

Virus classification

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There is no evidence that viruses possess a common ancestor or are in any way phylogenetically related. Nevertheless, classification along the lines of the Linnean system into families, genera, and species has been partially successful. In the early 1970s the International Committee on Taxonomy of Viruses (ICTV) was established. This article is a summary of the committee's most recent findings. Based on the organisms they infect, the first broad division is into vertebrate; algae, fungi, yeast, and protozoan; invertebrate; plant; and bacterial viruses. (However, viral families may fall into more than one of these classes.) Within these classes, other criteria for subdivision are used. Among these are general morphology: envelope or the lack of it; nature of the genome (deoxyribonucleic acid, DNA, or ribonucleic acid, RNA); structure of the genome [single-stranded (ss) or double-stranded (ds), linear or circular, fragmented or nonfragmented]; mechanisms of gene expression and virus replication (positive- or negative-strand RNA); serological relationship; host and tissue susceptibility; pathology (symptoms, type of disease). Information about many of these parameters has been available only since the 1950s, and was acquired after the introduction of tissue culture laboratory techniques.

Families and Genera of Viruses Infecting Vertebrates

The families of vertebrate viruses and the shapes and sizes of their characteristic members are presented in **Fig. 1**. Families are sometimes subdivided into subfamilies; the suffix -virinae may then be used. The subgroups of a family or subfamily are equivalent to the genera of the Linnean classification. *See also:* ANIMAL VIRUS.

DNA viruses

The vertebrate DNA viruses are divided into 10 families: Asfarviridae, Poxviridae, Iridoviridae, Hepadnaviridae, Herpesviridae, Polyomaviridae, Papillomaviridae, Adenoviridae, Circoviridae, and Parvoviridae.

Asfarviridae. The properties of this family are based on the sole genus *Asfivirus* (African swine fever virus). Virions consist of a nucleoprotein core structure (70–100 nm in diameter), surrounded by internal lipid layers and an icosahedral capsid (170–190 nm in diameter) and a lipid-containing envelope. The genome is a single molecule of linear dsDNA (170–190 kbp). African swine fever virus infects domestic and wild swine and can be transmitted by ticks, direct contact, fomites (disease-carrying objects), or mechanically by biting flies.

Poxviridae. The properties of this family are based on vaccinia virus of the *Orthopox* genus. The brick-shaped, (200 × 200 × 250)-nanometer particle contains a dumbbell-shaped nucleocapsid with a genome of dsDNA (170–250

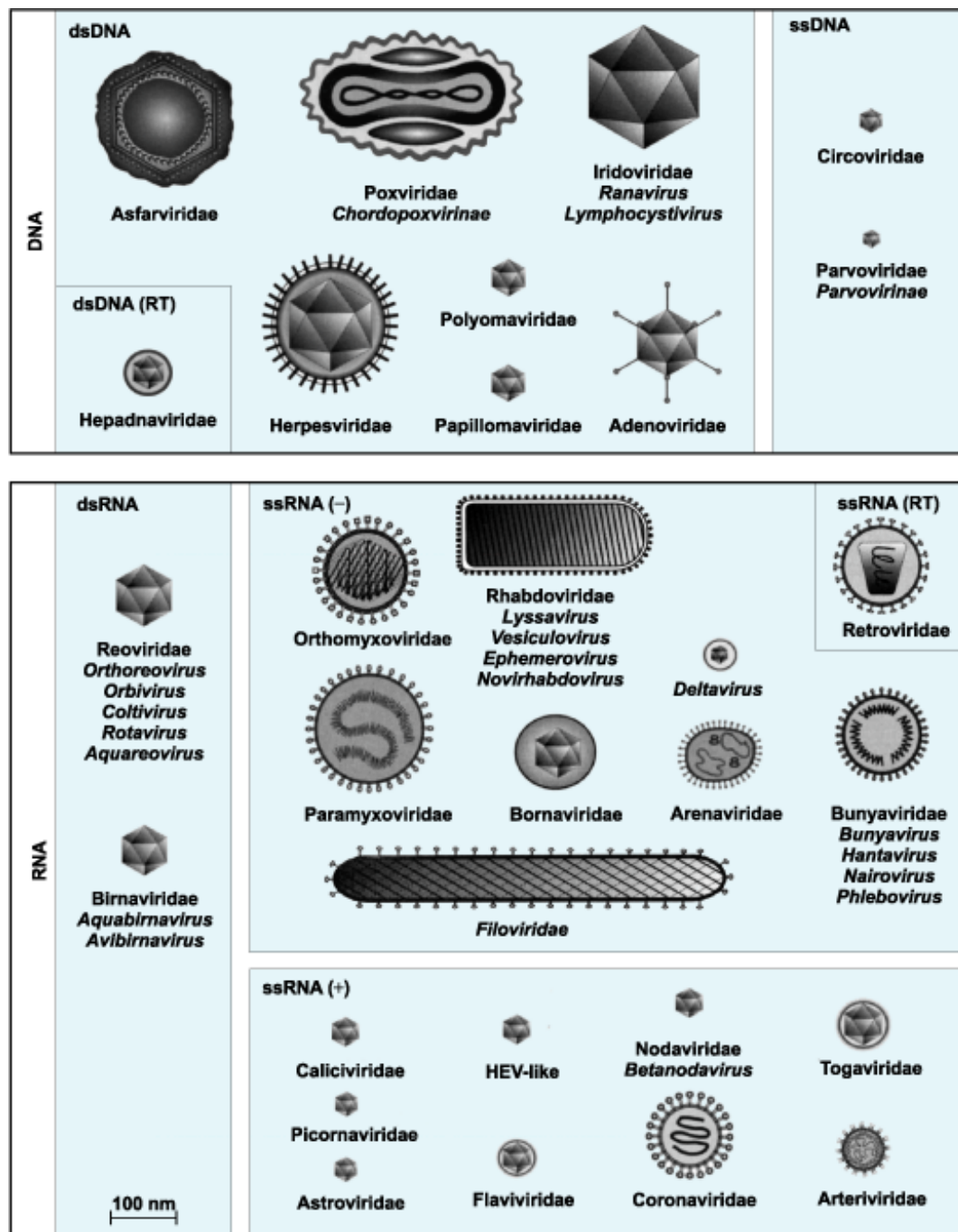


Fig. 1 Families and genera of viruses infecting vertebrates. Individual frames separate taxa of viruses containing double-stranded and single-stranded genomes. Large boxes separate taxa of viruses having DNA or RNA genomes. All diagrams have been drawn approximately to the same scale to provide an indication of the relative sizes of the viruses. (From M. H. V. van Regenmortel et al., eds., *Virus Taxonomy: 7th Report of the International Committee on Taxonomy of Viruses*, p. 30, copyright 2000, with permission from Elsevier)

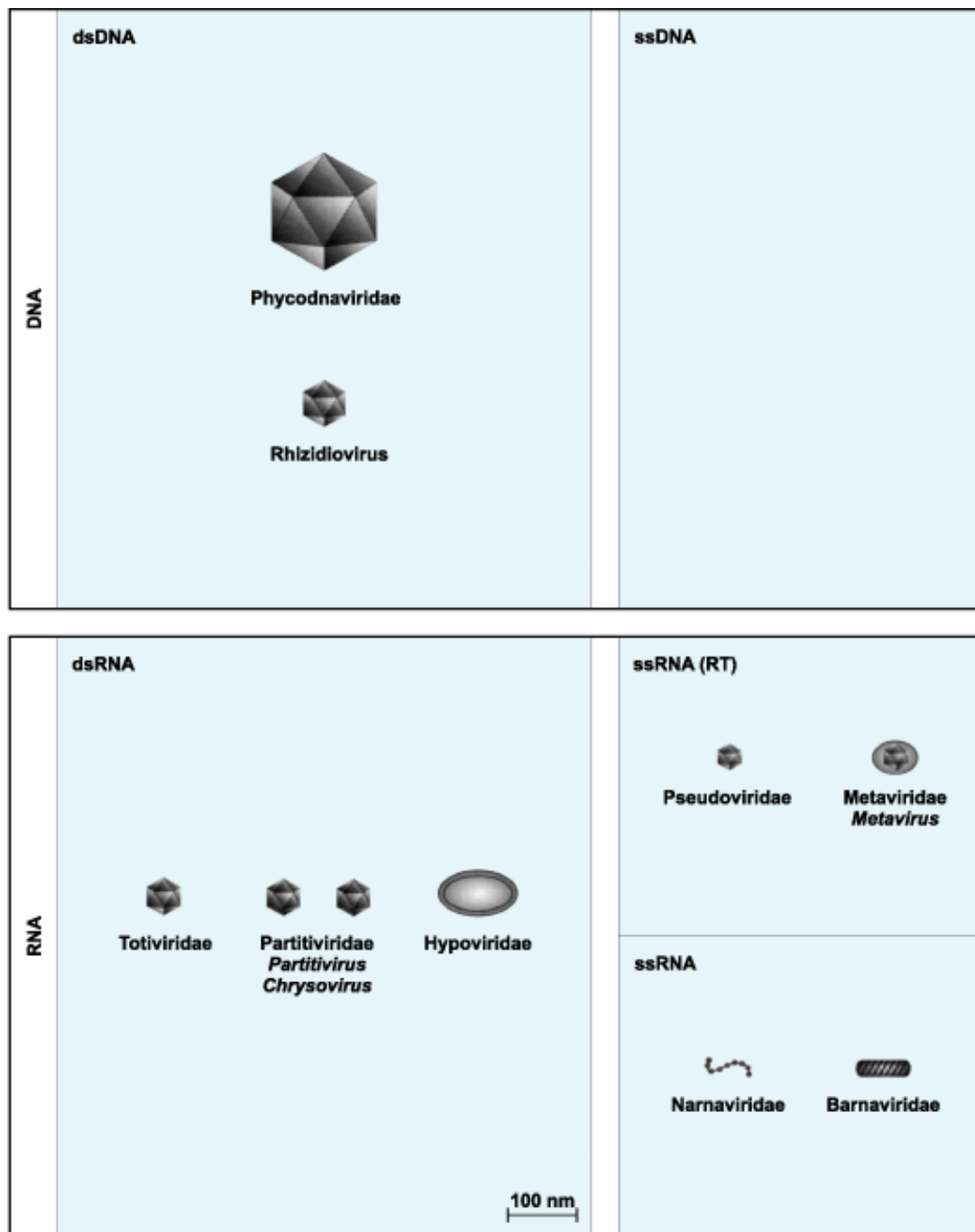


Fig. 2 Families and genera of viruses infecting algae, fungi, yeast, and protozoa. Individual frames separate taxa of viruses containing double-stranded and single-stranded genomes. Large boxes separate taxa of viruses having DNA or RNA genomes. All diagrams have been drawn approximately to the same scale to provide an indication of the relative sizes of the viruses. (From M. H. V. van Regenmortel et al., eds., *Virus Taxonomy: 7th Report of the International Committee on Taxonomy of Viruses*, eds., p. 31, copyright 2000, with permission from Elsevier)

kbp). At least 30 structural proteins have been reported. In spite of the lipid-containing envelope, most of these viruses are ether-resistant (some members of the poxviridae are, however, ether-sensitive). Generally, members of the Poxviridae are sensitive to common detergents, formaldehyde, oxidizing agents, and temperatures greater than 40°C (104°F). The large genome encodes a great number of enzymes which lead to a more autonomous virus replication than that of any other family. Unlike any other DNA virus, the poxvirus replicates in the cell cytoplasm, independent of functions found in the cell nucleus. Poxviridae are divided into two subfamilies: Chordopoxvirinae (which infects vertebrates) and Entomopoxvirinae (which infects invertebrates; **Fig. 3**). Genera of Chordopoxvirinae include *Orthopoxvirus* (human smallpox), *Leporipoxvirus* (rabbit myxoma), *Avipoxvirus* (chickenpox), *Capripoxvirus* (sheeppox), *Suipoxvirus* (swinepox), *Molluscipoxvirus* (molluscum contagiosum), *Yatapoxvirus* (Yaba monkey tumor virus), and *Parapoxvirus* (pseudocowpox). *See also*: SMALLPOX.

Iridoviridae. These are mostly insect viruses except for the genus *Ranavirus* (frog viruses) and the genus *Lymphocystivirus* (fish viruses). The icosahedral virion is 120–200 nm in diameter but may be up to 350 nm, with a dsDNA genome (between 140 and 303 kbp). Several structural proteins and also lipids (not in a lipid bilayer envelope) are contained in the capsid. Viruses released from cells may have a plasma-derived outer envelope. The viruses are sensitive to treatment with ether.

Hepadnaviridae. Hepadnaviruses are spherical, sometimes pleomorphic (variably formed) viruses. The virion particles are 40–48 nm in diameter after negative staining. An outer envelope surrounds an icosahedral nucleocapsid core containing the viral genome, the viral polymerase, and associated cellular proteins. The genome consists of a single molecule of circular DNA (3.0–3.3 kbp) that is partially single stranded. The family includes two genera: *Orthohepadnavirus* (hepatitis B virus) and *Avihepadnavirus* (duck hepatitis B virus). *Hepadnavirus* infection induces overproduction of surface proteins, which are secreted as lipoprotein particles together with virus to the blood. Empty viruslike particles consisting of excess virus envelope material are present in much greater numbers than complete virions in most individuals. *See also*: HEPATITIS.

Herpesviridae. In this family the particle is 120–200 nm in diameter. Its double-stranded linear DNA (125 to 240 kbp in size) is packed in a liquid crystalline array which fills the entire volume of the icosahedral capsid (100–125 nm). This package is surrounded by a lipid bilayer envelope and several glycoproteins. The space between the icosahedral capsid and the envelope, the tegument, is filled with at least 15 distinct polypeptides. Viral infectivity is destroyed by lipid solvents and detergents. The subfamilies of this group are Alphaherpesvirinae (herpes simplex virus group), Betaherpesvirinae (cytomegalovirus group), and Gammaherpesvirinae (lymphoproliferative virus group). Epstein-Barr (EB) virus is the cause of Burkitt's lymphoma in the malaria belt and nasopharyngeal carcinoma in China. It is also the causative agent of infectious mononucleosis. *See also*: CYTOMEGALOVIRUS INFECTION; EPSTEIN-BARR VIRUS; HERPES.

Polyomaviridae. This group is characterized by a nonenveloped icosahedron (72 capsomers), 40 nm in diameter, which contains five to seven unique structural proteins. Double-stranded circular DNA (5 kbp) is complexed

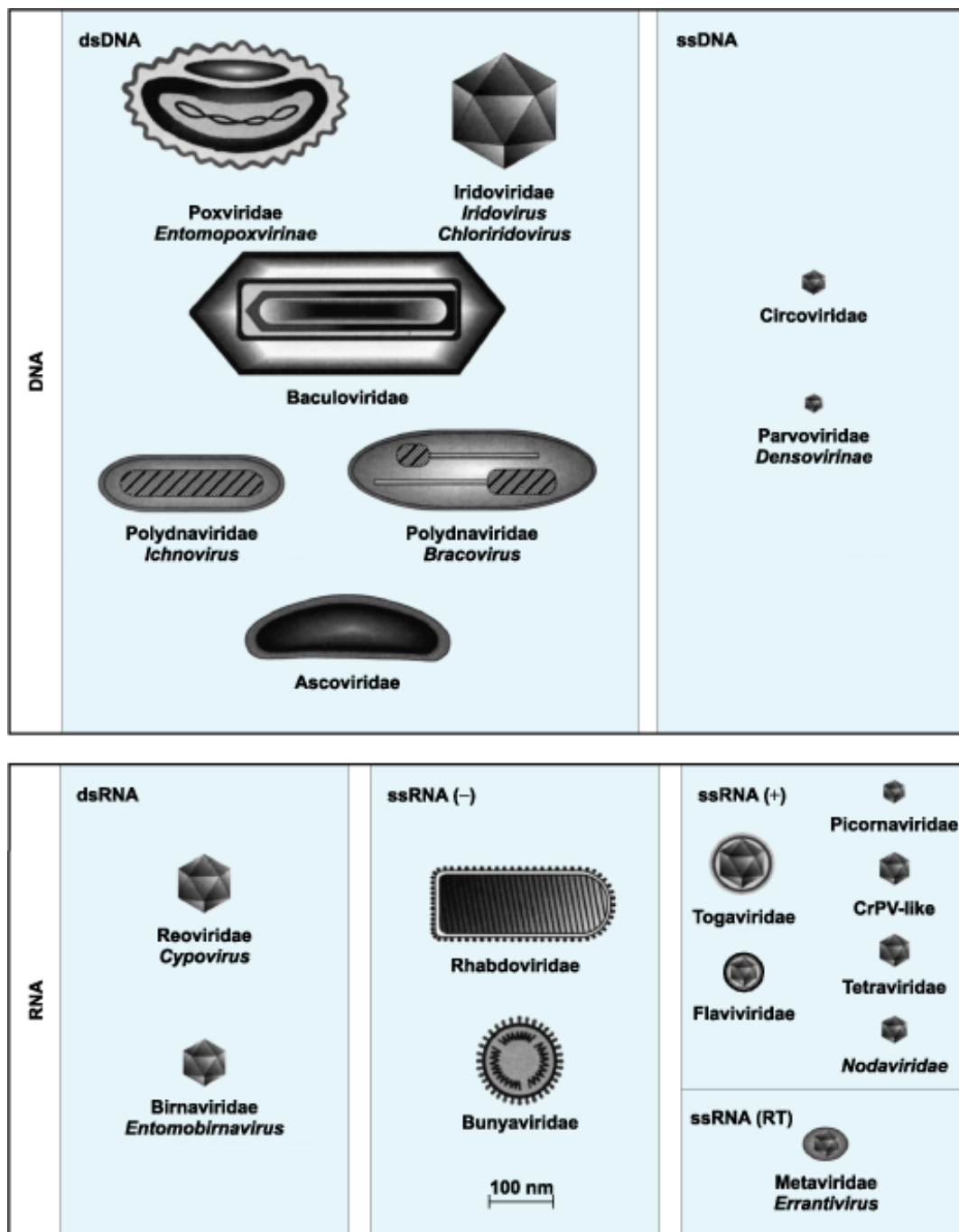


Fig. 3 Families and genera of viruses infecting invertebrates. Individual frames separate taxa of viruses containing double-stranded and single-stranded genomes. Large boxes separate taxa of viruses having DNA or RNA genomes. All diagrams have been drawn approximately to the same scale to provide an indication of the relative sizes of the viruses. (From M. H. V. van Regenmortel et al., eds., *Virus Taxonomy: 7th Report of the International Committee on Taxonomy of Viruses*, p. 32, copyright 2000, with permission from Elsevier)

inside the nucleocapsid to histone proteins of host cell origin. The sole genus in this family is *Polyomavirus*. Polyomaviruses include *JC polyomavirus*, which causes the rare disease known as progressive multifocal leukoencephalopathy in humans, and Simian virus 40, which causes a similar disease in rhesus monkeys.

Papillomaviridae. This family consists of nonenveloped icosahedral virions 55 nm in diameter. The capsid is composed of 72 capsomers in skewed arrangement. The genome consists of a single molecule of circular dsDNA (6800–8400 bp). The sole genus in this family is *Papillomavirus*. Species include human papillomaviruses and bovine papillomaviruses. Human papillomavirus spreads by close contact with warts. Specific human cancers, including cervical and penile cancers, have been linked to specific types of Papillomaviruses.

Adenoviridae. This group is characterized by a nonenveloped icosahedron of 252 capsomers, 70–90 nm in diameter, which contains at least 12 unique structural proteins. The 12 vertex capsomers (pentons) exhibit one (in the mammalian group) or two (in the avian group) filamentous projections (fibers) involved in attachment to the host cell. The genome, a double-stranded linear DNA (26–45 kbp), has been sequenced for human adenovirus. The family comprises two genera, *Mastadenovirus* (mammalian, including human) and *Aviadenovirus* (avian), each containing a large number of members. *See also*: ADENOVIRIDAE.

Circoviridae. This family, containing the sole genus *Circovirus*, is characterized by nonenveloped icosahedral virions. The particles range in size 12–27 nm in diameter. Virions contain circular single-stranded DNA (2.0 kbp). Species in the genus include porcine circovirus and chicken anemia virus.

Parvoviridae. These virions are nonenveloped, 18–26 nm in diameter with icosahedral symmetry with 32 capsomers. Parvoviridae are the smallest viruses, containing three or four structural proteins and a ssDNA genome of 4–6 kbp. This family includes two subfamilies, Parvovirinae and Densovirinae. The subfamily includes the genera *Parvovirus*, *Erythrovirus*, and *Dependovirus*. *Dependovirus* comprises defective viruses that require a helper virus (usually an adenovirus) for their replication. The other genera, *Parvovirus* and *Erythrovirus*, are autonomous. The subfamily Densovirinae and the genus *Dependovirus* produce, without preference, particles which contain either the positive or the negative DNA strand. Parvoviruses contain only the negative strand. Densoviruses infect arthropods only and will be discussed in a subsequent section.

Single-stranded, positive-sense RNA viruses

RNA vertebrate viruses may be either single-stranded or double-stranded. The single-stranded ones are further subdivided into positive-strand and negative-strand RNA viruses, depending on whether the RNA contains the messenger RNA (mRNA) nucleotide sequence or its complement, respectively. The RNA genes may be located on one or several RNA molecules (nonfragmented or fragmented genomes, respectively).

The single-stranded, positive-sense RNA vertebrate viruses contain eight families: Caliciviridae, Picornaviridae, Astroviridae, Flaviviridae, Nodaviridae, Coronaviridae, Togaviridae, and Arteriviridae. In addition, a genus of HEV-like viruses is found in this group but has not yet been assigned to a family.

Caliciviridae. These icosahedral particles, 27–40 nm in diameter, exhibit 32 visible cup-shaped depressions and contain 90 dimers of the major structural protein. Although their single-stranded RNA (7.4–8.3 kb) serves as mRNA, a smaller mRNA fragment has also been detected. Caliciviruses infect a broad range of animals that includes cattle, swine, and humans. Genera in this family include *Lagovirus*, *Vesivirus*, Norwalk-like viruses, and Sapporo-like viruses. The prototype of this virus group is the vesicular exanthema of swine virus (VESV).

Picornaviridae. This family contains the genera *Enterovirus* (human polio), *Cardiovirus* (mengo), *Rhinovirus* (common cold), *Hepatovirus* (hepatitis A virus), *Parechovirus* (human parechovirus), and *Aphtovirus* (foot-and-mouth disease). The nonenveloped viral capsids are icosahedral, 22–30 nm in diameter, composed of 60 identical units, consisting of three surface proteins each. Viruses contain one single-stranded RNA molecule of 7–8.5 kb in size. A small protein, VPg, is covalently bound at its 5' end instead of the cap structure, and is polyadenylated at the 3' end. Viruses are insensitive to ether, chloroform, or nonionic detergents. *See also*: ENTEROVIRUS; PICORNAVIRIDAE; RHINOVIRUS.

Astroviridae. Virions are 28–30 nm in diameter, spherical, and nonenveloped. A five- or six-pointed star is discernible on the surface of about 10% of particles. This family contains a sole genus, *Astrovirus*. A single molecule of infectious, positive-sense ssRNA (6.8–7.9 kb in size) makes up the viral genome. A poly(A) tract is located at the 3' end of the genome. *Astroviruses* have been detected in stool samples from humans, cats, cattle, and several other animals. Astroviruses cause acute, nonbacterial gastroenteritis in children and immunocompromised adults.

HEV-like viruses. These virions are icosahedral (27–34 nm) and nonenveloped. The genome is a positive-sense ssRNA molecule of approximately 7.2 kb, with a 3'-poly(A) tail. Hepatitis E virus is associated with outbreaks and sporadic cases of fecally transmitted acute hepatitis in tropical and subtropical countries.

Flaviviridae. These virions are 40–60 nm in diameter, spherical in shape, and contain a lipid envelope. A sole capsid protein makes up the capsid, while two or three virus-encoded membrane proteins are found in the envelope. The genome is a positive-sense ssRNA molecule, 9.6–12.3 kb in size. Genera in this group include *Flavivirus* (yellow fever virus), *Pestivirus* (bovine viral diarrhea virus), and *Hepacivirus* (hepatitis C virus). *See also*: YELLOW FEVER.

Nodaviridae. These virions are nonenveloped, roughly spherical in shape, 29–32 nm in diameter, with icosahedral symmetry. Two ssRNA molecules (mol wt 1.1 and 0.48×10^6 , respectively) serve as mRNAs and are both required for infectivity. Genera include *Alphanodavirus* (Nodamura virus) and *Betanodavirus* (striped jack nervous necrosis virus). All members of the Alphanodaviruses are insect viruses, although serological evidence suggests that Nodamura virus also naturally infects pigs. The Betanodaviruses were isolated from juvenile marine fish, and are associated with significant problems in commercial fish hatcheries.

Coronaviridae. Genera in this family include *Coronavirus* (severe acute respiratory syndrome or SARS) and *Torovirus* (equine torovirus). The spherical, enveloped particle is 120–160 nm in diameter, and exhibits large

(20 nm) spikes projecting from the surface. The nucleocapsid is helical and is surrounded by an internal core shell of approximately 65 nm. One ssRNA molecule ranges in size from 27.6 to 31 kb. Coronaviruses are known to infect a large number of animals as well as humans.

Togaviridae. This group contains the genera *Alphavirus* (Western equine encephalitis virus) and *Rubivirus* (rubella virus). The icosahedral nucleocapsid (40 nm in diameter) contains the capped and polyadenylated RNA (9–11.8 kb). The envelope contains two viral glycoprotein spikes. Many of these viruses are transmitted by insects and are the cause of human diseases, including several types of encephalitis. Rubella virus causes German measles, a benign childhood disease that causes severe fetal defects in pregnant women exposed to the virus. The viruses are spherical, enveloped particles 70 nm in diameter. *See See also*: RUBELLA.

Arteriviridae. The sole genus in this family is *Arterivirus* (equine arteritis virus). These virions are spherical with a diameter of 45–60 nm. The nucleocapsid is surrounded by a lipid envelope. The genome consists of a single copy of a linear ssRNA that ranges in length from 12.7 to 15.7 kb. The host range of arteriviruses is limited, with horses, donkeys, swine, and monkeys infected by their respective species.

Single-stranded, negative-sense RNA viruses

The nucleocapsid of negative-sense RNA animal viruses contains an RNA-dependent RNA polymerase required for the transcription of the negative strand into the positive mRNAs. Virion RNA is neither capped nor polyadenylated. The group is divided into seven families: Orthomyxoviridae, Paramyxoviridae, Filoviridae, Rhabdoviridae, Bornaviridae, Arenaviridae, and Bunyaviridae. In addition, a genus known as *Deltavirus* found in this group is not assigned to a specific family.

Orthomyxoviridae. This group contains the genera *Influenzavirus A* (human influenza type A), *B*, and *C*, as well as the genus *Thogotovirus*. These are enveloped, spherical, pleomorphic particles 80–120 nm in diameter, with helical nucleocapsids. Their fragmented genome consists of 6–8 RNA molecules, with genome sizes ranging from 10 to 14.6 kb. Surface projections for *Influenza A virus* are formed by the two major glycoproteins HA (hemagglutinin) and NA (neuraminidase). Serological classification by the World Health Organization (WHO) is based on these two neutralization antigens. *See See also*: INFLUENZA.

Paramyxoviridae. This group contains the subfamilies Paramyxovirinae and Pneumovirinae. The Paramyxovirinae include the genera *Respirovirus* (Sendai virus), *Rubulavirus* (mumps), and *Morbillivirus* (measles). The Pneumovirinae includes the genera *Pneumovirus* (respiratory syncytial virus) and *Metapneumovirus* (turkey rhinotracheitis virus). The enveloped, spherical particle, 150 nm in diameter, contains a single-stranded, nonfragmented RNA of approximately 15,000 nucleotides. *See See also*: PARAMYXOVIRUS; RESPIRATORY SYNCYTIAL VIRUS; SENDAI VIRUS.

Filoviridae. This group includes two genera, the Marburg-like viruses and the Ebola-like viruses. Virions are pleomorphic but have mainly filamentous shape, sometimes with extensive branching. Length varies greatly

between particles but the diameter is uniform (about 80 nm). Virions have a lipid membrane envelope derived from the host cell plasma membrane, with surface projections of viral glycoprotein of about 10 nm in length. The genome is a nonsegmented, negative-stranded, linear RNA molecule of about 19 kb in size. The natural reservoir of filoviruses is still unknown. Human disease is fatal in 25% of Marburg virus infections and in 50–90% of Ebola virus cases. *See also*: EBOLA VIRUS.

Rhabdoviridae. This group contains the genera *Vesiculovirus* (vesicular stomatitis Indiana virus), *Lyssavirus* (rabies), *Ephemerovirus* (bovine ephemeral fever virus), *Novirhabdovirus* (infectious hematopoietic necrosis virus), *Cytorhabdovirus* (lettuce necrotic yellows virus), and *Nucleorhabdovirus* (potato yellow dwarf virus). The particles are enveloped, bullet-shaped, and measure about 100–430 nm long by 45–100 nm in diameter. The outer surface of virions is covered with projections 5–10 nm long and about 3 nm in diameter. The nucleocapsid is 30–70 nm in diameter and exhibits helical symmetry. The genome consists of a single molecule of linear, negative-sense ssRNA about 11–15 kb in size. They contain five types of structural proteins: L, G, N, P, and M. Spikes are formed by G glycoprotein, and the M (matrix) protein occupies the space between the nucleocapsid and the envelope. The RNA is complexed with the N protein to form the helical nucleocapsid. Virus infectivity is rapidly inactivated at 56°C (133°F) or through exposure to lipid solvents.

Bornaviridae. The sole genus in this family is *Bornavirus* (Borna disease virus). The virions have a spherical morphology with a diameter of 90 ± 10 nm containing an internal core of 50–60 nm and a limiting outer membrane envelope that appears to be covered with projections approximately 7 nm long. The genome consists of a single molecule of a linear, nonsegmented negative-stranded RNA of 8.9 kb in size. Horses and sheep have been regarded as the main natural hosts of Borna disease virus, and the virus can cause a fatal neurological disease in these animals.

Arenaviridae. The sole genus in this family is *Arenavirus*, typified by the lymphocytic choriomeningitis virus. Its enveloped, spherical, pleomorphic particle is 50–300 nm in diameter. In section it exhibits granular appearance, due to ribosomes of host cell origin. A dense lipid envelope is covered by club-shaped projections 8–10 nm in length. The genome consists of two ssRNA molecules, L and S, of about 7.5 kb and 3.5 kb in size. Virus infectivity is inactivated by treatment with organic solvents or by exposure to ultraviolet (UV) and gamma irradiation. The reservoir hosts for this family are almost all rodents.

Bunyaviridae. This large family has been subdivided into five genera: *Bunyavirus* (bunyamwera), *Hantavirus* (Hantaan virus), *Phlebovirus* (Rift Valley fever virus), *Nairovirus* (Dugbe virus), and *Tospovirus* (tomato spotted wilt virus; **Fig. 4**). The virions are generally spherical or pleomorphic, 80–120 nm in diameter, and display surface glycoprotein projections of 5–10 nm embedded in a lipid bilayered envelope approximately 5 nm thick. The envelopes are usually derived from Golgi membranes in the host cell or sometimes cellular surface membranes. The genome contains three molecules of ssRNA, designated L (large), M (medium), and S (small), which total 11–19 kb. Viruses in the genera *Bunyavirus*, *Nairovirus*, and *Phlebovirus* are capable of alternately replicating

in vertebrates and arthropods. Aerosol transmission occurs in hantaviral infections, while plant-to-plant transmission by thrips (tiny winged insects in the genus *Thysanoptera*) is necessary for Tospoviruses.

Deltavirus. These virions are roughly spherical with an average diameter of 36–43 nm. An outer envelope contains lipid and three envelope proteins obtained from the coinfecting helper *hepadnavirus*. An inner nucleocapsid of 19 nm comprises the RNA genome of hepatitis delta virus (HDV) and approximately 70 copies of the only HDV-encoded protein, known as delta antigen. The genome consists of a single molecule of circular negative-sense ssRNA about 1.7 kb in length. HDV requires the presence of a helper *hepadnavirus* to provide envelope proteins. It is therefore considered a subviral satellite virus. Natural HDV infection is found only in humans with hepatitis B virus as helper virus.

Double-stranded RNA viruses

The dsRNA vertebrate viruses contain two groups, the Reoviridae and the Birnaviridae.

The Reoviridae include the nine genera *Orthoreovirus* (mammalian orthoreovirus), *Orbivirus* (bluetongue virus), *Rotavirus* (Rotavirus A), *Coltivirus* (Colorado tick fever virus), *Aquareovirus* (Aquareovirus A), *Cypovirus* (Cypovirus 1; see Fig. 3), *Fijivirus* (Fiji disease virus), *Phytoreovirus* (wound tumor virus in plants and insects), and *Oryzavirus* (rice ragged stunt virus). (See Fig. 4 for *Fijivirus*, *Phytoreovirus*, and *Oryzavirus*.) The nonenveloped virions within this family have icosahedral symmetry but may appear spherical in shape. They each have a capsid, which is made up of concentric protein layers organized in one, two, or three distinct capsid shells. The overall diameter of the capsid is 60–80 nm. The nine genera may be divided into two groups: one group contains those viruses in which virus particles have relatively large spikes situated at the 12 vertices of the icosahedron; the second group includes those genera with relatively smooth or almost spherical virus particles lacking surface projections. Virions from some genera can leave infected cells by budding, acquiring a membrane envelope derived from the cellular membranes; however, this envelope appears to be transient in most cases. The virions contain a genome of 10, 11, or 12 linear segments of dsRNA. The properties of the reoviruses vary according to the genus. *Rotavirus*, in particular, has become recognized as a frequent cause of human diarrhea.

DNA and RNA reverse transcribing viruses

Vertebrate viruses in this category include the families Hepadnaviridae, discussed under the DNA virus category previously, and the Retroviridae.

The Retroviridae contains the genera *Alpharetrovirus* (avian leucosis virus), *Betaretrovirus* (mouse mammary tumor virus), *Gammaretrovirus* (murine leukemia virus), *Deltaretrovirus* (bovine leukemia virus), *Epsilonretrovirus* (Walleye dermal sarcoma virus), *Lentivirus* (human immunodeficiency virus or HIV), and *Spumavirus* (chimpanzee foamy virus). These virions are spherical, enveloped, and 80–100 nm in diameter. Surface projections made of glycoprotein are about 8 nm in length. The internal core contains the viral

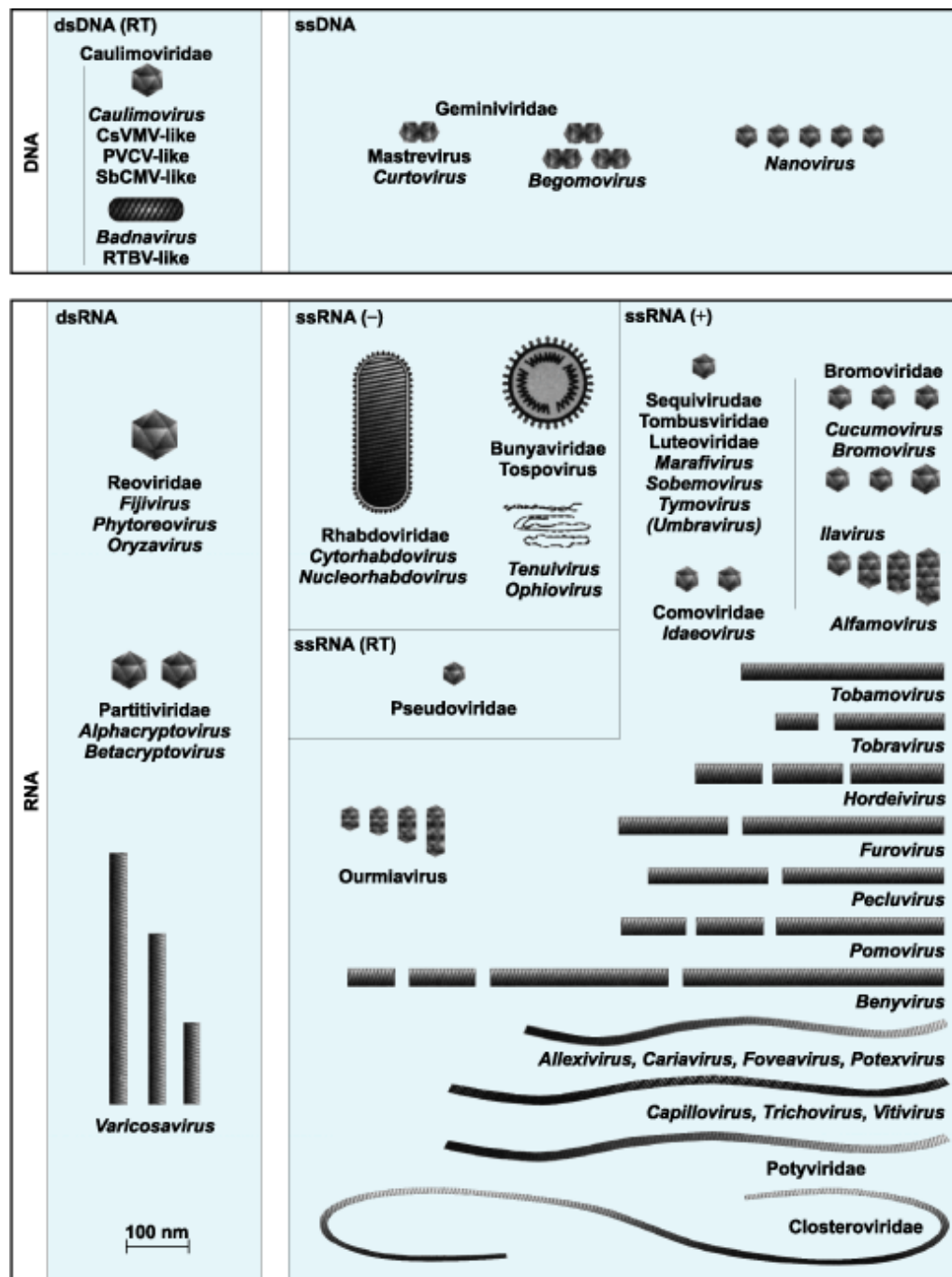


Fig. 4 Families and genera of viruses infecting plants. Individual frames separate taxa of viruses containing double-stranded and single-stranded genomes. Large boxes separate taxa of viruses having DNA or RNA genomes. All diagrams have been drawn approximately to the same scale to provide an indication of the relative sizes of the viruses. (From M. H. V. van Regenmortel et al., eds., *Virus Taxonomy: 7th Report of the International Committee on Taxonomy of Viruses*, p. 33, copyright 2000, with permission from Elsevier)

nucleocapsid, which is apparently spherical. The viral genome consists of a dimer of linear, positive-sense, ssRNA, each monomer 7–11 kb in length. There are two envelope proteins encoded by viral genes. Other proteins include a protease and a reverse transcriptase, which is essential to the process of producing a DNA copy of the RNA genome. This copy is then integrated into the host cell chromosome in a successful infection. Retroviruses have been implicated in human as well as animal leukemias, lymphomas, sarcomas, and immunodeficiencies, such as acquired immune deficiency syndrome (AIDS). *See also:* ACQUIRED IMMUNE DEFICIENCY SYNDROME (AIDS).

Families of Viruses Infecting Algae, Fungi, Yeast, and Protozoa

The shapes and sizes of characteristic members of the families of viruses that infect algae, fungi, yeast, and protozoa are presented in **Fig. 2**.

DNA viruses

Viruses in this group include one family, the Phycodnaviridae, and a genus known as *Rhizidiovirus* that is not assigned to a specific family.

Phycodnaviridae. Three genera include *Chlorovirus* (*Paramecium bursaria Chlorella virus 1*), *Prasinovirus* (*Micromonas pusilla virus SP1*), *Prymnesiovirus* (*Chrysochromulina brevifilum virus CbV-PW1*), and *Phaeovirus* (*Ectocarpus siliculosus virus 1*). These virions are nonenveloped, polyhedral particles with a shell surrounding an electron-dense core. They are 130–190 nm in diameter, with flexible, hairlike appendages extending from some of the vertices. The large genome consists of a dsDNA ranging from 160 to 380 kbp in size. The phycodnaviruses are ubiquitous in freshwater or seawater, and infect freshwater and marine algae worldwide.

Rhizidiovirus. These virions are isometric, 60 nm in diameter. The genome consists of a single molecule of dsDNA. *Rhizidiomyces virus* infects the fungus *Rhizidiomyces*. The virus appears to be transmitted in a latent form in the zoospores of the fungus. No other viruses have been identified in this genus.

Double-stranded RNA viruses

RNA viruses infecting algae, fungi, yeast, and protozoa include dsRNA viruses, ssRNA viruses, and ssRNA viruses that use reverse transcriptase. The double-stranded RNA viruses include three families: Totiviridae, Partitiviridae, and Hypoviridae.

Totiviridae. Genera in this family include *Totivirus* (*Saccharomyces cerevisiae virus L-A*), *Giardiavirus* (*Giardia lamblia virus*), and *Leishmanivirus* (*Leishmania RNA virus 1-1*). These virions have isometric symmetry and are 30–40 nm in diameter, nonenveloped, and lack surface projections. The genome consists of a single molecule of linear dsRNA, 4.6–7.0 kbp in size. These viruses are associated with latent infections of their fungal or protozoal hosts.

Partitiviridae. Genera in this family include *Partitivirus* (*Gaeumannomyces graminis virus*), *Chrysovirus* (*Penicillium chrysogenum virus*), *Alphacryptovirus* (White clover cryptic virus 1), and *Betacryptovirus* (White clover cryptic virus 2) [see Fig. 4 for *Alphacryptovirus* and *Betacryptovirus*]. These virions are isometric, nonenveloped, 30–40 nm in diameter, and contain two unrelated linear dsRNA segments (1.4–3.0 kbp in size). These viruses are associated with latent infections of their fungal and plant hosts.

Hypoviridae. The sole genus in this family is *Hypovirus* (*Cryphonectria hypovirus 1*). No true virions are associated with members of this family. Pleomorphic vesicles 50–80 nm in diameter, lacking any detectable viral structural proteins but containing dsRNA (9–13 kbp in size), are the only virus-associated particles that can be isolated from infected fungal tissue. Members infect the chestnut blight fungus, *Cryphonectria parasitica*.

Single-stranded RNA viruses

This group contains two families: *Narnaviridae* and *Barnaviridae*.

Narnaviridae. Two genera are found in this family: *Narnavirus* (*Saccharomyces cerevisiae narnavirus 20S RNA*) and *Mitovirus* (*Cryphonectria parasitica mitovirus 1-NB631*). No true virions are found associated with members of the genus *Narnavirus*. The *Narnavirus* genomes form ribonucleoprotein complexes containing linear single-stranded RNA of 2.5-kb and RNA-dependent RNA polymerases. These viruses infect the fungus *Saccharomyces cerevisiae*. The genus *Mitovirus* contains no reported virions. A single segment of dsRNA of 2.7 kb can be isolated from mitochondria of infected isolates. The virus infects members of the chestnut blight fungus, *Cryphonectria parasitica*.

Barnaviridae. The sole genus of this family is *Barnavirus* (mushroom bacilliform virus). Virions are nonenveloped, rod-shaped, and lack surface projections. Virions range 18–20 nm in width and 48–53 nm in length. The genome consists of a single linear molecule of a positive-sense ssRNA, 4.0 kb in size. The virus infects the common cultivated button mushroom.

Single-stranded RNA viruses using reverse transcriptase

Viruses in this category include two families: *Pseudoviridae* and *Mataviridae*.

Pseudoviridae. Two genera are found in the family *Pseudoviridae*: *Pseudovirus* (*Saccharomyces cerevisiae Ty1 virus*) and *Hemivirus* (*Drosophila melanogaster copia virus*). The morphology of virus particles of this family is poorly known and variable. Both viruses make similar-looking particles, but those of *Saccharomyces cerevisiae Ty1 virus* are cytoplasmic whereas those of *Drosophila melanogaster copia virus* are nuclear. The major virion RNA molecule consists of a single strand of RNA of approximately 5–6 kb. A viral reverse transcriptase is used to copy the RNA and make a dsDNA “provirus,” which is integrated into the host genome.

Metaviridae. Two genera are found in the family Metaviridae: *Metavirus* (*Saccharomyces cerevisiae* Ty3 virus) and *Errantivirus* (*Drosophila melanogaster* gypsy virus; Fig. 3). Morphology of particles is poorly characterized. Members include species which produce primarily or exclusively intracellular particles. Extracellular particles are enveloped with ovoid cores. Membranes are found in some members, apparently derived from the host cell. These viruses contain a reverse transcriptase as well as the positive strand RNAs.

Families and Genera of Viruses Infecting Invertebrates

The families of invertebrate viruses and the shapes and sizes of their characteristic members are presented in Fig. 3.

Double-stranded DNA viruses

These contain five families: Poxviridae, Baculoviridae, Iridoviridae, Polydnaviridae, and Ascoviridae.

Poxviridae. These viruses were previously described under vertebrate DNA viruses. However, the members of the subfamily Entomopoxvirinae strictly infect insects. Genera in this subfamily include *Entomopoxvirus* A, B, and C.

Baculoviridae. These are insect viruses. Two genera include *Nucleopolyhedrovirus* (*Autographa californica* multiple nucleopolyhedrovirus) and *Granulovirus* (*Cydia pomonella* granulovirus). The virions contain enveloped rod-shaped nucleocapsids. Nucleocapsid dimensions range 30–60 nm in diameter and 250–300 nm in length. The circular supercoiled dsDNA ranges 80–180 kbp in size.

Iridoviridae. These viruses were previously described under vertebrate DNA viruses. However, two genera of this family, *Iridovirus* and *Chloriridovirus*, strictly infect insects.

Polydnaviridae. These virions consist of nucleocapsids of uniform size (approximately 85 nm by 330 nm). A two-unit membrane envelope surrounds the ellipsoid nucleocapsid. Genomes consist of multiple dsDNA molecules of variable size, ranging from 2.0 to more than 31 kbp. The genera in this family are *Ichnovirus* (*Campoletis sonorensis* ichnovirus) and *Bracovirus* (*Cotesia melanoscela* bracovirus). These viruses have only been isolated from wasps; Polydnaviruses are unique among viruses in having obligate associations with parasitic wasps. The viral genome is inserted as a provirus into the host genome, from which new genome molecules are replicated.

Ascoviridae. These virions are bacilliform in shape, measuring about 130 nm in diameter by 200–400 nm in length. An envelope surrounds the inner particle. The sole genus in this family is *Ascovirus* (*Spodoptera frugiperda* ascovirus 1a). These viruses cause disease in insects only, and are found primarily in lepidopterous larvae.

Single-stranded DNA viruses

This group includes only two families, the Parvoviridae and Circoviridae, which were previously described under vertebrate DNA viruses. The subfamily Densovirinae includes three genera responsible for infecting invertebrates: *Densovirus*, *Iteravirus*, and *Brevidensovirus*.

Double-stranded RNA viruses

These include two families: Reoviridae and Birnaviridae.

Reoviridae. These viruses were previously described under vertebrate RNA viruses. Only one genus in this family infects invertebrates: *Cypovirus* (*Cypovirus 1*). *Cypoviruses* have only been isolated from arthropods.

Birnaviridae. These viruses were previously described under vertebrate RNA viruses. Only one genus in this family infects invertebrates: *Entomobirnavirus* (*Drosophila X virus*).

Single-stranded, negative-sense RNA viruses

These include two families: Rhabdoviridae and Bunyaviridae.

Rhabdoviridae. These viruses were previously described under vertebrate RNA viruses. A large number of rhabdoviruses have not been assigned to an existing genus and there are a number of ungrouped viruses. An example is *Sigma virus*, which infects *Drosophila* species, conferring CO₂ sensitivity to infected insects.

Bunyaviridae. These viruses were previously described under vertebrate RNA viruses. They are capable of alternately replicating in vertebrates and arthropods, causing disease in the vertebrates while having little or no effect on the arthropods (ticks, mosquitoes, and other arthropod disease vectors).

Single-stranded, positive-sense RNA viruses

These include five families: Togaviridae, Flaviviridae, Picornaviridae, Tetraviridae, and Nodaviridae. They also contains the unassigned genus referred to as cricket paralysis like viruses.

Togaviridae. These viruses were previously described under vertebrate RNA viruses. The viruses in the genus *Alphavirus* are transmitted biologically between vertebrates by mosquitoes and other blood-feeding arthropods. Typically, infection in the arthropods becomes permanent.

Flaviviridae. These viruses were previously described under vertebrate RNA viruses. The viruses in the genus *Flavivirus* are usually transmitted biologically between vertebrates by mosquitoes and other blood-feeding arthropods.

Picornaviridae. These viruses were previously described under vertebrate RNA viruses. Transmission by arthropod vectors is not known, although *Encephalomyocarditis virus* has been isolated from mosquitoes and ticks.

Tetraviridae. Two genera are found in this family: *Betatetravirus* and *Omegatetravirus*. These virions are nonenveloped, roughly spherical, about 40 nm in diameter, and contain a single, positive-sense ssRNA segment of about 6.5 kb. All virus species are isolated from *Lepidoptera* species (moths and butterflies).

Nodaviridae. These viruses were previously described under vertebrate RNA viruses. All species of the *Alphanodaviruses* were isolated in nature from insects.

Cricket paralysis-like viruses. This genus is not yet assigned to a family. These virions are roughly spherical with a diameter of 30 nm and no envelope. The virions exhibit icosahedral symmetry. The genome consists of a single molecule of linear, positive-sense ssRNA of 9–10 kb in size. All members of this genus have been isolated from invertebrate species.

Single-stranded RNA viruses using reverse transcriptase

This group contains only the family Metaviridae. These viruses were previously described under RNA viruses infecting algae, fungi, yeast, and protozoa. Members of the genus *Errantivirus* are known to infect species of *Drosophila*.

Families and Genera of Viruses Infecting Plants

The families of plant viruses and the shapes and sizes of their characteristic members are presented in Fig. 4. A number of plant viruses are placed into groups, rather than families. *See also*: PLANT VIRUSES AND VIROIDS.

Double-stranded DNA viruses

These include only the family Caulimoviridae. These virions are either bacilliform or isometric depending on the genus. There is no envelope. The genome consists of a single molecule of circular dsDNA of 7.2–8.1 kbp. Virions contain a reverse transcriptase. Genera in this family include *Caulimovirus*, Petunia vein clearing-like viruses, Soybean chlorotic mottle-like viruses, Cassava vein mosaic-like viruses, *Badnavirus*, and Rice tungro bacilliform-like viruses. The host ranges of most virus species are narrow. Many virus species are spread by vegetative propagation.

Single-stranded DNA viruses

These include one family, the Geminiviridae, and one unassigned genus called *Nanovirus*.

Geminiviridae. These virions apparently consist of two incomplete icosahedra with a total of 22 pentameric capsomers. The genome consists of a single molecule of circular ssDNA, 2.5–3.0 kb in size. Genera include *Mastrevirus*, *Curtovirus*, and *Begomovirus*. *Geminiviridae* are transmitted in nature by arthropods, in most cases by a single species.

Nanovirus. This genus is not yet assigned to a family. These virions are 17–20 nm in diameter, icosahedral, and lack envelopes. The genome is composed of several species of circular ssDNA approximately 1 kb in size. These viruses infect plants, including a range of leguminous species.

Double-stranded RNA viruses

These include two families, Reoviridae and Partitiviridae and the unassigned genus *Varicosavirus*.

Reoviridae. These viruses were previously described under vertebrate RNA viruses. Three genera in this family infect plants: *Fijivirus*, *Phytoreovirus*, and *Oryzavirus*. Viruses in these genera are typically transmitted between plants by arthropod vectors such as leafhoppers.

Partitiviridae. These viruses were previously described under RNA viruses infecting algae, fungi, yeast, and protozoa. Two genera are known to infect plants: *Alphacryptovirus* and *Betacryptovirus*. There are no known natural vectors for these viruses. The plant cryptoviruses are transmitted by ovule and by pollen to the seed embryo.

Varicosavirus. This genus is not yet assigned to a family. Virions are rod-shaped, about 320–360 nm in length, with a diameter of about 18 nm. The genome consists of dsRNA of two sizes, 7 kbp and 6.5 kbp. Viruses are transmitted by fungi of the genus *Olpidium* and are therefore soil- or waterborne. The type species for this genus is Lettuce big-vein virus.

Single-stranded negative-sense RNA viruses

These include two families, Rhabdoviridae and Bunyaviridae, plus two unassigned genera.

Rhabdoviridae. These viruses were previously described under vertebrate RNA viruses. Two genera in this family infect plants: *Cytorhabdovirus* and *Nucleorhabdovirus*. The viruses are primarily distinguished on the basis of the sites of virus maturation (cytoplasm: *Cytorhabdovirus*; nucleus: *Nucleorhabdovirus*).

Bunyaviridae. These viruses were previously described under vertebrate RNA viruses. One genus in this family is known to infect plants: *Tospovirus* (tomato spotted wilt virus). These viruses are known to be transmitted by thrips.

Tenuivirus. This genus is not yet assigned to a family. Virions have a thin filamentous shape, consisting of nucleocapsids 3–10 nm in diameter, with lengths proportional to the size of their RNA. The ssRNA genome consists of four or more segments, ranging in size from 11.9 to 9 kb. Plant hosts of tenuiviruses are all in the family Graminae.

Ophiovirus. This genus is not yet assigned to a family. Virions are naked filamentous nucleocapsids about 3 nm in diameter, with the shortest length about 760 nm. The genome consists of ssRNA of 11–12 kb in size. The natural hosts are dicotyledonous for two species, and tulip for the third species.

Single-stranded positive-sense RNA viruses

These include many families and unassigned genera, as follows.

Sequiviridae. Particles are isometric, about 30 nm in diameter. The genome consists of one molecule of infective, positive-sense RNA, 9–12 kb in size. Two genera are found in this family: *Sequivirus* (parsnip yellow fleck virus) and *Waikavirus* (rice tungro spherical virus). Transmission of these viruses is by aphids or leafhoppers; transmission is thought to be dependent on a self-encoded helper protein.

Comoviridae. Virions are nonenveloped, 28–30 nm in diameter, and exhibit icosahedral symmetry. Genomes consist of two molecules of linear positive-sense ssRNA. Genera include *Comovirus* (cowpea mosaic virus), *Fabavirus* (broad bean wilt virus 1), and *Nepovirus* (tobacco ringspot virus). All members of the family have biological vectors: comoviruses are transmitted by beetles, fabaviruses by aphids, and many nepoviruses are transmitted by nematodes.

Potyviridae. Virions are flexible filaments (helical symmetry) with no envelope and are 11–15 nm in diameter. A single molecule of positive-sense ssRNA of 8.5–10 kb in size makes up the genome. Genera in this family include *Potyvirus* (potato virus Y), *Ipomovirus* (sweet potato mild mottle virus), *Macluravirus* (Maclura mosaic virus), *Rymovirus* (ryegrass mosaic virus), *Tritimovirus* (wheat streak mosaic virus), and *Bymovirus* (barley yellow mosaic virus). All members of the family *Potyviridae* form cytoplasmic cylindrical inclusion bodies during infection. Some members have a narrow host range, while most members infect an intermediate number of plants. Transmission to most hosts is accomplished by mechanical inoculation.

Sobemovirus. This genus is not yet assigned to a family. Virions are about 30 nm in diameter and exhibit icosahedral symmetry. The genome consists of a single molecule of positive-sense ssRNA, approximately 4.1–4.5 kb in size. The representative virus for this genus is southern bean mosaic virus. Sobemoviruses infect both monocotyledonous and dicotyledonous plants, but the natural host range of each species is narrow.

Marafivirus. This genus is not yet assigned to a family. These virions exhibit icosahedral symmetry, are 28–32 nm in diameter, do not have an envelope, and contain one molecule of linear, positive-sense ssRNA, about 6.5 kb in size. The representative virus for this genus is *Maize rayado fino virus*.

Luteoviridae. Virions are 25 to 30 nm in diameter, exhibit icosahedral symmetry, and have no envelope. The genome consists of a single molecule of linear, positive-sense ssRNA of about 5800 nts. Three genera are found in this family: *Luteovirus* (barley yellow dwarf virus), *Polerovirus* (potato leafroll virus), and *Enamovirus* (pea enation mosaic virus-1). Transmission is by specific aphid vectors.

Umbravirus. This genus is not yet assigned to a family. Umbraviruses do not form conventional virus particles. Evidence suggests that the infective RNA is protected in lipid-containing structures. The representative virus is carrot mottle virus.

Tombusviridae. This is a very large family of plant viruses, with eight genera identified: *Aureusvirus*, *Avenavirus*, *Carmovirus*, *Dianthovirus*, *Machlomovirus*, *Necrovirus*, *Panicovirus*, and *Tombusvirus*. Virions exhibit an icosahedral symmetry with virions from the genera *Aureusvirus*, *Avenavirus*, *Carmovirus*, *Dianthovirus*, and *Tombusvirus* having a rounded outline, a diameter of about 32–35 nm, and a granular surface due to the presence of 90 projections known as P domains. Virions in the genera *Machlomovirus*, *Necrovirus*, and *Panicovirus* lack the protruding domain and appear smooth. The genome consists of a single molecule of positive-sense, linear ssRNA ranging in size from 3.7 to 4.7 kb. The exceptions are the *Dianthovirus* virions, which contain two genomic RNAs. A characteristic virus representative is the *Tomato bushy stunt virus* (genus: *Tombusvirus*).

Tobamovirus. This genus is not yet assigned to a family. The representative for this genus is the tobacco mosaic virus, which is characterized by particles with a rigid helical rod, 18 nm in diameter and 300–310 nm in length. The genome consists of a single molecule of positive-sense linear ssRNA, 6.3–6.6 kb in size.

Tobravirus. This genus is not yet assigned to a family. Tobacco rattle virus is the best-known member of this group, which is characterized by two types of nonenveloped, rigid helical rods 21–23 nm in diameter either 180–215 nm or 46–115 nm in length, depending on the isolate. The genome consists of two molecules of linear positive-sense ssRNA; the first is 6.8 kb and the second ranges in size from 1.8 kb to about 4.5 kb.

Hordeivirus. This genus is not yet assigned to a family. Virions in this group are nonenveloped, elongated, and rigid; they are helically symmetric and about 20 nm in diameter and 110–150 nm in length. The genome contains three molecules of positive-sense ssRNA, each approximately 3–4 kb in size. The representative virus for this genus is the barley stripe mosaic virus.

Furovirus. This genus is not yet assigned to a family. Virions in this group are nonenveloped, hollow rods; they are helically symmetric and about 20 nm in diameter and 140–160 nm or 260–300 nm in length. The genome contains two molecules of linear, positive-sense ssRNA, with the first molecule about 6–7 kb and the second molecule about 3.5–3.6 kb in size. The representative virus for this genus is the soil-borne wheat mosaic virus.

Pomovirus. This genus is not yet assigned to a family. Virions in this group are nonenveloped, rod-shaped particles; they are helically symmetric and about 20 nm in diameter, with predominant lengths of 65–80, 150–160, and 290–310 nm. The genome contains three molecules of linear, positive-sense ssRNA, with the first molecule about

6 kb, the second about 3–3.5 kb, and the third 2.5–3 kb in size. The representative virus for this genus is the potato mop-top virus.

Pecluvirus. This genus is not yet assigned to a family. Virions in this group are nonenveloped, rod-shaped particles; they are helically symmetric and about 21 nm in diameter, with two predominant lengths of 190 and 245 nm. The genome contains two molecules of linear, positive-sense ssRNA, with the first molecule about 5900 nts and the second molecule about 4500 nts. The representative virus for this genus is the peanut clump virus.

Benyvirus. This genus is not yet assigned to a family. Virions in this group are nonenveloped, rod-shaped particles; they are helically symmetric and about 20 nm in diameter, with predominant lengths of about 85, 100, 265, and 390 nm. The genome contains four molecules of linear, positive-sense ssRNA, ranging in size from 1.3 kb to 6.7 kb. The representative virus for this genus is the beet necrotic yellow vein virus.

Bromoviridae. Virions in this group are either spherical with icosahedral symmetry (diameter 26–35 nm) or bacilliform (diameters of 18–26 nm and lengths from 30 to 85 nm). Genomes consist of three linear, positive-sense ssRNAs (total genome length is approximately 8 kb). Genera in this group include the *Alfamovirus* (alfalfa mosaic virus), *Bromovirus* (brome mosaic virus), *Cucumovirus* (cucumber mosaic virus), *Ilarvirus* (tobacco streak virus), and *Oleavirus* (olive latent virus 2). The natural host range of the viruses ranges from very narrow (genus *Bromovirus*) to extremely broad (genus *Cucumovirus*). Transmission predominantly occurs by insects, usually as a mechanical vector and not a persistent infection of the insect. Several viruses in this family are responsible for major disease epidemics in crop plants.

Ourmiavirus. This genus is not yet assigned to a family. Virions in this group constitute a series of particles with conical ends and cylindrical bodies 18 nm in diameter. There is no envelope. The genome contains three segments of linear, positive-sense ssRNA. The representative virus for this genus is the *Ourmia melon virus*.

Idaeovirus. This genus is not yet assigned to a family. The virions are isometric, about 33 nm in diameter, and not enveloped. The genome contains three segments of linear, positive-sense ssRNA of about 5.5 kb, 2.2 kb, and 1 kb in size. The representative virus for this genus is the raspberry bushy dwarf virus.

Closteroviridae. Virions in this group are very flexuous filaments with helical symmetry, about 12 nm in diameter, with the length varying according to the genus and/or the individual species. The genome consists of a single molecule of linear, positive-sense ssRNA ranging in size from 15.3 to 19.3 kb. Genera include *Closterovirus* (beet yellows virus) and *Crinivirus* (lettuce infectious yellows virus). The host ranges of individual virus species are restricted. Natural vectors include aphids and whiteflies.

Capillovirus. This genus is not yet assigned to a family. The virions are nonenveloped flexuous filaments with helical symmetry, about 12 nm in diameter and 640–700 nm in length. The genome contains linear, positive-sense ssRNA of 6.5–7.4 kb in size. The representative virus for this genus is the apple stem grooving virus.

Trichovirus. This genus is not yet assigned to a family. These virions are nonenveloped flexuous filaments with helical symmetry, about 12 nm in diameter and 640–760 nm in length. The genome contains a single linear, positive-sense ssRNA of 7.5 kb in size. The representative virus for this genus is the apple chlorotic leaf spot virus.

Vitivirus. This genus is not yet assigned to a family. Virions are nonenveloped flexuous filaments with helical symmetry, about 12 nm in diameter and 725–825 nm in length. The genome contains a single linear, positive-sense ssRNA of 7.5 kb in size. The representative virus for this genus is the grapevine virus A virus.

Tymovirus. This genus is not yet assigned to a family. Virions are nonenveloped, icosahedral particles with a diameter of about 30 nm. The genome contains a single linear, positive-sense ssRNA of 6.3 kb in size. The representative virus for this genus is the turnip yellow mosaic virus.

Carlavirus. This genus is not yet assigned to a family. These virions are nonenveloped flexuous filaments with helical symmetry, 12–15 nm in diameter and 610–700 nm in length. The genome contains a single linear, positive-sense ssRNA of 7.4–7.7 kb in size. The representative virus for this genus is the carnation latent virus.

Potexvirus. This genus is not yet assigned to a family. These virions are nonenveloped flexuous filaments with helical symmetry, 13 nm in diameter and 470–580 nm in length. The genome contains a single linear, positive-sense ssRNA of 5.9–7.0 kb in size. The representative virus for this genus is the potato virus X.

Allexivirus. This genus is not yet assigned to a family. Virions in this group are nonenveloped highly flexible filaments, 12 nm in diameter and 800 nm in length. The genome contains a single linear, positive-sense ssRNA of 9.0 kb in size. The representative virus for this genus is the shallot virus X.

Foveavirus. This genus is not yet assigned to a family. These virions are nonenveloped flexuous filaments with helical symmetry, 12 nm in diameter and 800 nm in length. The genome contains a single linear, positive-sense ssRNA of 8.4–9.3 kb in size. The representative virus for this genus is the apple stem pitting virus.

Single-stranded RNA viruses using reverse transcriptase

This group contains only one family, the Pseudoviridae. These viruses were previously described under RNA viruses infecting algae, fungi, yeast, and protozoa. Members of this family are commonly referred to as LTR retrotransposons, and as such form an intrinsic and significant part of the genome of many plants.

Families and Genera of Viruses Infecting Bacteria

The families of bacteria, *Mycoplasma*, and Archeae viruses and the shapes and sizes of their characteristic members are presented in **Fig. 5**. Bacterial viruses are also known as bacteriophages or phages. They may be tailed or nontailed. *See also:* BACTERIOPHAGE.

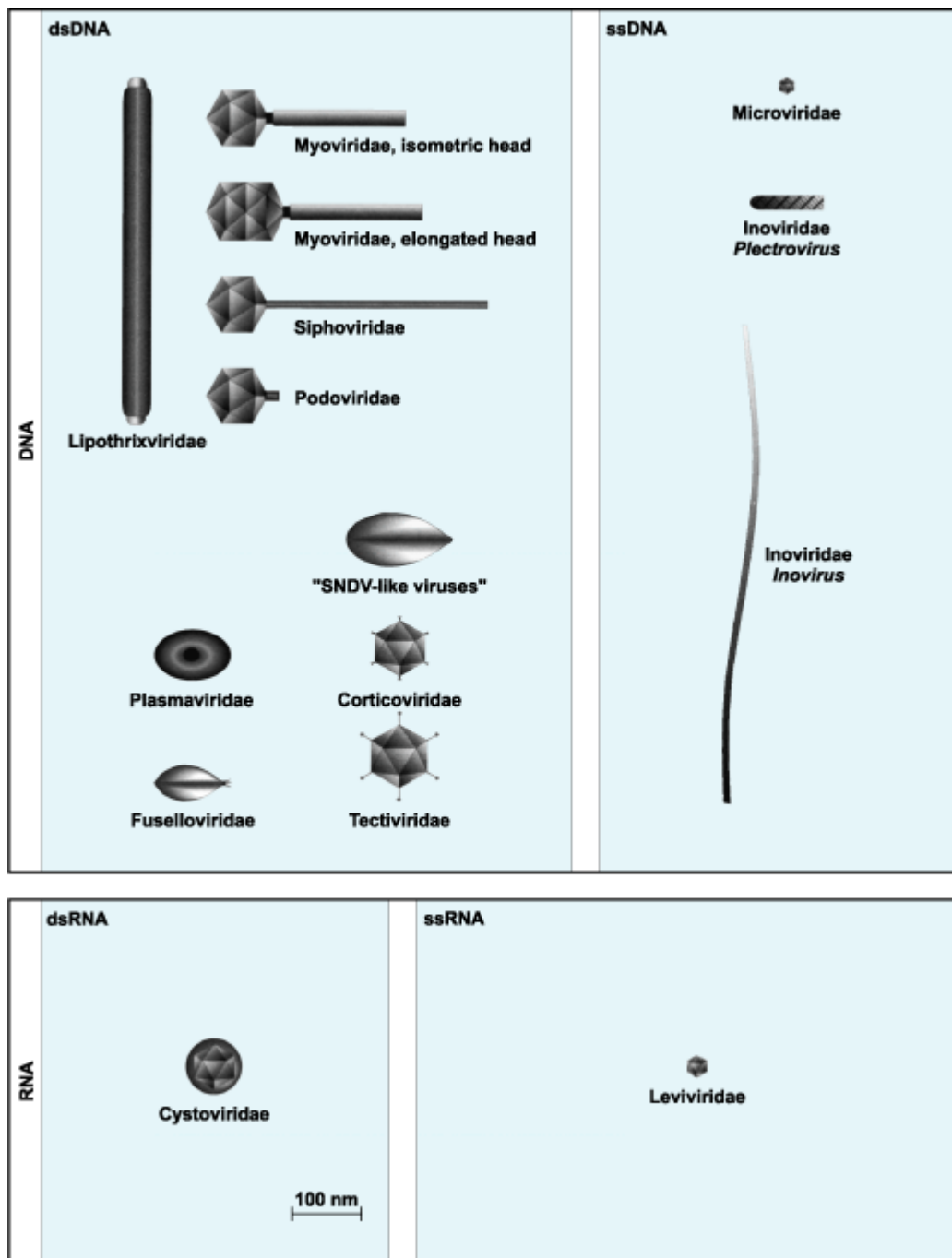


Fig. 5 Families and genera of viruses infecting bacteria. Individual frames separate taxa of viruses containing double-stranded and single-stranded genomes. Large boxes separate taxa of viruses having DNA or RNA genomes. All diagrams have been drawn approximately to the same scale to provide an indication of the relative sizes of the viruses. (From M. H. V. van Regenmortel et al., eds., *Virus Taxonomy: 7th Report of the International Committee on Taxonomy of Viruses*, p. 34, copyright 2000, with permission from Elsevier)

Double-stranded DNA viruses

These include nine families and one unassigned genus.

Myoviridae. These virions have contractile tails with a central core surrounded by a helical contractile sheath. The head is elongated (or icosahedral), 110 by 80 nm, and the tail measures 113 by 16 nm. Particles contain at least 21 structural proteins, two or three inside the head. Many enzymatic activities are present. The tail has a collar, base plate, six fibers, six spikes, and a central tube. Fibers initiate attachment events. Genomes range in size 34–160 kbp. Genera include T4-like viruses, P1-like viruses, P2-like viruses, Mu-like viruses, SPO1-like viruses, and ϕ -H-like viruses (which infect Archaea). These viruses infect bacteria, with the exception of the ϕ -H-like viruses.

Siphoviridae. These virions have long, noncontractile, thin tails, 65–570 nm long and 7–10 nm in diameter, which are often flexible. Tails are built of stacked disks of six subunits. Genera in this family include λ -like viruses, T1-like viruses, T5-like viruses, L5-like viruses, c2-like viruses, and ψ M1-like viruses. Heads are primarily icosahedral, and genomes consist of dsDNA of varying sizes. These viruses infect bacterial species including *Enterobacteria*, *Mycobacterium*, *Lactococcus*, and the archaea species *Methanobacterium*.

Podoviridae. These virions have short, noncontractile tails about 20 × 8 nm in dimension. Genera include the T7-like viruses, P22-like viruses, and the ϕ 29-like viruses. Heads are assembled first and tail subunits are added to the completed head. Phage heads are icosahedral. The genomes contain dsDNA of varying sizes. These viruses infect a wide number of bacterial species, including *Enterobacteria*, *Pseudomonas*, *Vibrio*, and *Caulobacter*.

Tectiviridae. Virus particles in this family are nonenveloped and icosahedral, 63 nm in diameter, and have 20-nm-long spikes at the 12 vertices. There are two shells, the outer rigid and 3 nm thick, while the inner is 6 nm thick, containing a lipoprotein vesicle. There are 15 virus-specific proteins associated with the lipoprotein vesicle. The genome consists of linear dsDNA of 14.7–15.7 kbp in size. During attachment to pili of gram-negative bacteria, following the ejection of nucleic acid, a transient tail of 60 nm length develops. The well-known *Enterobacteria phage PRD1* is in this group.

Corticoviridae. The virus particles are icosahedral and 60 nm in diameter, with brushlike spikes at the 12 vertices. The particle contains circular, dsDNA about 9 kbp in size. The virion also contains the enzyme transcriptase. A representative virus is *Alteromonas phage PM2*.

Plasmaviridae. This family of enveloped DNA phages includes the *Acholeplasma phage L2*. The particles are rounded, pleomorphic (50–125 nm in diameter), and show a small densely stained center. The double-stranded, circular DNA of the genome is 1.2 kbp in size. Virus is released by budding from *Acholeplasma* host cells, without killing the host.

Lipothrixviridae. These virions are rigid rods with a helical core, 410 nm long and 38 nm in diameter, with protrusions arising asymmetrically from both ends. The genome consists of one molecule of linear dsDNA of 15.9 kbp. A representative virus is *Thermoproteus virus 1*.

Rudiviridae. These virions are nonenveloped stiff rods, 23 nm in diameter by 500–780 nm in length. The genome is linear dsDNA, 33–36 kbp in size. A representative virus is *Sulfolobus virus SIRV-1*.

Fuselloviridae. These virions are lemon-shaped (60 by 100 nm), slightly flexible in appearance with short tail fibers attached to one pole. The genome contains circular, positively supercoiled dsDNA of 15.4 kbp in size. A representative virus is *Sulfolobus virus 1*.

Sulfolobus SNDV-like viruses. This genus is not yet assigned to a family. These virions are droplet-shaped, 80 by 180 nm. The genome is covalently closed circular dsDNA about 20 kbp in size. A representative virus is *Sulfolobus virus SNDV*.

Single-stranded DNA viruses

These include two families, Inoviridae and Microviridae.

Inoviridae. This family is characterized by nonenveloped rod-shaped phages which contain a single-stranded circular DNA genome within a cylindrical protein shell. Lengths vary from 700 nm to 2000 nm, although the diameter remains constant at about 7 nm. The genome consists of one molecule of infectious, circular positive-sense ssDNA. Genera in this family include *Inovirus* (*Enterobacteria phage M13*) and *Plectrovirus* (*Acholeplasma phage MV-L51*). Members of this family infect *Enterobacteria*, *Pseudomonas*, *Vibrio*, *Xanthomonas*, and *Acholeplasma*.

Microviridae. Virions exhibit icosahedral symmetry with projections at each of the 12 vertices. No envelope is present. Diameter of particles range from 26 to 32 nm. The genome for this family consists of one molecule of circular, positive-sense ssDNA, ranging in size from 4.4 to 6.0 kbp. Genera include *Microvirus*, *Spiromicrovirus*, *Bdellovirus*, and *Chlamydia microvirus*. A representative virus for this family is *Enterobacteria phage ϕ X 174*. Microviridae infect *Enterobacteria*, *Bdellovibrio*, *Spiroplasma melliferum*, and *Chlamydia psittaci*.

Double-stranded RNA viruses

These include only the family Cystoviridae. The virions are enveloped, spiked bacteriophages about 85 nm in diameter. The envelope surrounds an icosahedral nucleocapsid (58 nm in diameter). The genome consists of three linear dsRNA segments of 6.4, 4.0, and 2.9 kbp in size. A representative virus is *Pseudomonas phage ϕ 6*, which attaches to the pili of *Pseudomonas*.

Single-stranded RNA viruses

These include only the family Leviviridae. Virions are spherical and exhibit icosahedral symmetry (diameter of 26 nm). No envelope is present. The genome consists of one molecule of positive-sense ssRNA ranging in size from 3466 to 4276 nts. Two genera are found in this family: *Levivirus* (*Enterobacteria phage MS2*) and *Allolevivirus* (*Enterobacteria phage Q β*). These viruses attach to pili of male *Enterobacteria*, *Caulobacter*, and *Pseudomonas*.

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