SECTION I

INTRODUCTION TO PLANT VIRUSES

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CHAPTER

1

What Is a Virus?

This chapter discusses broad aspects of virology and highlights how plant viruses have led the subject of virology in many aspects.

OUTLINE

I. INTRODUCTION

Plant viruses are widespread and economically important plant pathogens. Virtually all plants that humans grow for food, feed, and fiber are affected by at least one virus. It is the viruses of cultivated crops that have been most studied because of the financial implications of the losses they incur. However, it is also important to recognise that many "wild" plants are also hosts to viruses. Although plant viruses do not have an immediate impact on humans to the extent that human viruses do, the damage they do to food supplies has a significant indirect effect. The study of plant viruses has led the overall understanding of viruses in many aspects.

II. HISTORY

Although many early written and pictorial records of diseases caused by plant viruses are available, they are do not go back as far as records of human viruses. The earliest known written record of what was very likely a plant

virus disease is a Japanese poem that was written by the Empress Koken in A.D. 752 and translated by T. Inouye:

> In this village
> It looks as if frosting continuously
> For, the plant I saw
> In the field of summer
> The colour of the leaves were yellowing

The plant, which has since been identified as *Eupatorium lindleyanum*, has been found to be susceptible to *Tobacco leaf curl virus*, which causes a yellowing disease.

In Western Europe in the period from about 1600 to 1660, many paintings and drawings were made of tulips that demonstrate flower symptoms of virus disease. These are recorded in the Herbals of the time and some of the earliest in the still-life paintings of artists such as Ambrosius Bosschaert. During this period, blooms featuring such striped patterns were prized as special varieties, leading to the phenomenon of "tulipomania" (Box 1.1).

Because of their small genomes, viruses have played a major role in elucidating many of the concepts in molecular biology, and the study of plant viruses has produced several of the major findings for virology in general. The major steps in reaching the current understanding of viruses are shown in the timeline in Figure 1.1.

Details of these "breakthroughs" can be found in Hull (2002; plant viruses), Fenner, (2008; vertebrate viruses), and Ackermann (2008; bacterial viruses). Plant viruses played a major role in determining exactly what a virus was. In the latter part of the nineteenth century, the idea that infectious disease was caused by microbes was well established, and filters were available that would not allow the known bacterial pathogens to pass through. In 1886, Mayer (see Figure 1.2A) described a disease of tobacco that he called *Mosaikkrankheit*, which is now known to be caused by the *Tobacco mosaic virus* (TMV). Mayer demonstrated that the disease could be transmitted to healthy plants by inoculation with extracts from diseased plants. A major observation was made in 1892 by Iwanowski, who showed that sap from tobacco plants displaying the disease described by Mayer was still infective after it had been passed through a bacteria-proof filter candle. However, based on previous studies, it was thought that this agent was a toxin. Iwanowski's experiment was repeated in 1898 by Beijerinck (see Figure 1.2B), who showed that the agent multiplied in infected tissue and called it *contagium vivum fluidum* (Latin for "contagious living fluid") to distinguish it from contagious corpuscular agents (Figure 1.2C).

Beijerinck and other scientists used the term *virus* to describe the causative agents of such transmissible diseases to contrast them with bacteria. The term *virus* had been used more or less synonymously with **bacteria** by earlier workers, but as more diseases of this sort were discovered, the unknown causative agents came to be called "filterable viruses." Similar properties were soon after reported for some viruses of animals (e.g., the filterable nature of

BOX 1.1

TULIPOMANIA

Tulips were introduced into the Netherlands in the late sixteenth century. Bulbs that produced "broken-coloured" flowers were in great demand and created a rapidly expanding market, leading to hyperinflation.

(continued)

BOX 1.1 *(continued)*

Semper Augustus tulip with flower colour break (one of the most favoured varieties)

One bulb cost 1,000 Dutch florins (guilders) in 1623, and by 1635, 6,000 florins. To understand the value of this, one Viceroy tulip bulb was exchanged for goods that were valued at almost 2,400 florins:

4 tons of wheat (448 florins)
8 tons of rye (558 florins)
4 fat oxen (480 florins)
8 fat pigs (240 florins)
12 fat sheep (120 florins)
2 hogsheads of wine (70 florins)
4 barrels of beer (3 florins)
2 barrels of butter (192 florins)
1,000 lbs cheese (120 florins)
1 bed with accessories (100 florins)
1 silver goblet (60 florins)

By 1636 there was much speculation, and futures were being taken out on these bulbs. In early 1637 one bulb was valued at 10,000 florins, but a few weeks later, the bubble burst and many people were left bankrupt. It was not until the 1920s that the viral aetiology of tulip flower breaking was discovered and that the symptoms were caused by an aphid-transmitted potyvirus. Today, 100 florins is equivalent to about U.S. $30,000.

Plant	Animal	Bacteria
Prehistory		
752 AD Plant virus in Japanese poem	1350 BC Smallpox recorded in Egypt	
1600-1637 Tulipomania	1796 Jenner developed smallpox vaccine	
Recognition of viral entity		
1886 Meyer Transmission of TMV		
1892 Iwanowski Filterability of TMV		
1898 Beijerink Viruses as an entity	1898 Filterability of PV and FMDV	
		1915. Filterability of phage
Biological age		
1900-1935 Descriptions of many viruses	1900– Descriptions of many viruses	1915- Descriptions of many viruses
	1901 Mosquito transmission of YFV	Early 1920s Infection cycle understood
Biophysical/biochemical age		
1935 Purification of TMV		
1936 TMV contains pentose nucleic acid		
1939 EM TMV rod-shaped particles	1940 VACV contains DNA	
	1949 PV grown in cultured cells	1940-1970 Phage genetics
1951 TYMV RNA in protein shell		
1956 Virus particles made of identical protein subunit		
1955/56 Infectious nature of TMV RNA		
1962 Structure of isometric particles		
1983 Structure of TBSV to 2.9Å	1985 Structure of poliovirus to 2.9Å	
Molecular age		
1960 Sequence of TMV coat protein	1979 Sequence of PV VPg	
	1970 Recognition of reverse transcriptase	
	1981 Infectious transcript of PV	1978 Infectious transcript of Qβ
1980 Sequence of CaMV DNA genome		
1982 Sequence of TMV RNA genome	1981 Sequence of poliovirus RNA genome	
1984 Infectious transcripts of multicomponent BMV		
1986 Transgenic protection of plants against TMV		
1996 Recognition of RNA silencing		
1997 Recognition of virus suppressors of silencing		

Abbreviations: BMV, *Brome mosaic virus*; CaMV, *Cauliflower mosaic virus*; FMDV, *Foot and mouth disease virus*; PV, *Poliovirus*; TBSV, *Tomato bushy stunt virus*; TMV, *Tobacco mosaic virus*; TYMV, *Turnip yellow mosaic virus*; VACV, *Vaccinia virus*; YFV, *Yellow fever virus*.

FIGURE 1.1 Timeline of development of virology.

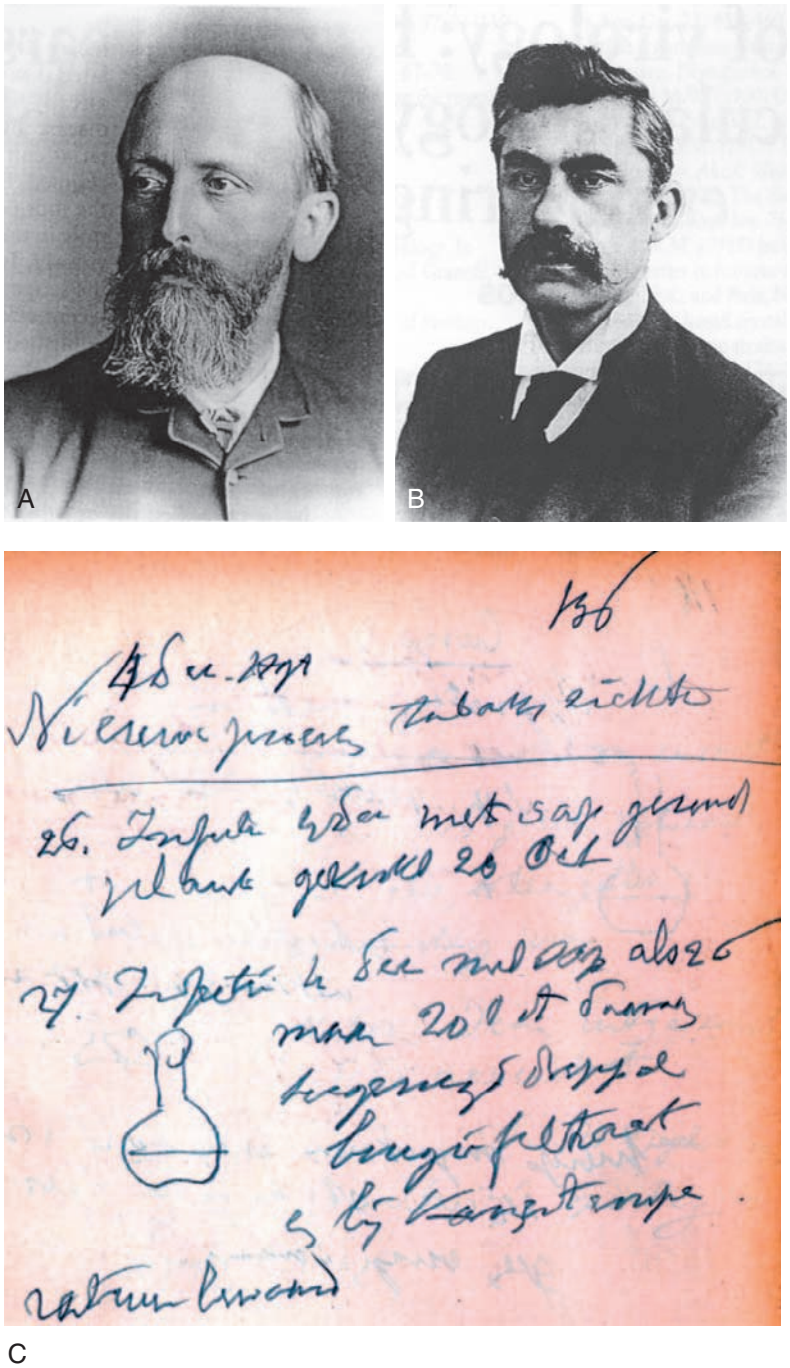

FIGURE 1.2 A. Adolf Eduard Mayer (1843–1942); B. Martinus Willem Beijerinck (1851–1931); C. Page from lab journal of W.M. Beijerinck from 1898 relating to TMV. A and B courtesy of the historical collection, Agricultural University, Wageningen, Netherlands; C. (© Kluyver Institute) Courtesy Curator Kluyver Laboratory Collection, Delft School of Microbiology Archive, Delft University of Technology.

the agent causing foot and mouth disease in 1898) and of bacteria in 1915. Over the course of time, the word *filterable* has been dropped, leaving just the term *virus*.

As shown in the timeline in Figure 1.1, in the subsequent development of virology, many of the studies ran in parallel for viruses of plants, vertebrates, invertebrates, and bacteria. In fact, when viewed overall, there is evidence of much cross-feeding between the various branches of virology. However, there were differences mainly due to the interactions that these viruses have with their hosts. For instance, vertebrates produce antibodies that counter viruses, whereas plants, invertebrates, and bacteria do not. Another factor that has contributed to advances is the simplicity of the system exemplified by studies on bacteriophage being linked to studies on bacterial genetics.

The development of plant, and other, virology can be considered to have gone through five major (overlapping) ages. The first two, Prehistory and Recognition of viral entity, were just described. After these two came the Biological age, between 1900 and 1935, when it was determined that plant viruses were transmitted by insects and that some of these viruses multiplied in, and thus were pathogens of, insects in a manner similar to some viruses of vertebrates. One of the constraints to plant virology was the lack of a quantitative assay, until Holmes in 1929 showed that local lesions produced in some hosts after mechanical inoculation could be used for the rapid quantitative assay of infective virus. This technique enabled properties of viruses to be studied much more readily and paved the way for the isolation and purification of viruses a few years later.

The Biochemical/Physical age started in the early 1930s. The high concentration at which certain viruses occur in infected plants and their relative stability was crucial in the first isolation and chemical characterisation of viruses because methods for extracting and purifying proteins were not highly developed. In 1935, Stanley announced the isolation of this virus in an apparently crystalline state but considered that the virus was a globulin containing no phosphorus. In 1936, however, Bawden and his colleagues described the isolation from TMV-infected plants of a liquid crystalline nucleoprotein containing nucleic acid of the pentose type. Around 1950, Markham and Smith showed that the RNA of *Turnip yellow mosaic virus* was encapsidated in a protein shell and was important for biological activity. This led to the classic experiments of Gierer, Schramm, Fraenkel-Conrat, and Williams in the mid-1950s that demonstrated the infectivity of naked TMV RNA and the protective role of the protein coat.

In parallel with these biochemical studies, physical studies in the late 1930s using X-ray analysis and electron microscopy confirmed that TMV had rod-shaped particles and obtained accurate estimates of the size of the rods. Attention turned to the structure of these particles, and in 1956, Crick and Watson suggested that the protein coats of small viruses are made up of numerous identical subunits arrayed either as helical rods or as a spherical shell with cubic symmetry. This led to Caspar and Klug (1962) formulating a general theory that delimited the possible numbers and arrangements of the protein subunits forming the shells of the smaller isodiametric viruses (see Chapter 5). Our recent knowledge of the larger viruses with more complex symmetries and structures has come from electron microscopy using negative-staining and ultrathin-sectioning methods.

The current Molecular age started in about 1960 when the full sequence of 158 amino acids in the coat protein of TMV was determined. The sequence of many naturally occurring strains and artificially induced mutants was also determined at about the same time. This work made an important contribution to establishing the universal nature of the genetic code and to our understanding of the chemical basis of mutation. This age continued with the sequencing of representatives of most, if not

all, virus genera leading to a greater understanding of how viruses function and interact with their hosts. The results from these studies are described in detail in this book and in the suggested further reading.

III. DEFINITION OF A VIRUS

A. How Viruses Differ from Other Plant Pathogens

In the size of their nucleic acids, viruses range from a monocistronic mRNA in the satellite virus of tobacco necrosis virus (STNV) to a genome larger than that of the smallest cells (Figure 1.3). A biologically more meaningful way of comparing genome sizes is to consider the information content—that is, the number of genes that they contain; some examples are given in Table 1.1. Before attempting to define what viruses are, we must consider briefly how they differ from other entities such as cellular parasites, plasmids, and transposable genetic elements. The three simplest kinds of parasitic cells are the Mycoplasmas, the *Rickettsiae*, and the *Chlamydiae*.

Mycoplasmas and related organisms are not visible by light microscopy. They are 150–300 nm in diameter with a bilayer membrane but no cell wall, and they contain RNA along with ribosomes and DNA. They replicate by binary fission, and some that infect vertebrates can be grown *in vitro*. Their growth is inhibited by certain antibiotics. Some mycoplasmas are plant pathogenic (see Chapter 3).

The ***Rickettsiae***, for example, the agent of typhus fever, are small, nonmotile bacteria, usually about 300 nm in diameter. They have a cell wall, plasma membrane, and cytoplasm with ribosomes and DNA strands. They are obligate parasites and were once thought to be related to viruses, but they are definitely cells because they multiply by binary fission, and they contain enzymes for ATP production.

The ***Chlamydiae***, for example, the agent that causes psittacosis, include the simplest known type of cell. They are obligate parasites that grow by infecting eukaryotic cells and lack an energy-generating system. They are as small as, or smaller than, many viruses. *Chlamydiae* have two phases to their life cycle. Inside host cells they take on an *intracellular* replicative form (termed the *reticulate body*) and rely on the host cell energy-yielding system; outside the cell they survive by forming infectious *elementary bodies* about 300 nm in diameter, which is smaller than some pox viruses. *Chlamydiae* can be grown only where their host cells grow and cannot be propagated in bacterial culture media.

Several criteria *do* and *do not* distinguish all viruses from all cells (see Table 1.2).

Plasmids are autonomous extrachromosomal genetic elements found in many kinds of bacteria. They consist of closed circular DNA. Some can become integrated into the host chromosome and replicate with it. Some viruses that infect prokaryotes have properties like those of plasmids and, in particular, the ability to integrate into the host cell chromosome. However, viruses differ from plasmids in the following ways:

1. Normal viruses have a particle with a structure designed to protect the genetic material in the extracellular environment and to facilitate entry into a new host cell.
2. Virus genomes are highly organised for specific virus functions of no known value to the host cell, whereas plasmids consist of genetic material that is often useful for the survival of the cell.
3. Viruses can kill cells or cause disease in the host organism, but plasmids cannot.

Transposons, or mobile genetic elements (sometimes called "jumping genes"), are sequences of DNA that can move around to different positions within the genome of a single cell, a process termed *transposition.* Two types of mobile genetic elements exist, based on their

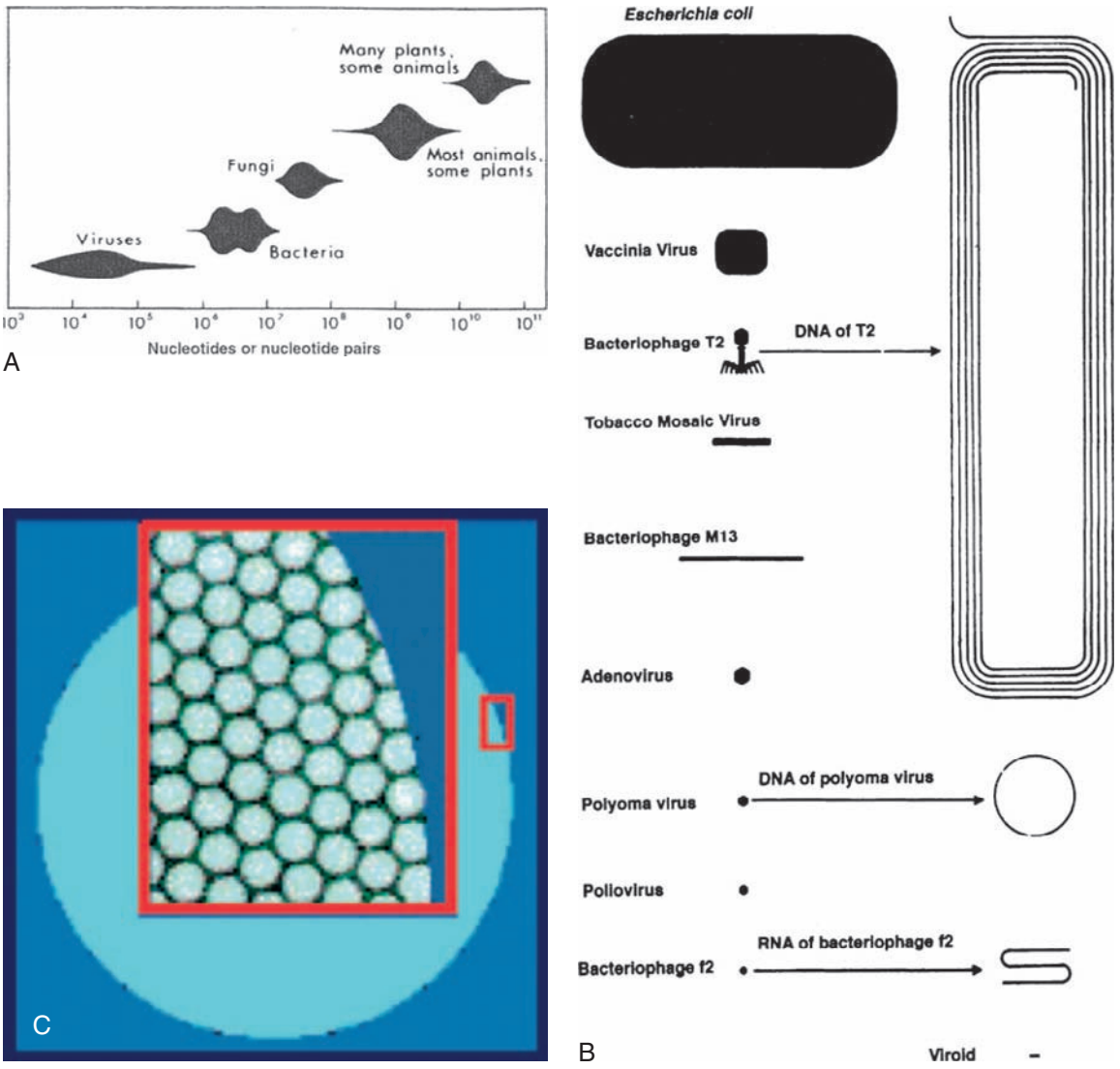

FIGURE 1.3 Size comparison of different organisms. A. Organisms classified according to genome size. The vertical axis gives an approximate indication of numbers of species within the size range of each group. B. Size comparison among a bacterium, several viruses, and a viroid. C. Comparison of size of rhinovirus and a pinhead. A. Modified from Hinegardner [1976; in *Molecular Evolution*, (F.J. Ayala, Ed.), pp. 179-199, Sinauer, Sunderland, MA]; B. With kind permission from Springer Science + Business Media: *Arch. Virol.*, Interference between proflavine treated reovirus and related and unrelated viruses, vol. 15, 1965, pp. 200–2009, E. Zalan; *Arch. Virol.*, Die Interferenz zwischen dem Polyoma-virus and dem Stomatitis-vesicularis-Virus in der Maus, vol. 15, 1965, pp. 210-219, D. Falke; *Arch. Virol.*, Properties of a new attenuated type 3 polio-virus, vol. 15, 1965, pp. 220-233, J. Šimon. C. http://web.uct.ac.za/depts/mmi/stannard/linda.html.

mechanism of transposition. Class I mobile genetic elements, or *retrotransposons*, move in the genome by being *transcribed* to RNA and then back to DNA by *reverse transcriptase*. Class II mobile genetic elements move directly from one position to another within the genome using a *transposase* to "cut and paste" them within the genome. In many properties, retrotransposons

TABLE 1.1 Information Content of Genomes of Various Organisms

Type of Organism	Example	Size of Genome	Number of Genes (Open Reading Frames)
Higher plant	Rice	3.9×10^8 kbp	>37,000
Vertebrate	Human	3.3×10^9 kbp	20,000–25,000
Invertebrate	Drosophila	1.2×10^8 kbp	~13,400
	Yeast	1.2×10^7 kbp	~5,770
Eubacteria	*Escherichia coli*	4.6×10^6 kbp	4,377
Mycoplasma	*Mycoplasma genitalium*	5.8×10^5 kbp	485
Large virus infecting vertebrates	*Vaccinia virus*	190 kbp	~250
Large virus infecting chlorella-like algae	*Paramecium bursarum Chlorella virus 1*	330 kbp	697
Large virus infecting invertebrates	*Autographa californica multiple nucleopolyhedrosis*	133.9 kbp	~150
Small virus infecting angiosperms	*Tobacco mosaic virus*	6395 nt	4
Smallest known virus	*Tobacco necrosis satellite virus*	1239 nt	1

TABLE 1.2 Distinguishing Criteria for Viruses

Criteria That Distinguish Viruses from Cells	Criteria That Do Not Distinguish Viruses from Cells
1. Lack of continuous membrane separating virus from host during replication	1. Size
2. Absence of protein-synthesising system	2. Nature and size of genome
3. Contain either DNA or RNA	3. Contain both DNA and RNA
4. Replication is by synthesis of a pool of components and not by binary fission	4. Absence of rigid cell envelope
	5. Obligate cell parasitism
	6. Absence of energy-yielding system
	7. Complete dependence on host cell for amino acids

resemble retroviruses, and they are classified as Metaviruses and Pseudoviruses. However, there is debate as to whether these are really viruses in the strictest sense. We can now define a virus, as shown in Box 1.2.

To be identified positively as a virus, an agent must normally be shown to be transmissible and to cause disease in at least one host. One of the basic tenets of pathology is that to prove that a disease is caused by a certain infectious agent, one must fulfill Koch's postulates, which were devised for bacteria; modifications of the postulates have been suggested to account for specific properties of viruses (Table 1.3). Today, however, it is not always possible to fulfill these postulates for viruses. For instance, plant cryptoviruses rarely cause detectable disease and are not transmissible by any mechanism except through seeds or pollen. Usually, it is satisfactory to show a clear association of the viral genome sequence with the disease after eliminating the possibility of joint infection with another virus.

BOX 1.2

DEFINITION OF A VIRUS

A *virus* is a set of one or more nucleic acid template molecules, normally encased in a protective coat or coats of protein or lipoprotein, that is able to organise its own replication only within suitable host cells. Within such cells, virus replication is (1) dependent on the host's protein-synthesising machinery, (2) organised from pools of the required materials rather than by binary fission, (3) located at sites that are not separated from the host cell contents by a lipoprotein bilayer membrane, and (4) continually giving rise to variants through several kinds of change in the viral nucleic acid.

TABLE 1.3 Koch's Postulates for Bacteria and Viruses

Bacteria	Viruses[a]
1. Demonstrate that the agent is regularly found in the diseased host	1. Isolation of virus from diseased host
2. Cultivate the agent on a suitable medium	2. Cultivate virus in experimental host or host cells
3. Reproduce the disease in the host by reintroducing the cultured agent	3. Prove lack of larger pathogens
4. Reisolate the agent from the artificially infected host	4. Produce comparable disease in original host species or in related ones
	5. Reisolate the virus

[a]Rivers (1937).

The structure and replication of viruses have the following features.

1. The infectious nucleic acid may be DNA or RNA (but never both) and be single- or double-stranded. If the nucleic acid is single-stranded it may be of positive or negative sense. (Positive sense has the sequence that would be used as an mRNA for translation to give a virus-coded protein.)
2. The mature virus particle may contain polynucleotides other than the genomic nucleic acid.
3. Where the genetic material consists of more than one nucleic acid molecule, each may be housed in a separate particle or all may be located in one particle.
4. The genomes of viruses vary widely in size, encoding between 1 and about 250 proteins. Plant viral genomes are at the small end of this range, mostly encoding between 1 and 12 proteins. The plant virus-coded proteins may have functions in virus replication, in virus movement from cell to cell, in virus structure, and in transmission by invertebrates or fungi. Animal and bacterial viruses may contain more genes associated with their interactions with their hosts.
5. Viruses undergo genetic change. Point mutations occur with high frequency as a result of nucleotide changes brought about by errors in the copying process during genome replication. Other kinds of genetic change may be due to recombination, reassortment of genome pieces, loss of genetic material, or acquisition of nucleotide sequences from unrelated viruses or the host genome.

6. Enzymes specified by the viral genome may be present in the virus particle. Most of these enzymes are concerned with nucleic acid synthesis.
7. Replication of many viruses takes place in distinctive virus-induced structures in the cell.
8. Some viruses share with certain nonviral nucleic acid molecules the property of integration into host-cell genomes and translocation from one integration site to another.
9. A few viruses require the presence of another virus for their replication.

B. Are Viruses Alive?

This question is asked very frequently. The definitions of a *living organism* vary widely, with the most accepted one being "A living organism has cellular structure and is manifest by growth through metabolism, reproduction, and the power of adaptation to the environment through changes that originate internally." While viruses reproduce and adapt, they are not cellular and do not metabolise; they rely on their host cell metabolism. Thus, technically they are not living organisms and the term *virus life cycle* should not be used; *virus replication cycle* describes the making of a new virus particle from an input particle.

IV. CLASSIFICATION AND NOMENCLATURE OF VIRUSES

In all studies of natural objects, humans seem to have an innate desire to name and to classify everything. It has been said that taxonomy is "the craft of making dead things look alive." Virologists are no exception. Virus classification, as with all other classifications, arranges objects with similar properties into groups, and even though this may be a totally artificial and human-driven activity without any natural base, it does have certain properties:

- It gives a structured arrangement of the organisms so that the human mind can comprehend them more easily.
- It helps with communication among virologists and between virologists and other interested parties.
- It enables properties of new viruses to be predicted.
- It could reveal possible evolutionary relationships.

In theory, it is possible to consider the problems of naming and classifying viruses as separate issues. In practice, however, naming soon comes to involve classification.

From the 1930s to 1960s, various classification systems were proposed for plant (and other) viruses. This led to much confusion, and at the International Congress for Microbiology, held in Moscow in 1966, the first meeting of the International Committee for the Nomenclature of Viruses was held. An organisation was set up for developing an internationally accepted taxonomy and nomenclature for all viruses. Rules for the nomenclature of viruses were laid down. This committee developed into the International Committee for Taxonomy of Viruses (ICTV), which has since produced eight reports, the most recent being Fauquet *et al*. (2005). These reports give the definitive descriptions of the various taxa of viruses.

A. Virus Classification

A detailed list of the criteria used for virus classification and taxonomy is given in Murphy *et al*. (1995). The criteria come under four major headings: virion properties, such as size and shape, type of genome, properties of proteins; genome organisation and replication; antigenic properties; and biological properties, such as host range, pathogenicity, and transmission.

A problem arises as to how much weight is put onto each character. In practice, the nature and sequence of the genomic nucleic acid are the major characters that are used, but other properties, such as particle shape and composition, antigenic relationships, and biology, are also considered to be important. Any classification of viruses should be based not only on evolutionary history, as far as this can be determined from the genotype, but should also be useful in a practical sense. Most of the phenotypic characters used today in virus classification will remain important even when the nucleotide sequences of most viral genomes have been determined.

B. Families, Genera, and Species

The main building block of a biological classification is the species. In day-to-day practice, virologists use the concept of a "virus" as being a group of fairly closely related strains, variants, or pathovars. A virus defined in this way is essentially a species in the sense suggested for angiosperms and defined by the ICTV. In 1991, the ICTV accepted the concept that viruses exist as species, adopting the following definition:

> A viral species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche. [**Polythetic** denotes a taxonomic group classified on the basis of several characters, as opposed to a monothetic group.]

The species has formed the basis of modern virus classification being established in subsequent ICTV reports, especially the seventh and eighth, in which a List of Species-Demarcating Criteria is provided for each genus. This enables viruses to be differentiated as species and tentative species, which are viruses that have not yet been sufficiently characterised to ensure that they are distinct and not strains of an existing virus or do not have the full characteristics of the genus to which they have been assigned. Of the 1,037 plant viruses listed in the eighth ICTV report, 751 are true species and 286 are tentative species. Further studies will provide enough data to classify the tentative species. A common problem is determining whether a new virus is truly a new species or a strain of an existing species. Conversely, what was considered to be a strain may, on further investigation, turn out to be a distinct species. This is due to the population structure of viruses that, because of continuous production of errors in replication, can be considered a collection of quasi-species. The concept of quasi-species is discussed in more detail following.

With the species forming the basis of the classification system, they can be grouped into other taxa on various criteria. To date, the taxonomic levels of *order*, *family*, and *genus* have been defined by the ICTV, and it is likely that there will be pressure for further higher and intermediate taxa. No formal definition for a *genus* exists, but it is usually considered "a population of virus species that share common characteristics and are different from other populations of species." Currently, 80 genera of plant viruses are recognised. In some cases—such as the *Rhabdoviridae*—numerous viruses are recognised that obviously belong to that family but for which there is not enough information to place them either in existing genera or for creating new genera; these viruses are listed as "unassigned." Genera are named either after the type species—for example, *Caulimovirus* after *Cauliflower mosaic virus*—or are given a descriptive name, often from a Greek or Latin word, for a major feature of the genus—for example, *Closterovirus*, from the Greek κλωστηρ (kloster), which is a spindle or thread, or that describes the virus particle shape, such as *Geminivirus*, from the Latin *geminus*, meaning "twins."

Similarly, genera are grouped together into families on common characteristics (Table 1.4). There are 17 families recognised for plant viruses; some, such as *Reoviridae* and *Rhabdoviridae*, are in common with animal virus families.

TABLE 1.4 Criteria Demarcating Different Virus Taxa

I Order
Common properties between several families including:
Biochemical composition
Virus replication strategy
Particle structure (to some extent)
General genome organisation
II Family
Common properties between several genera including:
Biochemical composition
Virus replication strategy
Nature of particle structure
Genome organisation
III Genus
Common properties with a genus including:
Virus replication strategy
Genome size, organisation, and/or number of segments
Sequence homologies (hybridisation properties)
Vector transmission
IV Species
Common properties within a species including:
Genome arrangement
Sequence homologies (hybridisation properties)
Serological relationships
Vector transmission
Host range
Pathogenicity
Tissue tropism
Geographical distribution

Seventeen of the genera have not yet been assigned to families and are termed "floating genera." The acquisition of further data on these floating genera, together with changing attitudes on virus classification, will no doubt lead to the designation of further plant virus families. The family is either named after the type member genus—for example, *Caulimoviridae,* named after the genus *Caulimovirus*—or given a descriptive name, as with the genus, for a major feature of the family—for example, *Geminiviridae*, which describes the virus particles.

Only three orders have been accepted thus far by the ICTV. The *Mononegavirales* contains, among other families, the *Rhabdoviridae,* which contains two plant virus families. In practice, genome nucleic acid sequence data are increasingly being used to delimit genera, species, and strains (Figure 1.4). A detailed discussion of virus classification, the currently accepted taxa, and how the ICTV operates are provided in Fauquet *et al*. (2005).

C. Naming Viruses (Species)

Questions of virus nomenclature have generated more heat over the years than the much more practically important problems of how to delineate distinct virus species. When a family or genus is approved by the ICTV, a type species is designated. Some virologists favour using the English vernacular name as the official species name. Using part of a widely known vernacular name as the official species name may frequently be a very suitable solution, but it could not always apply (e.g., with newly discovered viruses). Other virologists favour serial numbering for viruses (species). The experience of other groups of microbiologists is that, although numbering or lettering systems are easy to set up in the first instance, they lead to chaos as time passes and changes must be made in taxonomic groupings. The idea of Latinized binomial names for viruses was supported by the ICTV for many years but never implemented for any viruses.

In successive editions of the ICTV reports, virus names in the index have been listed by the vernacular name (usually English) followed by the family or genus name—for example,

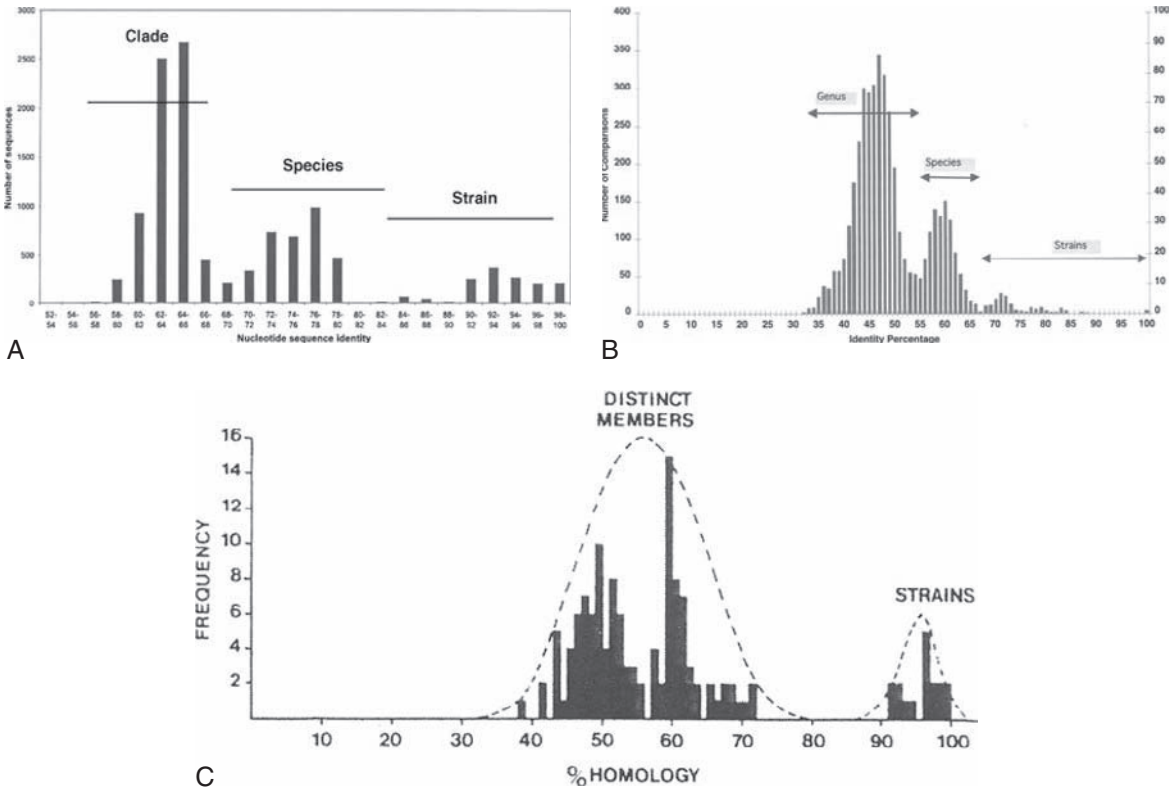

FIGURE 1.4 Differentiation of taxa by pairwise identities of sequences of variants of A. RT/RNaseH nucleotide sequences of *Banana streak virus* isolates; B. Nucleic acid sequences of the L1 gene of members of the Family *Papillomaviridae*; C. Amino acid sequences of coat proteins of potyviruses. A. With kind permission from Springer Science+ Business Media: *Arch. Virol.,* The diversity of *Banana streak virus* isolates in Uganda, vol. 150, 2005, pp. 2407-2420, G. Harper; B. From Virus Taxonomy, 8th Report of the National Committee on the Taxonomy of Viruses, Fauquet *et al.*, p. 5, Copyright Elsevier (2005); C. Reichmann *et al.* (*Journal of General Virology* 73, 1–16, 1992).

tobacco mosaic *Tobamovirus*, Fiji disease *Fijivirus*, and *Lettuce necrotic yellows rhabdovirus*. This method for naming a plant virus is becoming increasingly used in the literature.

D. Acronyms or Abbreviations

Abbreviations of virus names have been used for many years to make the literature easier to read and more succinct to present. The abbreviation is usually in the form of an acronym using the initial letters of each word in the virus name. As the designation of the acronym was by the author of the paper, it was leading to much overlap and confusion. For instance, among plant viruses, AMV was used to designate *Alfalfa mosaic virus* and *Arabis mosaic virus* and could also justifiably be used for *Abutilon mosaic virus*, *Agropyron mosaic virus*, *Alpina mosaic virus*, *Alstromeria mosaic virus*, *Alternantha mosaic virus*, *Aneilema mosaic virus*, or *Anthoxanthum mosaic virus*. Therefore, in 1991 the Plant Virus section of the ICTV initiated a rationalisation of plant virus acronyms and has subsequently updated the list regularly in ICTV reports (Box 1.3).

There are no efforts to create a common acronym system for viruses from different kingdoms. Thus, CMV can mean *Cucumber*

BOX 1.3

RULES FOR VIRUS ABBREVIATIONS OR ACRONYMS

- Abbreviations should be as simple as possible.
- An abbreviation must not duplicate any other previously coined term or one still in use.
- The word *virus* in a name is abbreviated as *V*.
- The word *viroid* in a name is abbreviated as *Vd.*
- *M* is usually used for "mosaic" and *Mo* for "mottle."
- The word *ringspot* is abbreviated as *RS* and *symptomless* as *SL.*
- Abbreviations for single words should not normally exceed two letters.
- Where a particular combination of letters has been adopted for a particular plant, subsequent abbreviations for viruses of that host should use the same combination.
- The second (or third) letter of a host plant abbreviation is in lowercase—for example, Ab for Abutilon.
- When several viruses have the same name and are differentiated by a number, the abbreviation will have a hyphen between the letters and number—for example, *Plantain virus 6* is abbreviated as PlV-6.
- When viruses end with a letter, the letter is added to the end of the abbreviation without a hyphen—for example, *Potato virus X* is abbreviated PVX.
- When viruses are distinguished by their geographical location, a minimum number of letters (two or three) are added to the abbreviation with a hyphen—for example, *Tomato yellow leaf curl virus* from Thailand is TYLCV-Th.
- When a virus name comprises a disease name and the words *associated virus,* these are abbreviated *aV*—for example, *Grapevine leafroll associated virus 2* is abbreviated GLRaV-2.

A set of guidelines is laid out in Fauquet and Mayo (1999). Although these and the acronyms derived from them, are not officially sanctioned by the ICTV, the acronyms are used in the ICTV reports.

mosaic virus (of plants), *Canine minute virus* (of vertebrates), or *Clo Mor virus* (of invertebrates). Thus, acronyms have to be taken in context.

E. Plant Virus Classification

The current classification of plant viruses is shown in Figure 1.5.

F. Virus Strains

A virus species is not a uniform population because in each infected cell, a wide range of variants is present. This situation is termed a *quasi-species* (Box 1.4).

The quasi-species concept makes it difficult to strictly define a *strain.* However, one must describe variants within a species and, in reality, take a pragmatic approach. Characters have to be weighed up as to how they would contribute to making subdivisions and to communication, not only between virologists but also to plant pathologists, extension workers, farmers, and many other groups. An example is the luteovirus *Beet western yellows virus* (BWYV), which has a wide host range, including sugar beet in the United States. For many years, *Beet mild yellows virus*, which infected sugar beet in Europe, was regarded as a strain of BWYV. Confusion arose when it was discovered that the European luteovirus that was most closely related to BWYV did not infect sugar beet but was common in the oilseed rape crop. This caused many problems in explaining

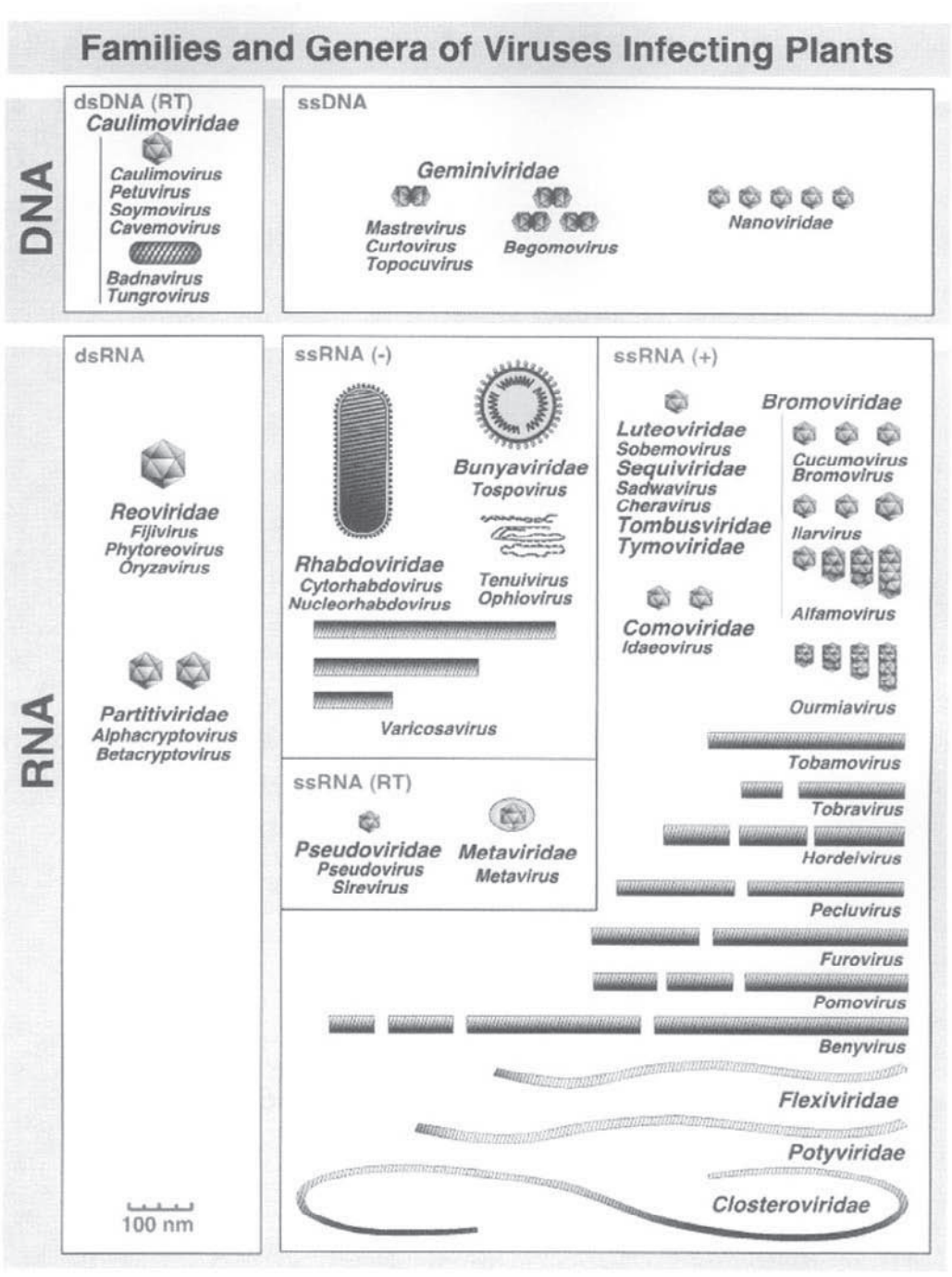

FIGURE 1.5 Classification of plant viruses. From Virus Taxonomy, 8th Report of the National Committee on the Taxonomy of Viruses, Fauquet *et al.*, p. 18, Copyright Elsevier (2005).

BOX 1.4

QUASI-SPECIES

A *quasi-species* is a population structure in which collections of closely related genomes are subjected to a continuous process of genetic variation, competition, and selection. Usually, the distribution of mutants or variants is centred on one or several master sequences. The selection equilibrium is meta-stable and may collapse or change when an advantageous mutant appears in the distribution.

In this case, the previous quasi-species will be substituted by a new one characterised by a new master sequence and a new mutant spectrum. The stability of a quasi-species depends on the complexity of the genetic information in the viral genome, the copy fidelity on replication of the genome, and the superiority of the master sequence.

A quasi-species has a physical, chemical, and biological definition. In the physical definition, a quasi-species can be regarded as a cloud in sequence space, which is the theoretical representation of all the possible variants of a genomic sequence. For an ssRNA virus of 10 kb, the sequence space is 410,000. Thus, the quasi-species cloud represents only a very small proportion of the sequence space and is constrained by the requirements of gene and nucleic acid functions. Chemically, the quasi-species is a rated distribution of related nonidentical genomes. Biologically, a quasi-species is the phenotypic expression of the population, most likely dominated by that of the master sequence.

to farmers that the BWYV in their overwintering oilseed rape crop would not infect their beet crop the next year.

G. Use of Virus Names

The ICTV sets rules, which are regularly revised, on virus nomenclature and the orthography of taxonomic names (see the eighth ICTV report). The last word of a species is *virus,* and the suffix (ending) for a genus name is *-virus.* For a subfamily, it is *-virinae*; for a family, it is *-viridae*; and for an order, it is *-virales*. In formal taxonomic usage, the virus order, family, subfamily, genus, and species names are printed in italics (or underlined), with the first letter being capitalized; other words in species names are not capitalized unless they are proper nouns or parts of proper nouns. Also, in formal use, the name of the taxon should precede the name being used—for example, the family *Caulimoviridae*, the genus *Mastrevirus*, and the species *Potato virus Y*. An example of classification, nomenclature, and orthography is shown in Box 1.5.

In informal use, the family, subfamily, genus, and species names are written in lowercase Roman script, the taxon does not include the formal suffix, and the taxonomic unit follows the name being used—for example, the caulimovirus family, the mastrevirus genus, and the potato virus Y species. In even less formal circumstances, but still widely used, the taxonomic unit is omitted and the taxon for higher taxa can be in the plural—for example, caulimoviruses, mastreviruses, and potato virus Y.

BOX 1.5

EXAMPLE OF VIRUS CLASSIFICATION, NOMENCLATURE AND ORTHOGRAPHY

Taxa	Example	Suffix
Order	*Mononegavirales*	*-virales*
Family	*Rhabdoviridae*	*-viridae*
Subfamily		*-virinae*
Genus	*Nucleorhabdovirus*	*-virus*
Species	*Sonchus yellow net virus*	
Acronym	*SYNV*	

Informal usage arises from practicalities and can lead to the adoption of more formal use. For instance, the genus *Badnavirus* was not adopted in 1991 but was used widely in the literature and was adopted in the 1995 ICTV report. However, the year 2000 report limited its use to certain DNA viruses with bacilliform particles excluding *Rice tungro bacilliform virus*. As will be apparent in this book, it is necessary to distinguish the reverse transcribing DNA viruses that have isometric particles from those that have bacilliform particles; the informal usage will be *caulimoviruses* for the former and *badnaviruses* for the latter.

V. VIRUSES OF OTHER KINGDOMS

The eighth report from the ICTV (Fauquet *et al*., 2005) noted over 2,700 accepted, tentative, and unassigned virus species classified into 3 orders, 73 families (4 of these divided into subfamilies), and 287 genera. Most of these taxonomic groupings at the genus level are specific to viruses of plants, vertebrates, invertebrates, or prokaryotes, but some genera of viruses infect more than one kingdom. The overall classification is based on genome type, some very obvious differences exist between the genome types of plant, vertebrate, invertebrate, and prokaryotic viruses (Table 1.5).

TABLE 1.5 Numbers of Virus Species in Various Kingdoms

	Plant		Vertebrate		Invertebrate		Prokaryote		Fungi and Algae	
	Number	**% Total**	**Number**	**% Total**	**Number**	**% Total**	**Number**	**% Total**	**Number**	**% Total**
dSDNA	0	0	263	28.4	150	60.7	203	62.5	127	67.9
sSDNA	198	19.1	66	7.1	27	10.9	92	28.3	0	0
RT	66	6.4	62	6.7	24	9.7	0	0	13	7.0
dSRNA	48	4.6	75	8.1	38	15.4	24	7.4	33	17.6
sS-RNA	48	4.6	227	24.5	0	0	0	0	0	0
sS+RNA	677	65.3	234	25.2	8	3.2	6	1.8	14	7.5
Total	1,037		927		247		325		187	

Data from Fauquet *et al*. (2005), using numbers of assigned, unassigned, and tentative virus species.

VI. SUMMARY

- Plant viruses are important pathogens.
- The study of plant viruses has made important contributions to the understanding of viruses in general—for example, the recognition of viruses as pathogens, the structure of virus particles, and the infectious nature of RNA.
- This chapter defines a virus, contrasts it with similar agents, and discusses how viruses are classified.

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