Chapter 2

Virus Structure and Classification

2.1 COMMON CHARACTERISTICS OF VIRUSES

As described in Chapter 1, "The World of Viruses" viruses were initially characterized as filterable agents capable of causing disease. Since that time, advances in microscopy and scientific techniques have led to a better classification of viruses and their properties. Electron microscopy has allowed us to visualize viruses in great detail, while molecular and cellular assays have broadened our understanding of how viruses function and are related to one another. Taken together, we have learned that although they can be quite diverse, viruses share several common characteristics:

1. Viruses are Small in Size.

   The smallest of viruses are about 20 nm in diameter, although influenza and the human immunodeficiency virus have a more typical size, about 100 nm in diameter. Average human cells are 10–30 μm (microns) in diameter, which means that they are generally 100 to 1000 times larger than the viruses that are infecting them.

   However, some viruses are significantly larger than 100 nm. Poxviruses, such as the variola virus that causes smallpox, can approach 400 nm in length, and filoviruses, such as the dangerous Ebola virus and Marburg virus, are only 80 nm in diameter but extend into long threads that can reach lengths of over 1000 nm. Several very large viruses that infect amoebas have recently been discovered: megavirus is 400 nm in diameter, and pandoraviruses have an elliptical or ovoid structure approaching 1000 nm in length. It is a common mistake to think that all viruses are smaller than bacteria; most bacteria are typically 2000–3000 nm in size, but certain strains of bacteria called *Mycobacteria* can be 10 times smaller than this, putting them in the range of these large viruses. So although a characteristic of viruses is that they are all small in size, this ranges from only a few nanometers to larger than some bacteria (Fig. 2.1).

2. Viruses are **obligate intracellular parasites**, meaning that they are completely dependent upon the internal environment of the cell to create new infectious virus particles, or **virions**.

   All viruses make contact with and bind the surface of a cell to gain entry into the cell. The virus disassembles and its genetic material (made of nucleic acid) encodes the instructions for the proteins that will spontaneously assemble into the new virions. This is known as de novo replication, from the Latin for "from new." In contrast to cells, which grow in size and divide equally in two to replicate, viruses use the cell's energy and machinery to create and assemble new virions piece by piece, completely from scratch.

3. The genetic material of viruses can be composed of DNA or RNA.

   All living cells, whether human, animal, plant, or bacterial, have double-stranded DNA (dsDNA) as their genetic material. Viruses, on the other hand, have **genomes**, or genetic material, that can be composed of DNA *or* RNA (but not both). Genomes are not necessarily double-stranded, either; different virus types can also have single-stranded DNA (ssDNA) genomes, and viruses with RNA genomes can be single-stranded or double-stranded. Any particular virus will only have one type of nucleic acid genome, however, and so viruses are not encountered that have both ssDNA and ssRNA genomes, for example.

   Similarly to how the size of the virus particle varies significantly, the genome size can also vary greatly from virus to virus. A typical virus genome falls in the range of 7000–20,000 base pairs (bp) (7–20 kilobase pairs (kb)). Smaller-sized virions will naturally be able to hold less nucleic acid than larger virions, but large viruses do not necessarily have large genomes. While most viruses do not contain much nucleic acid, some dsDNA viruses have very large genomes: herpesviruses

Refresher: Orders of Magnitude and Scientific Notation

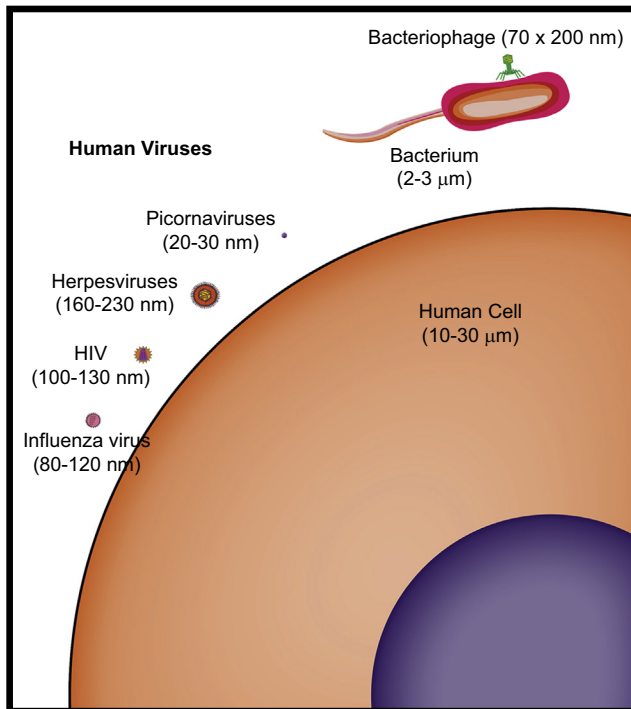| Virion size: Getting Smaller		Virus genome size: Getting Bigger	
1000 millimeters (mm) in a meter (m)	$1\,mm = 10^{-3}\,m$	1000 base pairs (nucleotide pairs, bp) in a kilobase pair (kb)	$1\,kb = 10^{3}\,bp$
1000 micrometers (μm, or microns) in a millimeter	$1\,\mu m = 10^{-6}\,m$	1000 kb in a megabase pair (mb)	$1\,mb = 10^{6}\,bp$
1000 nanometers (nm) in a micrometer	$1\,nm = 10^{-9}\,m$	1000 mb in a gigabase pair (gb)	$1\,gb = 10^{9}\,bp$

FIGURE 2.1   Virus and cell size comparison. Human viruses can vary in size but are generally in the range of 20–200 nm in diameter. In comparison, bacteria are generally 2–3 μM in length, and an average human cell is 10–30 μM.

have genomes that are 120–200 kb in total, and the very large pandoraviruses mentioned previously have the largest genomes: up to 2.5 million bases, rivaling the genome size of many bacteria! In comparison, eukaryotic cells have much larger genomes: a red alga has the smallest known eukaryotic genome, at 8 million base pairs; a human cell contains over 3 billion nucleotides in its hereditary material; the largest genome yet sequenced, at over 22 billion base pairs, is that of the loblolly pine tree.

> **Study Break**
> Describe the common characteristics of viruses.

2.2 STRUCTURE OF VIRUSES

The infectious virus particle must be released from the host cell to infect other cells and individuals. Whether dsDNA, ssDNA, dsRNA, or ssRNA, the nucleic acid genome of the virus must be protected in the process. In the extracellular environment, the virus will be exposed to enzymes that could break down or degrade nucleic acid. Physical stresses, such as the flow of air or liquid, could also shear the nucleic acid strands into pieces. In addition, viral genomes are susceptible to damage by ultraviolet radiation or radioactivity, much in the same way that our DNA is. If the nucleic acid
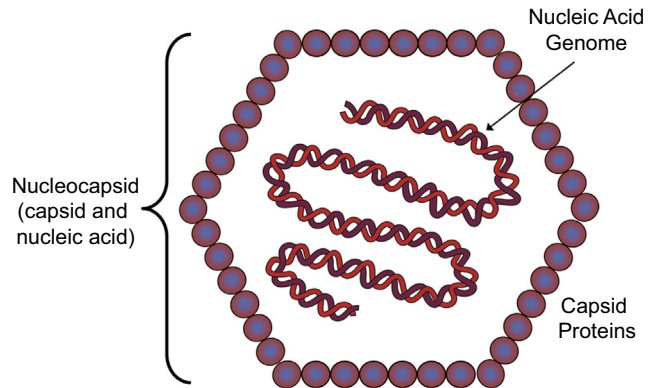

FIGURE 2.2   Basic virus architecture. Viral capsid proteins protect the fragile genome, composed of nucleic acid, from the harsh environment. The capsid and nucleic acid together are known as the nucleocapsid.

genome of the virus is damaged, then it will be unable to produce progeny virions.

In order to protect the fragile nucleic acid from this harsh environment, the virus surrounds its nucleic acid with a protein shell, called the **capsid**, from the Latin *capsa*, meaning "box." The capsid is composed of one or more different types of proteins that repeat over and over again to create the entire capsid, in the same way that many bricks fit together to form a wall. This repeating structure forms a strong but slightly flexible capsid. Combined with its small size, the capsid is physically very difficult to break open and sufficiently protects the nucleic acid inside of it. Together, the nucleic acid and the capsid form the **nucleocapsid** of the virion (Fig. 2.2).

Remember that the genomes of most viruses are very small. Genes encode the instructions to make proteins, so small genomes cannot encode many proteins. It is for this reason that the capsid of the virion is composed of one or only a few proteins that repeat over and over again to form the structure. The nucleic acid of the virus would be physically too large to fit inside the capsid if it were composed of more than just a few proteins.

In the same way that a roll of magnets will spontaneously assemble together, capsid proteins also exhibit self-assembly. The first to show this were H. Fraenkel-Conrat and Robley Williams in 1955. They separated the RNA genome from the protein subunits of tobacco mosaic virus, and when they put them back together in a test tube, infectious virions formed automatically. This indicated that no additional information is necessary to assemble a virus: the physical components will assemble spontaneously, primarily held together by electrostatic and hydrophobic forces.

Most viruses also have an **envelope** surrounding the capsid. The envelope is a lipid membrane that is derived from one of the cell's membranes, most often the plasma membrane, although the envelope can also come from the cell's endoplasmic reticulum, Golgi complex, or even the nuclear membrane,

FIGURE 2.3 **Comparison between a Naked and Enveloped Virion.** The capsid of an enveloped virion is wrapped with a lipid membrane derived from the cell. Virus attachment proteins located in the capsid or envelope facilitate binding of the virus to its host cell.

depending upon the virus. These viruses often have proteins, called **matrix proteins**, that function to connect the envelope to the capsid inside. A virus that lacks an envelope is known as a **nonenveloped** or **naked virus** (Fig. 2.3). Each virus also possesses a **virus attachment protein** embedded in its outermost layer. This will be found in the capsid, in the case of a naked virus, or the envelope, in the case of an enveloped virus. The virus attachment protein is the viral protein that facilitates the docking of the virus to the plasma membrane of the host cell, the first step in gaining entry into a cell.

2.2.1 Helical Capsid Structure

Each virus possesses a protein capsid to protect its nucleic acid genome from the harsh environment. Virus capsids predominantly come in two shapes: **helical** and **icosahedral**. The helix (plural: helices) is a spiral shape that curves cylindrically around an axis. It is also a common biological structure: many proteins have sections that have a helical shape, and DNA is a double-helix of nucleotides. In the case of a helical virus, the viral nucleic acid coils into a helical shape and the capsid proteins wind around the inside or outside of the nucleic acid, forming a long tube or rod-like structure (Fig. 2.4). The nucleic acid and capsid constitute the **nucleocapsid**. In fact, the protein that winds around the nucleic acid is often called the nucleocapsid protein. Once in the cell, the helical nucleocapsid uncoils and the nucleic acid becomes accessible.
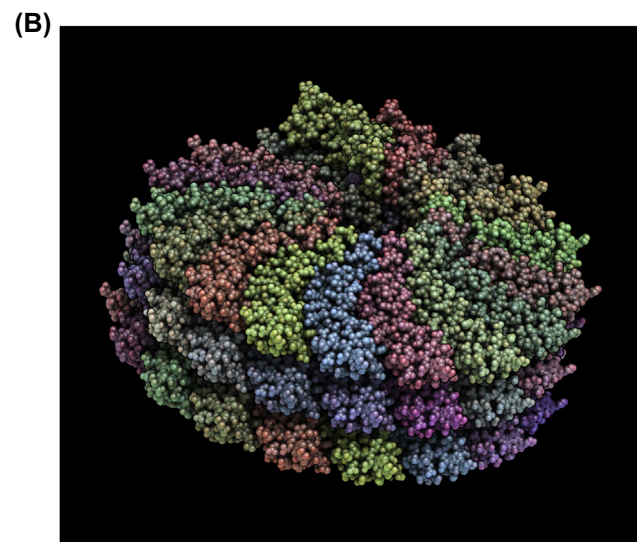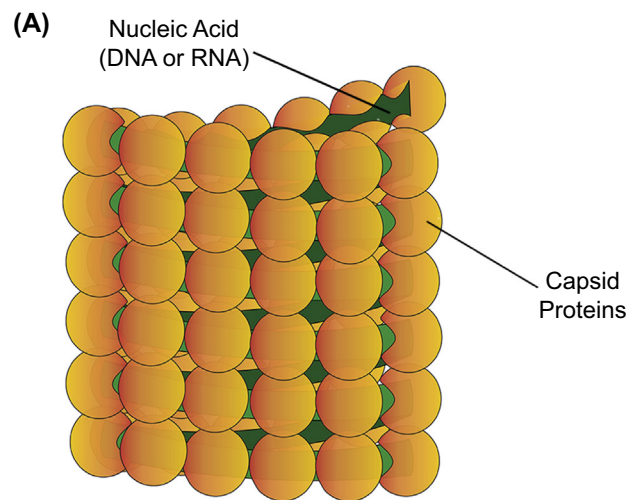
FIGURE 2.4 **Helical capsid structure.** (A) Viral capsid proteins wind around the nucleic acid, forming a helical nucleocapsid. (B) Helical structure of tobacco mosaic virus. Rendering of 49 subunits was performed using QuteMol (*IEEE Trans. Vis. Comput. Graph 2006, 12, 1237–44*) using a 2xea PDB assembly (*J. Struct. Biol. 2010, 171, 303–8*).

There are several perceived advantages to forming a helical capsid. First, only one type of capsid protein is required. This protein subunit is repeated over and over again to form the capsid. This structure is simple and requires less free energy to assemble than a capsid composed of multiple proteins. In addition, having only one nucleocapsid protein means that only one gene is required instead of several, thereby reducing the length of nucleic acid required. Because the helical structure can continue indefinitely, there are also no constraints on how much nucleic acid can be packaged into the virion: the capsid length will be the size of the coiled nucleic acid.

Helical viruses can be enveloped or naked. The first virus described, tobacco mosaic virus, is a naked helical virus. In fact, most plant viruses are helical, and it is very uncommon that a helical plant virus is enveloped. In contrast, all helical animal viruses are enveloped. These include well-known viruses such as influenza virus, measles virus, mumps virus, rabies virus, and Ebola virus (Fig. 2.5).

2.2.2 Icosahedral Capsid Structure

Of the two major capsid structures, the icosahedron is by far more prevalent than the helical architecture. In comparison to a helical virus where the capsid proteins wind around the nucleic acid, the genomes of icosahedral viruses are packaged completely within an icosahedral capsid that acts as a protein shell. Initially these viruses were thought to be spherical, but advances in electron microscopy and X-ray crystallography revealed these were actually icosahedral in structure.

An icosahedron is a geometric shape with 20 sides (or **faces**), each composed of an equilateral triangle. An icosahedron has what is referred to as **2–3–5 symmetry**, which is used to describe the possible ways that an icosahedron can rotate around an axis. If you hold an icosahedral die in your hand, you will notice there are different ways of rotating it (Fig. 2.6). Let's say you

In-Depth Look: Defining Helical Capsid Structure

A helix is mathematically defined by two parameters, the amplitude and the pitch, that are also applied to helical capsid structures. The **amplitude** is simply the diameter of the helix and tells us the width of the capsid. The **pitch** is the height or distance of one complete turn of the helix. In the same way that we can determine the height of a one-story staircase by adding up the height of the stairs, we can figure out the pitch of the helix by determining the **rise**, or distance gained by each capsid subunit. A staircase with 20 stairs that are each 6 inches tall results in a staircase of 10 feet in height; a virus with 16.3 subunits per turn and a rise of 0.14 nm for each subunit results in a pitch of 2.28 nm. This is the architecture of tobacco mosaic virus.
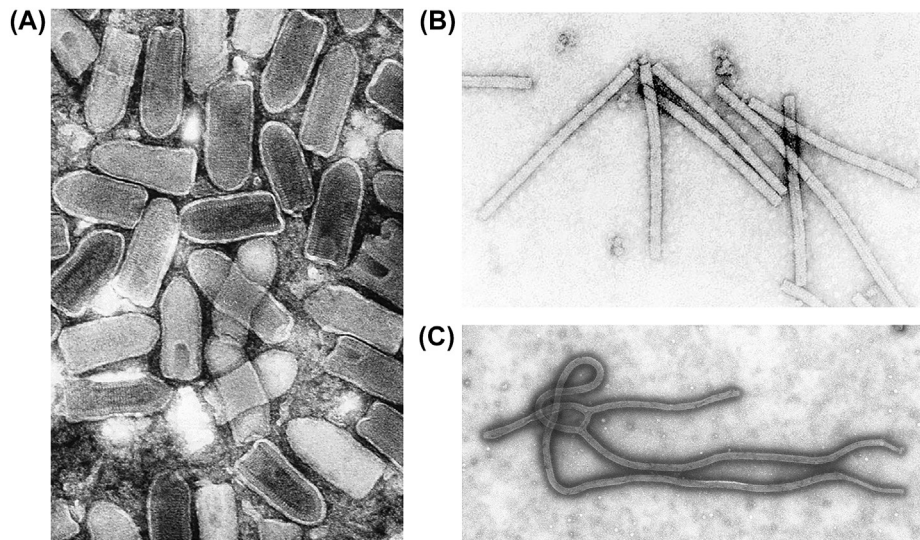
FIGURE 2.5   Electron micrographs of helical viruses. (A) Vesicular stomatitis virus forms bullet-shaped helical nucleocapsids. *(Image courtesy of CDC/Dr. Fred A. Murphy.)* (B) Tobacco mosaic virus forms long helical tubes. *(Image courtesy of the USDA Beltsville Electron Microscopy Unit.)* (C) The helical Ebola virus forms long threads that can extend over 1000 nm in length. *(Image courtesy of CDC/Cynthia Goldsmith.)*
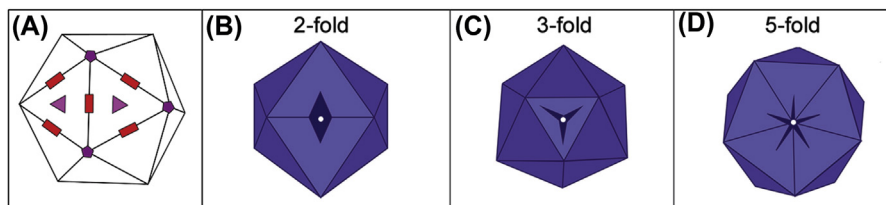
FIGURE 2.6   Icosahedron terminology and axes of symmetry. (A) Icosahedron faces (fuchsia triangles), edges (red rectangles), and vertices (violet pentagons) are indicated on the white icosahedron. (B) The twofold axis of symmetry occurs when the axis is placed through the center of an edge. The threefold axis occurs when the axis is placed in the center of a face (C), and the fivefold axis passes through a vertex of the icosahedron (D).

looked straight on at one of the **edges** of the icosahedron and poked an imaginary pencil through the middle of that edge. Your pencil would be right in the middle of a triangle facing up and a triangle facing down. If you rotate the icosahedron clockwise, you will find that in 180 degrees you encounter the same arrangement (symmetry): a triangle facing up and a triangle facing down. Continuing to rotate the icosahedron brings you back to where you began. This is known as the **twofold axis** of symmetry, because as you rotate the shape along this axis (your pencil), you encounter your starting structure twice in one revolution: once when you begin, and again when rotated 180 degrees. On the other hand, if you put your pencil axis directly through the center one of the small triangle **faces** of the icosahedron, you will encounter the initial view two additional times as you rotate the shape, for a total of three times. This is the **threefold axis.** Similarly, if your pencil axis goes through a **vertex** (or tip) of the icosahedron, you will find symmetry five times in one rotation, forming the **fivefold axis**. It is for this reason that an icosahedron is known to have 2–3–5 symmetry, because it has twofold, threefold, and fivefold axes of symmetry. This terminology is useful when dealing with an icosahedral virus because it can be used to indicate specific locations on the virus or where the virion has interactions with the cell surface. For instance, if a virus interacts with a cell surface receptor at the threefold axis, then you know this interaction occurs at one of the faces of the icosahedron. A protein protruding from the capsid at the fivefold axis will be found at one of the vertices (tips) of the icosahedron. All of the illustrations of viruses in Fig. 2.7 are viewed on the twofold axis of symmetry.

Study Break
How many twofold axes of symmetry are found in one icosahedron? How about the number of threefold or fivefold axes? How many faces, edges, and vertices are found in an icosahedron?

Viral proteins form each face (small triangle) of the icosahedral capsid. Viral proteins are not triangular, however, and so one protein subunit alone is not sufficient to form the entire face. Therefore, a face is formed from at least three viral protein subunits fitted together (Fig. 2.8). These can all be the same protein, or they can be three different proteins. The subunits together form what is called
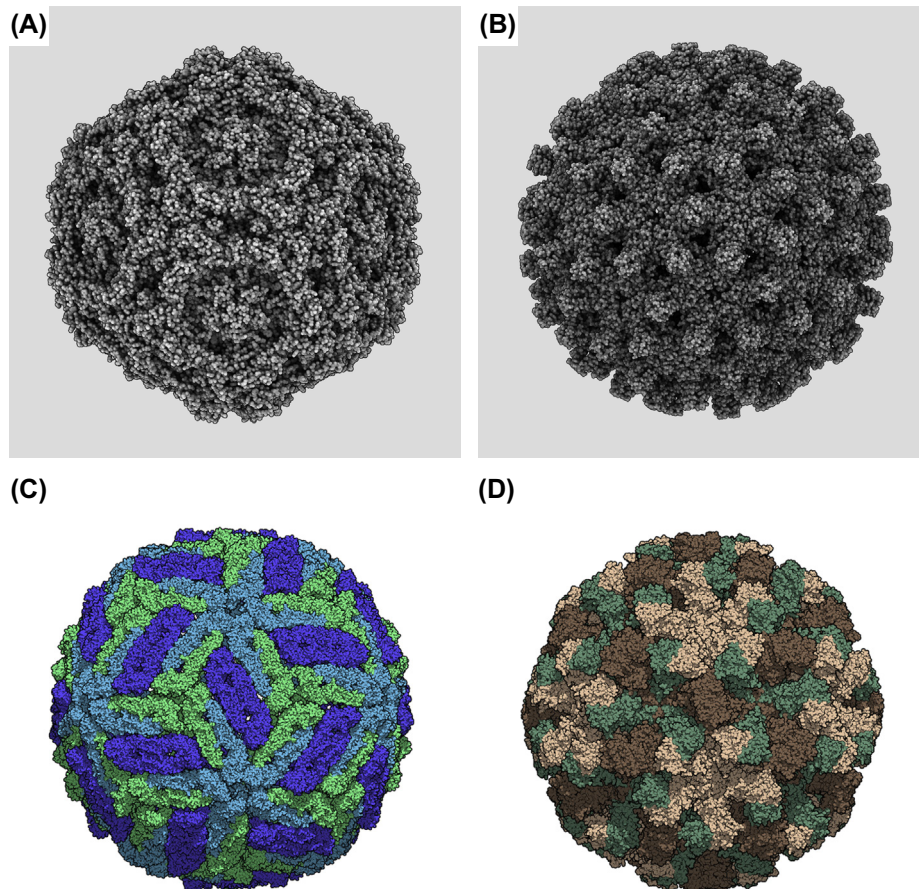
FIGURE 2.7 Illustrations of viruses, as viewed on the twofold axis of rotation. 3D surface reconstructions of parvovirus B19 (A), human hepatitis B virus (B), dengue virus (C), and Norwalk virus (D). *Illustrations created with QuteMol (IEEE. Trans. Vis. Comput. Graph 2006, 12, 1237–44) using 2G33 (J. Virol. 2006, 80, 11055–61), 1S58 (Proc. Natl. Acad. Sci. U. S. A. 2004, 101, 11628–33), 1K4R (Cell 2002, 108, 717–25), and 1IHM (Science 1999, 286, 287–90) PDB assemblies.*
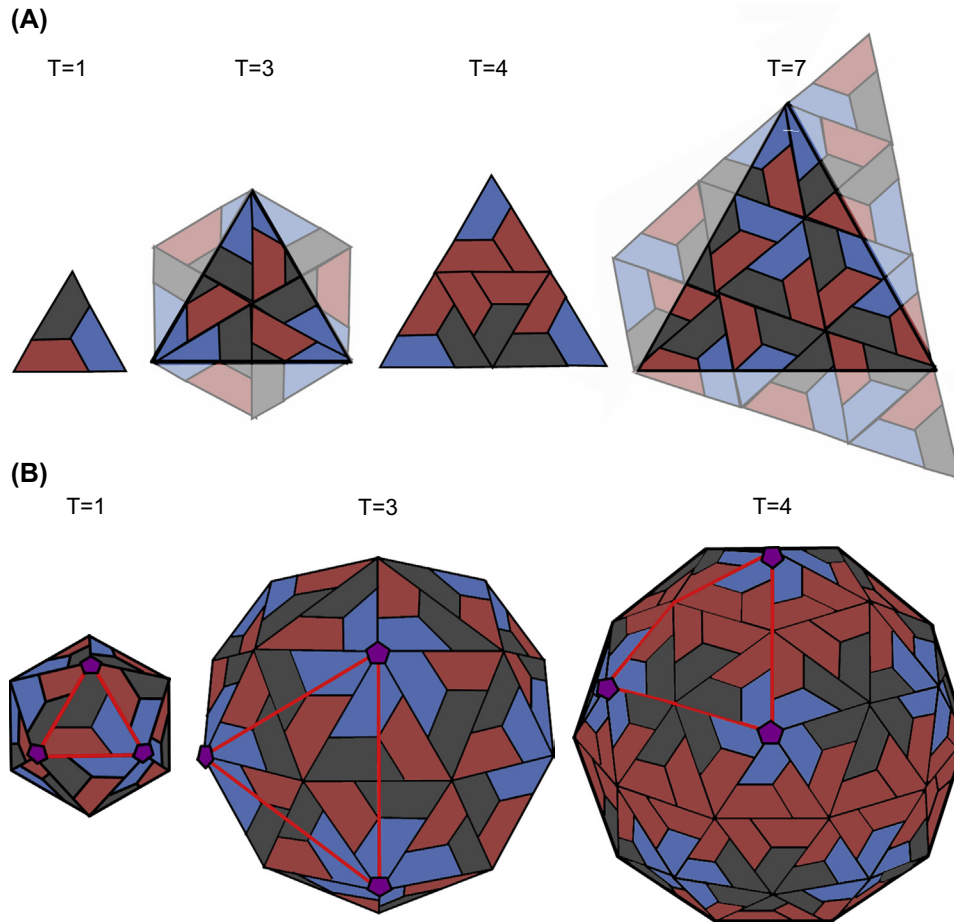
FIGURE 2.8   Capsid architecture and triangulation number. (A) Virus capsids are composed of viral protein subunits that form structural units. The triangulation number (T) indicates the number of structural units per face of the icosahedron. In a $T=1$ virus, one structural unit (composed of three different protein subunits: gray, red, and blue) create the icosahedron face. (B) Virion capsids with $T=1$, $T=3$, and $T=4$. The red lines outline a triangular face of the icosahedron, while the purple pentagons indicate the vertices (fivefold axes) of the icosahedron.

the **structural unit**. The structural unit repeats to form the capsid of the virion.

But how can some viruses form very large icosahedral capsids? The answer is repetition. The structural unit can be repeated over and over again to form a larger icosahedron side. The number of structural units that creates each side is called the **triangulation number (T)**, because the structural units form the triangle face of the icosahedron. In a $T=1$ virus, only one structural unit forms each icosahedron face (Fig. 2.8). In a $T=4$ virus, four structural units form the face. Sometimes the structural unit overlaps from one face to another: in a $T=3$ virus, three total structural units form the face, although this occurs as six half-units (half of each structural unit forms part of an adjacent face). Similarly, the structural units of a $T=7$ virus are also slightly skewed, compared to the triangle face. The geometry and math involved with icosahedral capsid structure

can be complex, and only the very basics are described here. In any case, by increasing the number of identical structural units on each face, the icosahedron can become progressively larger without requiring additional novel proteins to be produced. Some viruses have triangulation numbers over 25, even!

The proteins that compose the structural unit may form three dimensional structures known as **capsomeres** that are visible in an electron micrograph. In icosahedral viruses, capsomeres generally take the form of pentons (containing five units) or hexons (containing six units) that form a visible pattern on the surface of the icosahedron (See Fig. 13.11 for an example). Capsomeres are morphological units that arise from the interaction of the proteins within the repeated structural units.

Why does the icosahedral virus structure appear so often? Research has shown that proteins forming

icosahedral symmetry require lesser amounts of energy, compared to other structures, and so this structure is evolutionarily favored.

Many viruses that infect animals are icosahedral, including human papillomavirus, rhinovirus, hepatitis B virus, and herpesviruses (Fig. 2.9). Like their helical counterparts, icosahedral viruses can be naked or enveloped, as well. The type of viral nucleic acid (dsDNA, ssDNA, dsRNA, and ssRNA) does not correlate with the structure of the capsid; icosahedral viral capsids can contain any of the nucleic acid types, depending upon the virus.

2.2.3 Complex Viral Structures

The majority of viruses can be categorized as having helical or icosahedral structure. A few viruses, however, have a **complex** architecture that does not strictly conform to a simple helical or icosahedral shape. Poxviruses, geminiviruses, and many bacteriophages are examples of viruses with complex structure (Fig. 2.10). Poxviruses, including the viruses that cause smallpox or cowpox, are large oval or brick-shaped particles 200–400 nm long. Inside the complex virion, a dumbbell-shaped core encloses the viral DNA and is surrounded by two "lateral bodies," the function of which is currently unknown. The geminiviruses also exhibit complex structure. As their name suggests, these plant-infecting viruses are composed of two icosahedral heads joined together. **Bacteriophages**, also known as **bacterial viruses** or **prokaryotic viruses**, are viruses that infect and replicate within bacteria. Many bacteriophages also have complex structure, such as bacteriophage P2, which has an icosahedral head, containing the nucleic acid, attached to a cylindrical tail sheath that facilitates binding of the bacteriophage to the bacterial cell.
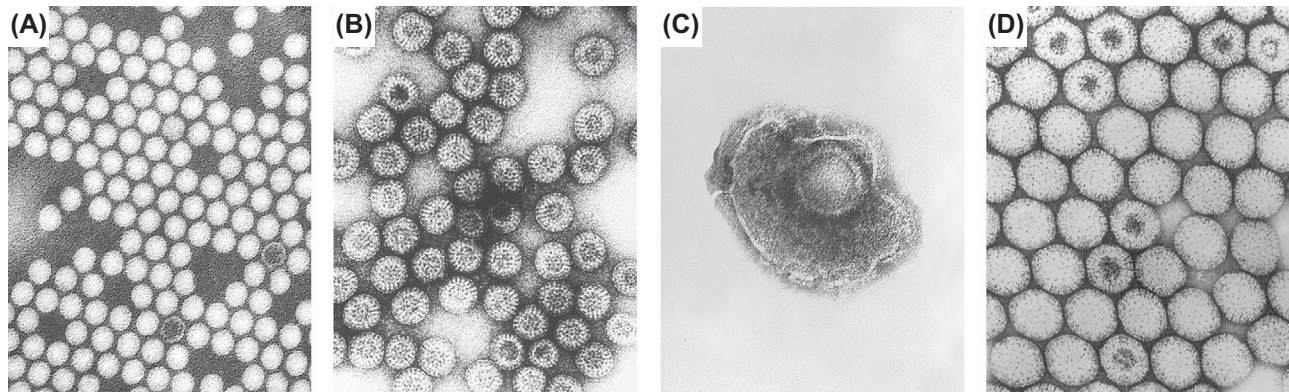
FIGURE 2.9 **Electron micrographs of icosahedral viruses.** Poliovirus (A), rotavirus (B), varicella–zoster virus (C), the virus that causes chickenpox and shingles, and reovirus (D). Note that C is enveloped. *Images courtesy of the CDC: Dr. Fred Murphy and Sylvia Whitfield (A), Dr. Erskine Palmer (B and D), and Dr. Erskine Palmer and B.G. Partin (C).*
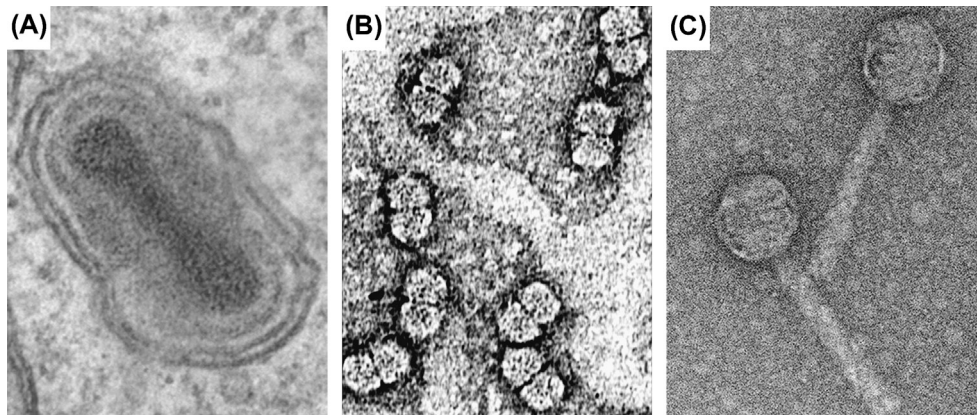
FIGURE 2.10 **Electron micrograph of viruses with complex architecture.** Vaccinia virus (A), a virus belonging to the poxvirus family, has a complex capsid architecture with a dumbbell-shaped core. Geminiviruses (B) have a double-icosahedron capsid. Bacteriophages, such as P2 (C), often have complex capsid structure. *Images courtesy of Ana Caceres et al. (A, PLoS Pathog. 2013, 9(11), e1003719), Kassie Kasdorf (B), and Mostafa Fatehi (C).*

2.3 VIRUS CLASSIFICATION AND TAXONOMY

The classification of viruses is useful for many reasons. It allows scientists to contrast viruses and to reveal information on newly discovered viruses by comparing them to similar viruses. It also allows scientists to study the origin of viruses and how they have evolved over time. The classification of viruses is not simple, however—there are currently over 2800 different viral species with very different properties!

One classification scheme was developed in the 1970s by Nobel laureate David Baltimore. The **Baltimore classification system** categorizes viruses based on the type of nucleic acid genome and replication strategy of the virus. The system also breaks down single-stranded RNA viruses into those that are positive strand (+) and negative strand (−). As will be further discussed in the next chapter, **positive-strand** (also positive-sense or plus-strand) RNA is able to be immediately translated into proteins; as such, messenger RNA (mRNA) in the cell is positive strand. **Negative-strand** (also negative-sense or minus-strand) RNA is not translatable into proteins; it first has to be transcribed into positive-strand RNA. Baltimore also took into account viruses that are able to **reverse transcribe**, or create DNA from an RNA template, which is something that cells are not capable of doing. Together, the seven classes are

- class I: dsDNA viruses
- class II: ssDNA viruses
- class III: dsRNA viruses
- class IV: positive-sense ssRNA viruses
- class V: negative-sense ssRNA viruses
- class VI: RNA viruses that reverse transcribe
- class VII: DNA viruses that reverse transcribe

There are a variety of ways by which viruses could be classified, however, including virion size, capsid structure, type of nucleic acid, physical properties, host species, or disease caused. Because of this formidable challenge, the **International Committee on Taxonomy of Viruses (ICTV)** was formed and has been the sole body charged with classifying viruses since 1966. **Taxonomy** is the science of categorizing and assigning names (**nomenclature**) to organisms based on similar characteristics, and the ICTV utilizes the same taxonomical hierarchy that is used to classify living things. It is important to note that viruses, since they are not alive, belong to a completely separate system that does not fall under the tree of life. Whereas a living organism is classified using

TABLE 2.1 Taxa Used to Classify Viruses

Taxon	Notes	Example
Order	Ends in -virales suffix; only about half of viruses are currently classified in orders.	*Picornavirales*
Family	Ends in -viridae suffix; subfamilies are indicated with -virinae suffix.	*Picornaviridae*
Genus	Ends in -virus suffix.	*Enterovirus*
Species	Generally the "common name" of the virus. Classifying and cataloging anything below the species classification (such as subtypes, serotypes, strains, isolates, or variants) is the responsibility of the specific field.	*Rhinovirus A* (Serotypes include Human rhinovirus 1, which includes strains human rhinovirus 1A and human rhinovirus 1B)

domain, kingdom, phylum, class, order, family, genus, and species **taxa** (singular: **taxon**), or categories, viruses are only classified using order, family, genus, and species (Table 2.1).

The ICTV classifies viruses based upon a variety of different characteristics with the intention of categorizing the most similar viruses with each other. The chemical and physical properties of the virus are considered, such as the type of nucleic acid or number of different proteins encoded by the virus. DNA technologies now allow us to sequence viral genomes relatively quickly and easily, allowing scientists to compare the nucleic acid sequences of two viruses to determine how closely related they are. Other virion properties are also taken into account, including virion size, capsid shape, and whether or not an envelope is present. The taxa of viruses that infect vertebrates are shown in Fig. 2.11; notice that some families are not yet classified into orders (refer to Table 2.1 for a refresher on how to distinguish the taxa by their suffixes). Also note the size difference between viruses of different families.

Currently, the ICTV has categorized seven orders of viruses (Table 2.2) that contain a total of 103 families classified within them. Seventy-seven virus families, however, have yet to be assigned to an order, including notable viruses such as the retroviruses, papillomaviruses, and poxviruses. New orders have been proposed, and it is likely that more will be created as the taxonomical process continues.
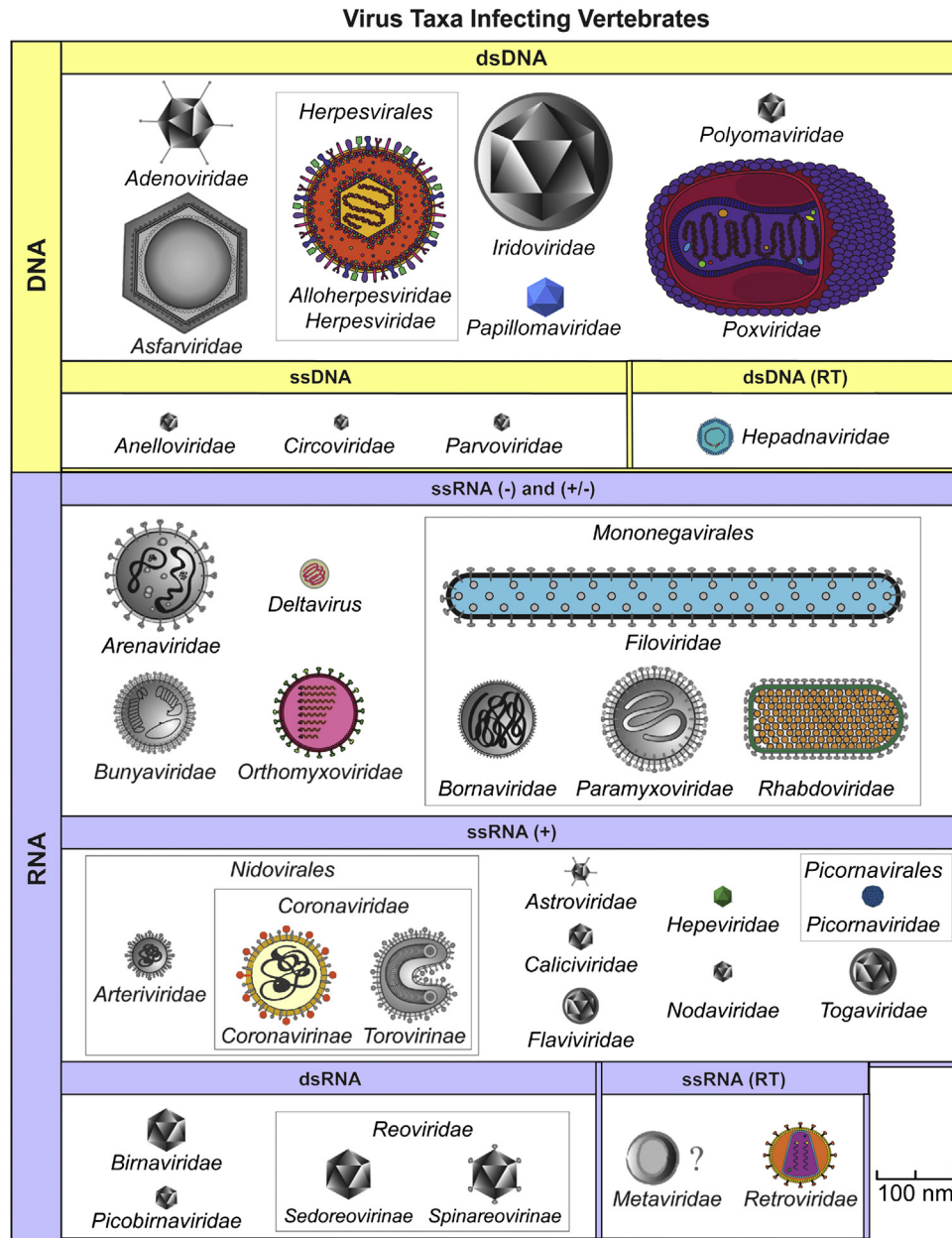
FIGURE 2.11   Taxa of viruses that infect vertebrates. Viruses are categorized based upon their type of nucleic acid (DNA viruses in yellow boxes and RNA viruses in blue boxes) and further classified based upon distinguishing characteristics. Note the nucleic acid, size, and architectural differences between viruses of different families. Viruses in color will be discussed in later chapters. *Modified with permission from Virus Taxonomy: Ninth Report of the International Committee on Taxonomy of Viruses, Elsevier, 2012.*

In-Depth Look: How Viruses are Named

The ICTV has established guidelines for naming newly discovered viruses. The Latin binomial names that are used for living organisms, where the genus and species are listed together (such as *Homo sapiens* or *Yersinia pestis*), are not used for naming viruses. Virus names should also not include any person's name (although historically this was how a few viruses were named), and selected names should be easy to use and meaningful.

When directly referring to a viral order, family, genus, or species the virus name should be written in italics with the first letter capitalized. When not referring specifically to viral classification, however, capitalization and italics are not required unless a proper name is encountered. For instance, "Some members of the *Arenaviridae* family can cause severe disease, including lymphocytic choriomeningitis virus and Lassa virus, which is named after the town in Nigeria where the first case occurred." The chart below gives some examples of where virus named originated (Table 2.3).

TABLE 2.2 Current Orders of the Virosphere

Order	Notes
Caudovirales	Tailed dsDNA viruses that infect members of the domains Bacteria and Archaea; name comes from Latin *cauda*, meaning "tail."
Herpesvirales	dsDNA viruses of vertebrates and invertebrates; from Greek *herpes*, meaning "creeping" or "spreading" (describing the rashes of these viruses).
Ligamenvirales	dsDNA viruses that infect the domain Archaea; from Latin *ligamen*, meaning "thread" or "string" (describing the linear structure of the viruses). Newest order, created in 2012.
Mononegavirales	"Negative-strand" ssRNA viruses of vertebrates, invertebrates, and plants; name derives from Latin for "one negative," referring to the single negative-strand RNA genome. Was the first order created, in 1990.
Nidovirales	"Positive-strand" ssRNA viruses of vertebrates and invertebrates; from Latin *nidus* meaning "nest" because they encode several proteins nested within one piece of mRNA.
Picornavirales	"Positive-strand" ssRNA viruses of vertebrates, invertebrates, and plants; from pico (small) + RNA + virales (viruses).
Tymovirales	"Positive-strand" ssRNA viruses of plants and invertebrates; Tymo is an acronym standing for Turnip Yellow Mosaic virus, found within this order.

ds, Double-stranded; *ss*, single-stranded.

TABLE 2.3 Name Origins of Selected Viruses

Name	Origin
Viruses named after the clinical conditions they cause	
Human immunodeficiency virus (HIV)	Causes the decline of the immune system, leading to immunodeficiency
Hepatitis virus	Although they are not in the same family, all hepatitis viruses cause liver inflammation (hepatitis)
Human papillomavirus (HPV)	Causes papillomas, benign epithelial tumors such as warts
Poxviruses	From pockes meaning "sac," referring to the blistery rash observed

Name	Origin
Rabies virus	From Latin *rabies*, meaning "madness," describing the symptoms seen with disease progression
Viruses named after their location of discovery	
Coxsackievirus	Named after Coxsackie, New York, the location from where the first specimens were obtained
Ebola virus	Named after the Ebola River in northern Democratic Republic of the Congo (formerly Zaire), where the virus first emerged in 1976
Marburg virus	Named after Marburg, a town in Germany, where an outbreak occurred in 1967
Nipah virus	First identified in the Malaysian village of Kampung Sungai Nipah in 1998
Norwalk virus	Named after a 1968 outbreak in children at an elementary school in Norwalk, Ohio
West Nile virus	First isolated from a woman in the West Nile district of Uganda in 1937
Viruses named after their properties	
Coronavirus	From Latin *corona*, meaning crown, referring to the crown-like appearance of the virions when viewed with an electron microscope
Herpesviruses	From Greek *herpein*, "to creep," referring to the lesions that slowly spread across the skin
Influenza virus	Originated in 15th century Italy, from an epidemic attributed to the "influence of the stars"
Picornaviruses	Pico meaning "small" + RNA viruses
Poliovirus	From Greek *polios*, meaning "gray," referring to the gray matter (cell bodies) in the spinal cord that it infects and damages
Viruses named after people (historically assigned; viruses can no longer be named after individuals)	
Epstein–Barr virus	Named after Michael Anthony Epstein and Yvonne Barr, who discovered the virus
JC Virus	Named after a patient, John Cunningham, from which the virus was isolated
Rous sarcoma virus	Discovered by Peyton Rous in 1911

SUMMARY OF KEY CONCEPTS

Section 2.1 Common Characteristics of Viruses

- Viruses are small. Most viruses are in the range of 20–200 nm, although some viruses can exceed 1000 nm in length. A typical bacterium is 2–3 µM in length; a typical eukaryotic cell is 10–30 µM in diameter.
- Viruses are obligate intracellular parasites and are completely dependent upon the cell for replication. Unlike cells that undergo mitosis and split in two, viruses completely disassemble within the cell and new virions (infectious particles) are assembled de novo from newly made components.
- While living things have dsDNA genomes, the genetic material of viruses can be composed of DNA or RNA, and single- or double-stranded. Most virus genomes fall within the range of 7–20 kb, but they range from 3 kb to over 2 mb.

Section 2.2 Structure of Viruses

- The simplest viruses are composed of a protein capsid that protects the viral nucleic acid from the harsh environment outside the cell.
- Virus capsids are predominantly one of two shapes, helical or icosahedral, although a few viruses have a complex architecture. In addition, some viruses also have a lipid membrane envelope, derived from the cell. All helical animal viruses are enveloped.
- Helical capsid proteins wind around the viral nucleic acid to form the nucleocapsid. A helix is mathematically defined by amplitude and pitch.
- An icosahedron is a geometric shape with 20 sides, each composed of an equilateral triangle. The sides are composed of viral protein subunits that create a structural unit, which is repeated to form a larger side and the other sides of the icosahedron. The triangulation number refers to the number of structural units per side.

Section 2.3 Virus Classification and Taxonomy

- The Baltimore classification system categorizes viruses based upon the type and replication strategy of the nucleic acid genome of the virus. There are seven classes.
- The ICTV was formed to assign viruses to a taxonomical hierarchy. The taxa used for classifying viruses are order, family, genus, and species. Because they are not alive, viruses are not categorized within the same taxonomical tree as living organisms.

FLASH CARD VOCABULARY

Virion	Triangulation number
Genome	Capsomere
Capsid	Bacteriophage
Nucleocapsid	Baltimore classification system
Enveloped virus	Positive-strand (positive-sense)
Naked (unenveloped) virus	Negative-strand (negative-sense)
Matrix proteins	Reverse transcribe
Virus attachment protein	Taxonomy
Helix	Nomenclature
Icosahedron: Face, edge, vertex	International Committee on Taxonomy of Viruses
Structural unit	Taxon

CHAPTER REVIEW QUESTIONS

1. Why are viruses considered obligate intracellular pathogens?
2. How does viral replication differ from cell replication?
3. What is the function of the capsid? Why must viruses repeat the same capsid protein subunits over and over again, rather than having hundreds of different capsid proteins?
4. Explain what 2–3–5 symmetry is, pertaining to an icosahedron.
5. What is a structural unit? In a $T = 3$ virus that has three subunits per structural unit, how many total subunits form the capsid?
6. List the seven groups of the Baltimore classification system.
7. What taxa are used to classify viruses? How does this differ from the classification of a living organism?
8. What viral properties are used to classify viruses?

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