13]