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Virus Taxonomy

Eighth Report of the International Committee on Taxonomy of Viruses

Edited by
C. M. Fauquet
M. A. Mayo
J. Maniloff
U. Desselberger
L. A. Ball

Virology Division International Union of Microbiological Societies

Virus Taxonomy

Classification and Nomenclature of Viruses

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Preface and Acknowledgments

The practical need to partition the world of the viruses into distinguishable, universally agreed upon entities is the ultimate justification for developing a virus classification system. The first internationally organized attempts to introduce some order in the bewildering variety of viruses took place at the International Congress of Microbiology held in Moscow in 1966. A Committee was created, later called The International Committee on Taxonomy of Viruses (ICTV) which was given the task of developing a single, universal taxonomic scheme for all the viruses infecting animals (vertebrates, invertebrates and protozoa), plants (higher plants and algae), fungi, bacteria and archaea. Since 1971 the ICTV, operating on behalf of the world community of virologists, has produced the following seven reports describing the current state of virus taxonomy:

ICTV Report	Editors	Reporting ICTV Proceedings at the International Congresses of Virology held in :
The First Report, 1971	P. Wildy	Helsinki, 1968
The Second Report, 1976	F. Fenner	Budapest, 1971 and Madrid, 1975
The Third Report, 1979	R.E.F. Mathews	The Hague, 1978
The Fourth Report, 1982	R.E.F. Mathews	Strasbourg, 1981
The Fifth Report, 1991	R.I.B. Francki, C.M. Fauquet, D.L. Knudson, F. Brown	Sendai, 1984; Edmonton, 1987 and Berlin, 1990
The Sixth Report, 1995	F.A. Murphy, C.M. Fauquet, D.H.L. Bishop, S.A. Ghabrial, A.W. Jarvis, G.P. Martell, M.A. Mayo, M.D. Summers	Glasgow, 1993
The Seventh Report, 2000	M.H.V. van Regenmortel, C.M. Fauquet, D.H.L. Bishop, E.B. Carstens, M.K. Estes, S.M. Lemon, J. Maniloff, M.A. Mayo, D.J. McGeoch, C.R. Pringle, R.B. Wickner	Jerusalem, 1996

The present Eighth Report of the ICTV builds on the accumulated taxonomic construction of its predecessors and records the proceedings of the Committee since 2000, including decisions reached at the eleventh and the twelfth International Congresses of Virology held in Sydney in 1999 and Paris in 2002 respectively, and at mid-term ICTV meetings in 2001, 2002, and 2003.

In 1991, the ICTV agreed that the hierarchical level of species would be defined and added to the categories of genus, subfamily, family and order which were already in use in the universal virus classification system. In this 8th Report, the list of recognized virus species has been further extended and the demarcation criteria used to discriminate between individual virus species in different genera have been spelled out as far as possible. This work is still incomplete and will continue to require the input of the more than 70 Study-Groups who provide the information codified in ICTV Reports. The present Report represents the work of more than 500 virologists world-wide, i.e. the members of the Study Groups, Subcommittees and the Executive Committee of the ICTV. The compilers of the Report wish to express their gratitude to all these virologists.

We are especially grateful to Dr. Claude M. Fauquet, his assistant Ms Patricia Cosgrove and his staff (Vince Abernathy, Joe Iskra, John Lewis, Ben Fofana, and Adrien Fauquet) for taking responsibility respectively for the clerical aspects, the website ICTVbook and ICTVnet, the formatting and layout of the 8th ICTV Report and for the drawing and scanning of all the diagrams and pictures.

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Contents

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Part I :
The Universal Taxonomy of Viruses in Theory and Practice

L. Andrew Ball
President of the International Committee on Taxonomy of Viruses

Taxonomy lies at the uneasy interface between biology and logic. The processing of information follows somewhat different rules in these two systems and the role of taxonomy is to reconcile them as tidily as possible. To this end, the International Union of Microbiological Societies (IUMS) charged the International Committee on Taxonomy of Viruses (ICTV) with the task of developing, refining, and maintaining a universal virus taxonomy. The goal of this undertaking is to categorize the multitude of known viruses into a single classification scheme that reflects their evolutionary relationships, i.e. their individual phylogenies. As discussed below however, the uncertainties that surround the origins of viruses and the complexities of their evolution create unique problems for virus taxonomy. Nevertheless, this volume - the 8th in the series of ICTV taxonomic reports - documents the overall success of this 38-year effort which has created a rational, largely satisfying, and above all useful taxonomic structure that facilitates communication among virologists around the world and enriches our understanding of virus biology. The 8th ICTV Report depicts the current status of virus taxonomy in 2004; it is a tribute to the hundreds of virologists who contributed to it. Periodic updates are published in the Virology Division News (VDN) section of *Archives of Virology* and posted on the ICTV website:
http://www.danforthcenter.org/iltab/ictvnet/asp/_MainPage.asp.

Viral taxa. The 7th ICTV Report (1) formalized for the first time the concept of the virus species as the lowest taxon (group) in a branching hierarchy of viral taxa. As defined therein, '*a virus species is a polythetic class of viruses that constitute a replicating lineage and occupy a particular ecological niche*' (2). A 'polythetic class' is one whose members have several properties in common, although they do not necessarily all share a single common defining property. In other words, the members of a virus species are defined collectively by a consensus group of properties. Virus species thus differ from the higher viral taxa, which are 'universal' classes and as such are defined by properties that are necessary for membership. These issues have been presented and debated at length in the literature (see reference 3 and citations therein), and they will not be revisited here except to reiterate a few basic points:

- Viruses are real physical entities produced by biological evolution and genetics, whereas virus species and higher taxa are abstract concepts produced by rational thought and logic (3). The virus/species relationship thus represents the front line of the interface between biology and logic.
- Viruses (including virus isolates, strains, variants, types, sub-types, serotypes, etc.) should wherever possible be assigned as members of the appropriate virus species, although many viruses remain unassigned because they are inadequately characterized.
- All virus species must be represented by at least one virus isolate.
- Almost all virus species are members of recognized genera. A few species remain unassigned in their families although they have been clearly identified as new species.
- Some genera are members of recognized sub-families.
- All sub-families and most genera are members of recognized families. Some genera are not yet assigned to a family; in the future they may either join an existing family or constitute a new family with other unassigned genera. For example, the family *Flexiviridae* was recently created by grouping the following (formerly unassigned) genera: *Potexvirus*, *Carlavirus*, *Allexivirus*, *Vitivirus*, *Mandarivirus, Foveavirus, Capillovirus,* and *Trichovirus.*
- Some families are members of the following recognized orders: *Caudovirales, Nidovirales* and *Mononegavirales*.
- The hierarchy of recognized viral taxa is therefore:

  (Order)
  Family
  (Sub-family)
  Genus
  Species
- Only the aforementioned taxa are recognized by the ICTV. Other groupings (from clade to super-family), may communicate useful descriptive information in some circumstances but they have no formally recognized taxonomic meaning. Similarly, the term 'quasi-species', although it captures an important concept (4), has no recognized taxonomic meaning.

The creation or elimination, (re)naming, and (re)assignment of a virus species, genus, (sub)family, or order are all taxonomic acts that require public scrutiny and debate, leading to formal approval by the full membership of the ICTV (see below). For detailed instructions on how to initiate this process, see Article 6 of the Statutes of the ICTV and Rule 3.20 of the International Code of Virus Taxonomy and Nomenclature in this volume. In contrast, the naming of a virus isolate and its assignment to a pre-existing species are not considered taxonomic acts and therefore do not require formal ICTV approval. Instead they will typically be accomplished by publication of a paper describing the virus isolate in the peer-reviewed virology literature.

The ~1550 virus species that were introduced for the first time in the 7th ICTV Report were assigned the common (mostly English) names of representative member viruses, and this practice has been extended to the ~1950 virus species listed in the 8th Report. The only distinction is that species names are italicized whereas virus names are not (1, 5). While the decisions that led to these new conventions have been vigorously debated (6-17), it is hard to imagine that the alternative – the creation *de novo* of ~1950 species names – would have been preferable to most virologists.

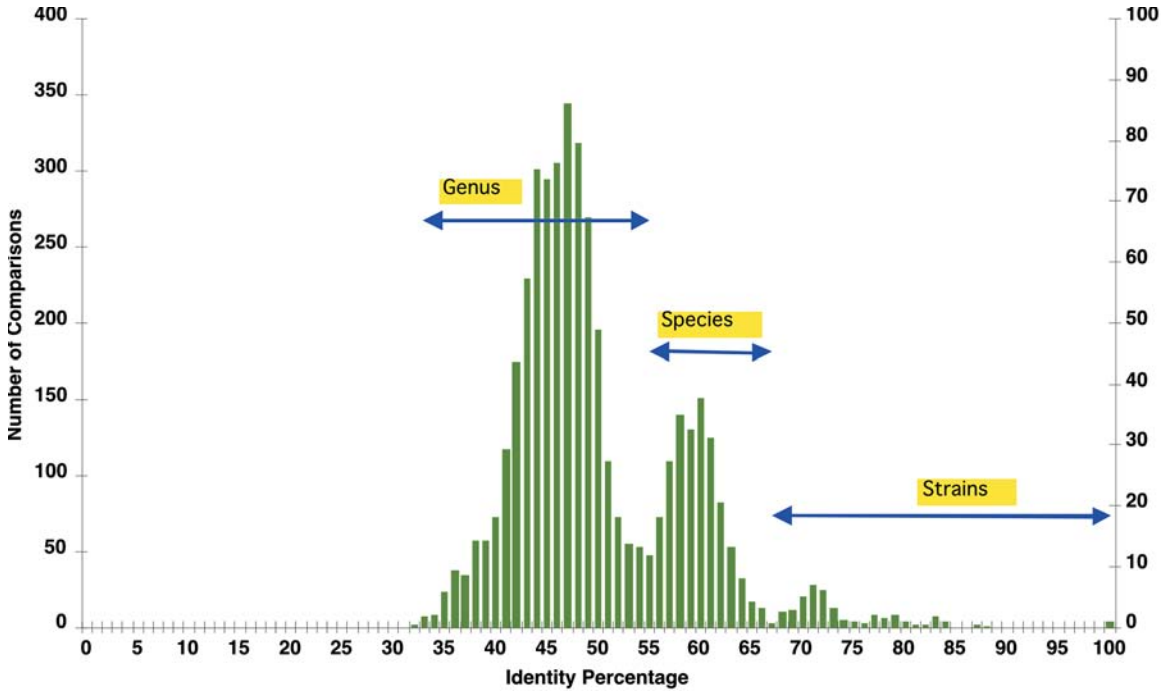

Figure 1. Distribution of pairwise identity percentages calculated for the sequences of the L1 gene of members of the family *Papillomaviridae* (Courtesy of C.M. Fauquet).

Demarcation criteria. Consistent assignment of viruses to taxa requires the specification of demarcation criteria, particularly at the species level where the differences are the smallest. Since virus species are polythetic, multiple demarcation criteria are needed to reliably delineate different species, and lists of the criteria used for each genus can be found in the corresponding descriptions. Within most genera, sequence comparisons are an increasingly dominant demarcation criterion because they provide a quantitative measure of divergence. In general, pairwise sequence identity profiles show well resolved peaks that represent typical evolutionary distances between strains, species, and genera within a given virus family (Figure 1). Different virus families may show similar overall patterns, but the absolute evolutionary distances between taxa may be different (2). Such genetic analyses provide a reassuring validation of taxonomic assignments, but they should not supersede species demarcation based on a balanced and multifaceted examination that includes phenotypic criteria. After all, virus taxonomy aims to classify organisms rather than simply to define the lineages of their genes.

Type species. Each genus contains a designated 'type species'. This is the virus species whose name typifies the name of the genus i.e. it is the 'nomenclatural type' of the genus, and its recognition creates an indissoluble link between the species and the genus. The type species is not necessarily the best characterized species in the genus and it may not even be a typical member (18). Rather, type species status is usually conferred on the species that necessitated the original creation and naming of the genus, and it should therefore seldom, if ever, be changed. Higher taxa do not have designated type species, and a proposal in the 4th ICTV Report (19) that each family should have a designated 'type genus' has since been revoked. The following definition of 'type species' has been proposed for the International Code of Virus Taxonomy and Nomenclature (18):

> "A type species is a species whose name is linked to the use of a particular genus name. The genus so typified will always contain the type species."

Abbreviations. As a general rule, there is no need to abbreviate the names of virus species because they will be used once or at most a few times in a typical paper (16). In contrast, it is convenient and appropriate to abbreviate the names of viruses, and this volume lists and uses many such abbreviations. However, there are many instances of identical abbreviations being used for very different viruses that infect plants, animals and insects. The ICTV does not formally define or endorse any particular virus name abbreviation, nor does it set rules for abbreviating virus names.

A practical guide to orthography (i.e. when to italicize). Once the distinction between a virus and a virus species is understood, when to use italics usually becomes clear: virus species names should be italicized, whereas the names of viruses themselves should not. However sentences written without the virus/species distinction in mind can be ambiguous as to whether they refer to a virus itself or to its species, and are best rewritten to resolve the ambiguity. Informal taxonomic names are widely used and should not be italicized or capitalized. For example, the informal name 'vesiculovirus' refers to a member of the genus *Vesiculovirus*; the informal name 'rhabdovirus' refers to a member of the family *Rhabdoviridae*; and the informal name 'mononegavirus' refers to a member of the order *Mononegavirales*. The International Code of Virus Taxonomy and Nomenclature in this volume gives more detailed instructions on how to correctly portray the names of viruses and their taxa.

Taxonomy and phylogeny. Since the universal scheme of virus taxonomy was derived from classical Linnaean systematics, it is well suited for classifying organisms that are related to one another via simple branched and diverging descent, with relatively long evolutionary distances between successive branch points. However, virus evolution differs from this simple paradigm in several ways. First, it seems unlikely that all viruses are descended from a single original 'protovirus'. Multiple origins appear more likely, but it is unclear how many there were or when they occurred. These uncertainties jeopardize the possibility of meaningful virus taxonomy above the level of order. Secondly, recombination and reassortment are common among some viruses, resulting in chimeric organisms with polyphyletic genomes (20, 21). It is logically impossible to accurately represent such multi-dimensional phylogeny in a monophyletic scheme. The incorporation of host genes into some viral genomes can further complicate the situation. Thirdly, viruses that can integrate into the genome of the host, such as the retroviruses and lysogenic bacteriophages, experience and respond to profoundly different selective pressures as they switch between vertical and horizontal modes of transmission by moving into and out of the host genome. Finally, viruses that infect both vertebrates and invertebrates (or other pairs of widely disparate hosts) can be expected to evolve very differently in their different host species. All these factors add complexity to virus evolution and compromise the relationship between taxonomy and phylogeny. The net result is that in any taxonomic arrangement some viruses and even some taxa will always be misfits.

Higher virus taxonomy. The uncertainties that surround the origins of viruses undermine the prospects for integrating all virus families into a single phylogenetic tree with a corresponding global taxonomy. While we can be confident that all members of a virus species and genus share common ancestors, this confidence begins to diminish at the higher taxonomic levels, which explains why there are so few recognized virus orders and no virus classes or higher taxa. However, as the abundance of sequence information and the power of methods for sequence comparisons increase it is likely that more distant phylogenetic relationships will become evident. The task of the ICTV is to recognize and reflect the collective judgment of the appropriate specialists on when to confer taxonomic status on such emergent relationships.

How to propose a taxonomic change. Any change of name or taxonomic status of a virus species, genus, sub-family, family, or order requires approval by the full membership of the ICTV before it is formally accepted by the scientific community. This includes the creation and naming of new taxa that may be deemed necessary to accommodate newly characterized viruses. For instructions on how to initiate this process, see Article 6 of the Statutes of the ICTV and Rule 3.20 of the International Code of Virus Taxonomy and Nomenclature in this volume. However most authors with new data

will be ready to publish before the approval process is complete, or in some cases before it has even begun. It should be recognized by authors, referees and editors that while such publications often make valuable contributions to the taxonomic debate, the proposals they contain have no formal status, nor do they establish any sort of nomenclatural precedence (see Rules 3.10 and 2.5 in the International Code of Virus Taxonomy and Nomenclature).

Anyone wishing to propose a taxonomic change should access the ICTV website at http://www.danforthcenter.org/iltab/ictvnet/asp/_MainPage.asp and complete the appropriate taxonomic proposal template. All taxonomic proposals are first circulated to the members of the appropriate Study Group and Subcommittee for specialist review and consideration, then posted for general comments on a site accessible to all ICTV members, and then reviewed by the Executive Committee at its next annual meeting. After further rounds of consideration and review, proposals that garner the support of a majority of EC members are submitted to the full ICTV for final ratification. Approved proposals are published in the ICTV Taxonomic Reports (i.e. this volume), and in the intervening years in the Virology Division News (VDN) section of *Archives of Virology*. A current taxonomic index of approved names of virus species and other taxa is available online at http://phene.cpmc.columbia.edu/.

ICTV database (ICTVdB). Since 1991, the ICTV has been working towards the development of a comprehensive and universal database containing virus isolate data. The goals of this initiative are to provide the research community and others with online tools for precisely identifying viruses at the isolate level from constellations of characteristics, and to create reliable links to the agreed virus taxonomy on the one hand and the genome sequence databases on the other (22-24). The ICTVdB website is http://phene.cpmc.columbia.edu/ and the anticipated launch date is summer 2005.

According to authoritative estimates, the majority of virus gene sequences in both GenBank and the EMBL databases are either unassigned or misassigned with respect to the virus isolates from which they were generated. In order to prevent any further deterioration in this deplorable situation, the ICTV Executive Committee decided that future proposals for the recognition of new virus species will be considered only when supported by both a sequence accession number and data from one or more isolates entered in the ICTV database (25). It is to be hoped that the entry of virus isolate data into the ICTVdB will soon become as routine as sequence deposition in publishing the description of a new virus.

Virus taxonomy 2004. The advent of nucleotide sequence determination has revolutionized biology and largely rationalized taxonomy, including that of viruses. The universal virus taxonomy presented in this Report provides a classification scheme that is supported by verifiable data and expert consensus. It is an indispensable framework both for further study of the ~1950 currently recognized virus species and for the identification and characterization of newly emergent viruses, whether they result from natural, accidental, or deliberate dissemination. The current health of virus taxonomy is due to the efforts of hundreds of virologists from around the world, but more volunteers are always needed. Those interested in contributing their expertise are encouraged to contact the relevant Study Group Chair or any member of the ICTV Executive Committee.

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Part II: The Viruses

Fauquet, C.M. and Mayo, M.A.

This report describes the taxa and viruses approved by the ICTV between 1970 and 2003. Descriptions of the most important characteristics of these taxa are provided, together with a list of species and tentative species and selected references. These descriptions represent the work of the chairpersons and members of the Subcommittees and Study-Groups of the ICTV. A glossary of abbreviations and terms is provided first, followed by a set of virus diagrams per type of host and listings of the taxa, by type of nucleic acid and size of the genome.

The different types of viruses infecting all sorts of hosts are depicted in three different ways: 1) virus diagrams are scale are represented per type of host, 2) the same diagrams are all assembled into the now famous "Virosphere" representing viruses by their biochemical structure and type of hosts, and 3) for the first time we are representing 4 pages of various virus structures at the atomic resolution level, to provide to the readers ideas about the variability and sizes of a range of viruses infecting vertebrates, invertebrates, fungi, protozoa, algae, bacteria, mycoplasma, and plants.

The names of orders, families, subfamilies, genera and species approved by the ICTV are printed in italics. Names that have not yet been approved are printed in quotation marks in standard type. Tentative species names, strain, serotype, genotype and isolate names are printed in standard type.

Throughout the Report, three categories of viruses of the various taxa have been defined: (1) *Type species:* pertains to the type species used in defining the taxon. As noted above, the choice of the type species by ICTV is not made with the kind of precision that must be used by international special groups and culture collections or when choosing substrates for vaccines, diagnostic reagents, etc. In this regard, the designation of prototype viruses and strains must be seen as a primary responsibility of international specialty groups. (2) *List of species:* other species and isolates of these species which on the basis of all present evidence definitely belong to the taxon. (3) *Tentative species:* pertains to those viruses for which there is presumptive but not conclusive evidence favoring membership of the taxon. A very limited number of species are pending ratification by the ICTV and they are marked with the sign ‡.

The ICTV has approved three orders, 73 families, 9 subfamilies, 287 genera and more than 5450 viruses belonging to more than 1950 species. Descriptions of virus satellites, viroids and the agents of spongiform encephalopathies (prions) of humans and several animal and fungal species are included. Finally a list of unassigned viruses is provided with a pertinent reference for each.

The VIIIth ICTV report is illustrated by 436 electron microscope pictures, diagrams of virus particles, diagrams of genome organization and phylogenetic trees. Most of those have been provided by the authors of the virus description but an important source of virus particle computer rendering images was the VIPER website (http://viperdb.scripps.edu/)(Reddy et al., (2001). Virus Particle Explorer (VIPER), a Website for virus capsid structures and their computational analysis. *J. Virol.* **75**:11943-11947).

Glossary of Abbreviations and Virological Terms

In addition to universally accepted abbreviations such as DNA and RNA, it is common practice to use abbreviations for virological and technical words in virology. In the Report, we have adopted commonly used abbreviations (e.g. CP for capsid protein and NC for nucleocapsid). These have been approved by the Executive Committee of ICTV for use in the ICTV Report but have no official status. The abbreviations will be used without definition throughout the book, except in a few instances where Study-Group conventions (e.g. C in place of CP for capsid protein) dictate different practice. In these instances, abbreviations are defined locally.

ABBREVIATIONS

aa	amino acid(s)
bp	base pair(s)
CF	complement fixing
CP	capsid/coat protein
CPE	cytopathic effect
D	diffusion coefficient
DI	defective interfering
DNAse	desoxyribonuclease
ds	double-stranded
gRNA	genomic RNA
HE	hemagglutination esterase
Hel	helicase
HI	hemagglutination inhibition
hr(s)	hour(s)
IRES	internal ribosome entry structure
kbp	kilobase pairs
kDa	kilodalton
min	minutes(s)
MP	movement protein
Mr	relative molar mass
mRNA	messenger RNA
Mtr	methyltransferase
N	nucleoprotein
NC	nucleocapsid
NES	nuclear export signal
NLS	nuclear localization signal
NNS	non-segmented negative strand
nt	nucleotide(s)
NTR	non-translated region
ORF	open reading frame
PAGE	poly acrylamid gel electrophoresis
PCR	polymerase chain reaction
Pol	polymerase
Pro	protease
RdRp	RNA-dependent RNA polymerase
Rep	replication associated protein
RF	replicative from
RFLP	restriction fragment length polymorphism
RI	replicative intermediate

RNAse	ribonuclease
RNP	ribonucleoprotein
RT	reverse transcriptase
sgRNA	subgenomic RNA
ss	single-stranded
T	triangulation number
UTR	untranslated region
VPg	genome-linked protein

RNA Replicases, Transcriptases and Polymerases

In the synthesis of viral RNA, the term polymerase has been replaced in general by two somewhat more specific terms: RNA replicase and RNA transcriptase. The term transcriptase has become associated with the enzyme involved in messenger RNA synthesis, most recently with those polymerases which are virion-associated. However, it should be borne in mind that for some viruses it has yet to be established whether or not the replicase and transcriptase activities reflect distinct enzymes rather than alternative activities of a single enzyme. Confusion also arises in the case of the small positive-sense RNA viruses where the term replicase (e.g., Qβ replicase) has been used for the enzyme capable both of transcribing the genome into messenger RNA via an intermediate negative-sense strand and of synthesizing the genome strand from the same template. In the text, the term replicase will be restricted as far as possible to the enzyme synthesizing progeny viral strands of either polarity. The term transcriptase is restricted to those RNA polymerases that are virion-associated and synthesize mRNA. The general term RNA polymerase (i.e., RNA-dependent RNA polymerase) is applied where no distinction between replication and transcription enzymes can be drawn (e.g., Qβ, R 17, *Poliovirus* and many plant viruses).

Other Definitions

Enveloped: possessing an outer (bounding) lipoprotein bilayer membrane.

Positive-sense (= plus strand, message strand) RNA: the strand that contains the coding triplets that are translated by ribosomes.

Positive-sense DNA: the strand that contains the same base sequence as the mRNA. However, mRNAs of some dsDNA viruses are transcribed from both strands and the transcribed regions may overlap. For such viruses this definition is inappropriate.

Negative sense (= minus strand): for RNA or DNA, the negative strand is the strand with base sequence complementary to the positive-sense strand.

Pseudotypes: enveloped virus particles in which the envelope is derived from one virus and the internal constituents from another.

Surface projections (= spikes, peplomers, knobs): morphological features, usually consisting of glycoproteins, that protrude from the lipoprotein envelope of many enveloped viruses.

Virion: morphologically complete virus particle.

Viroplasm: (= virus factory, virus inclusion, X-body): a modified region within the infected cell in which virus replication occurs, or is thought to occur.

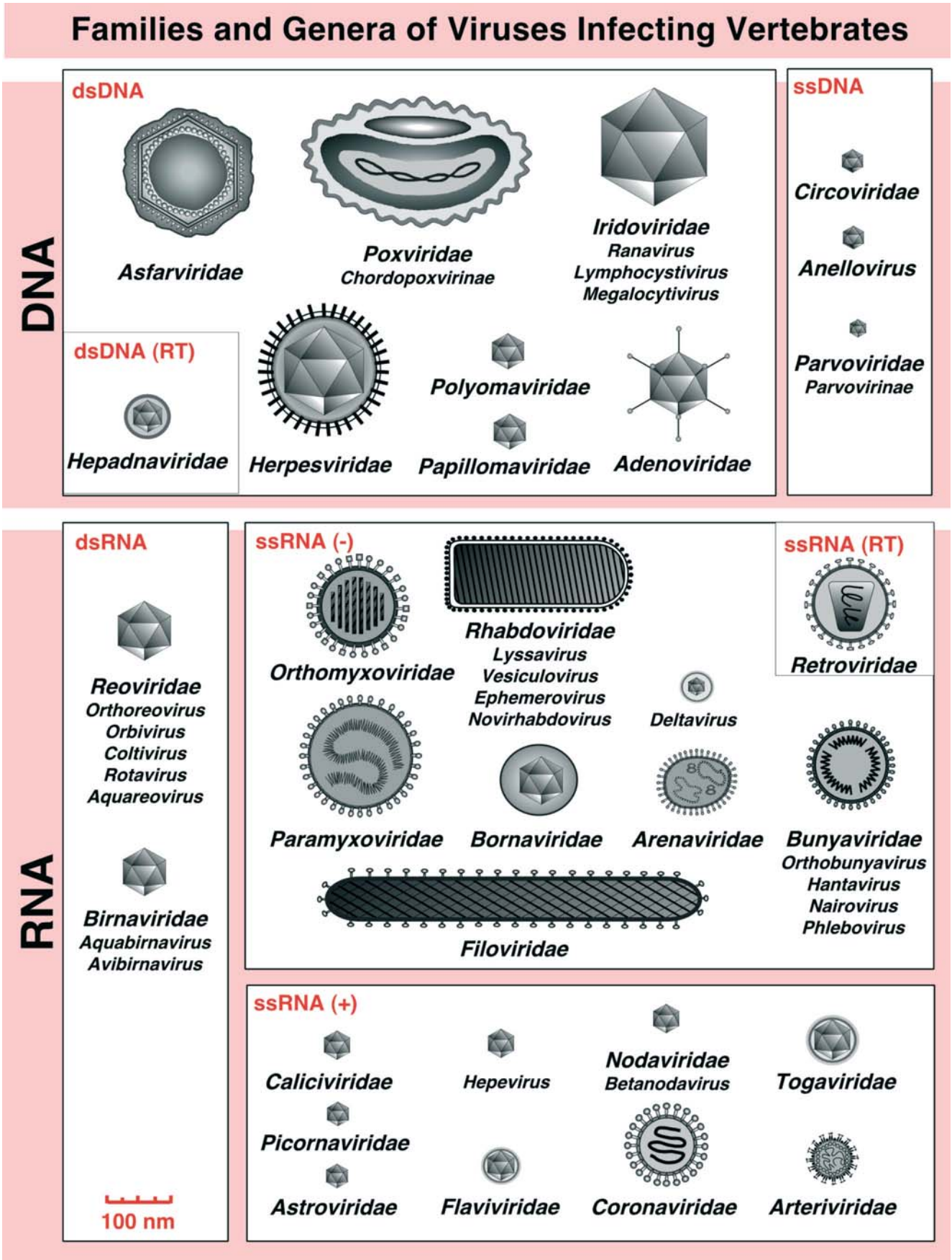
TABLE I. Families and Genera of Viruses Listed According to the Nature of the Genome

FAMILY OR UNASSIGNED GENUS	NATURE OF THE GENOME	PRESENCE OF AN ENVELOPE	MORPHOLOGY	GENOME CONFIGURATION	GENOME SIZE kbp or kb	HOST
Myoviridae	dsDNA	-	tailed phage	1 linear	34-169	B, Ar
Siphoviridae	dsDNA	-	tailed phage	1 linear	22-121	B, Ar
Podoviridae	dsDNA	-	tailed phage	1 linear	16-70	B
Tectiviridae	dsDNA	-	isometric	1 linear	15	B
Corticoviridae	dsDNA	-	isometric	1 circular supercoiled	10	B
Plasmaviridae	dsDNA	+	pleomorphic	1 circular supercoiled	12	Ms
Lipothrixviridae	dsDNA	+	Filament- or rod-shaped	1 linear	16-42	Ar
Rudiviridae	dsDNA	-	rod-shaped	1 linear	32-35	Ar
Fuselloviridae	dsDNA	+	lemon-shaped	1 circular supercoiled	15-18	Ar
Salterprovirus	dsDNA	+	Lemon-shaped	1 linear	14.5	Ar
Guttaviridae	dsDNA	+	droplet-shaped	1 circular	20	Ar
Poxviridae	dsDNA	+	pleomorphic	1 linear	130-375	V, I
Asfarviridae	dsDNA	+	spherical	1 linear	170-190	V
Iridoviridae	dsDNA	+/-	isometric	1 linear	135-303	V, I
Phycodnaviridae	dsDNA	-	isometric	1 linear	100-560	Al
Baculoviridae	dsDNA	+	Rod-shaped	1 circular supercoiled	80-180	I
Nimaviridae	dsDNA	+	Ovoid/bacilliform	1 circular	300	I
Herpesviridae	dsDNA	+	isometric	1 linear	125-240	V
Adenoviridae	dsDNA	-	isometric	1 linear	26-45	V
Rhizidiovirus	dsDNA	-	isometric	1 linear	27	F
Polyomaviridae	dsDNA	-	isometric	1 circular	5	V
Papillomaviridae	dsDNA	-	isometric	1 circular	7-8	V
Polydnaviridae	dsDNA	+	rod, fusiform	multiple supercoiled	150-250	I
Ascoviridae	dsDNA	+	Bacilliform, ovoidal, allantoid	1 circular	120-180	I
Mimivirus	dsDNA	-	isometric	1 circular	~800	Pr
Inoviridae	ssDNA	-	Rod-shaped, filamentous	1 + circular	5-9	B, Ms
Microviridae	ssDNA	-	isometric	1 + circular	4-6	B, Sp
Geminiviridae	ssDNA	-	isometric	1 or 2 +/- circular	3-6	P
Circoviridae	ssDNA	-	isometric	1 - or +/- circular	2	V
Anellovirus	ssDNA	-	isometric	1 - circular	3-4	V
Nanovirus	ssDNA	-	isometric	6-9 + circular	6-9	P
Parvoviridae	ssDNA	-	isometric	1 +/- linear	4-6	V, I
Hepadnaviridae	dsDNA-RT	+	spherical	1 linear	3-4	V
Caulimoviridae	dsDNA-RT	-	isometric, bacilliform	1 circular	7-9	P
Pseudoviridae	ssRNA-RT	-	spherical	1 + segment	5-9	P,I,Pr
Metaviridae	ssRNA-RT	-	spherical	1 + segment	4-10	F,P,I,V
Retroviridae	ssRNA-RT	+	spherical	1 dimer + segment	7-13	V
Cystoviridae	dsRNA	+	spherical	3 segments	13	B
Reoviridae	dsRNA	-	isometric	10-12 segments	19-32	V,I,P,F
Birnaviridae	dsRNA	-	isometric	2 segments	5-6	V, I
Totiviridae	dsRNA	-	isometric	1 segment	4-7	F, Pr
Partitiviridae	dsRNA	-	isometric	2 segments	3-6	P, F
Chrysoviridae	dsRNA	-	isometric	4 segments	13	F
Hypoviridae	dsRNA	-	pleomorphic	1 segment	9-13	F
Endornavirus	dsRNA	-	none	1 segment	14-18	P

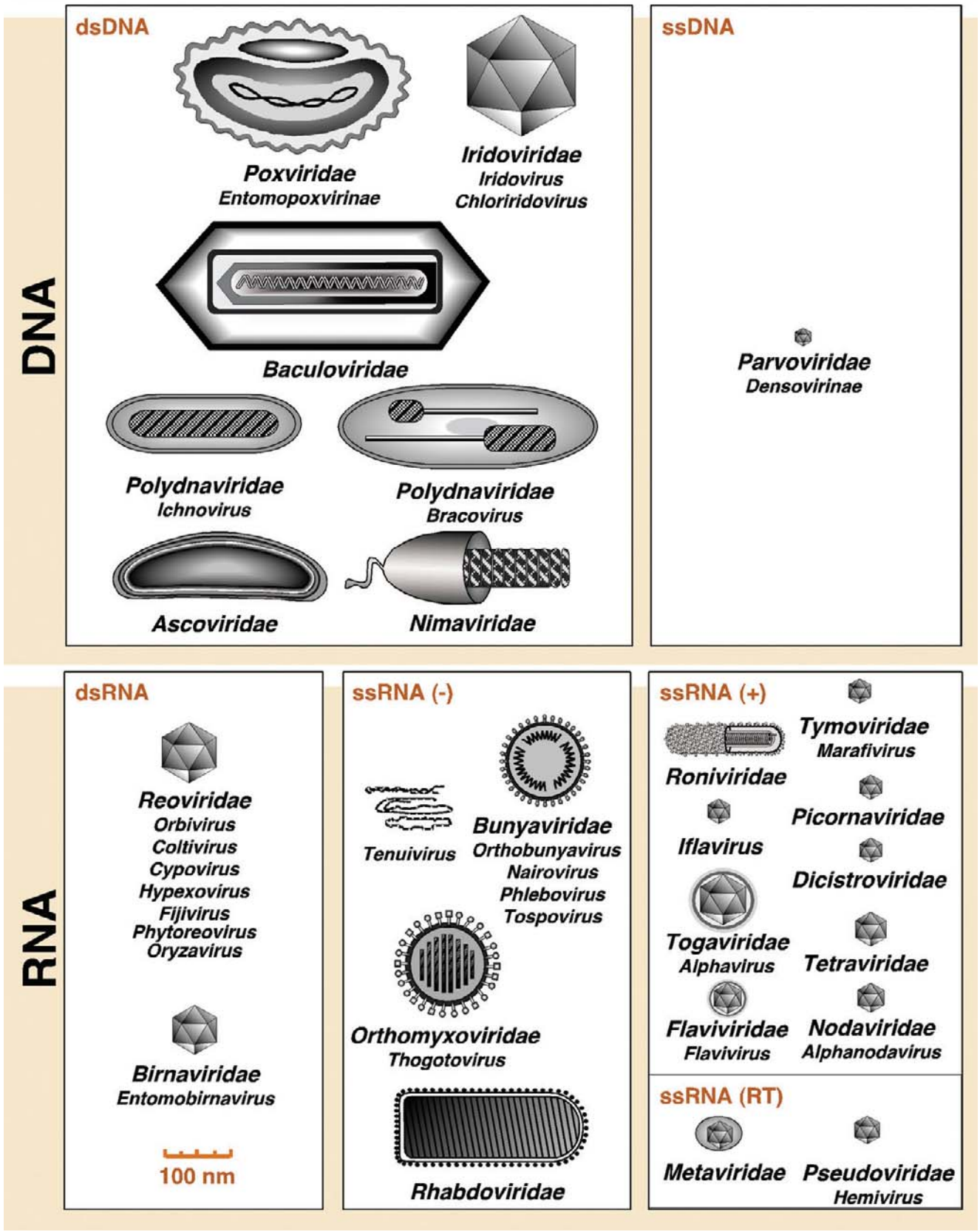
Family or Unassigned genus	Nature of the genome	Presence of an envelope	Morphology	Genome Configuration	Genome Size kbp or kb	Host
Bornaviridae	NssRNA	+	spherical	1 - segment	9	V
Rhabdoviridae	NssRNA	+	bullet-shaped, bacilliform	1 - segment	11-15	V, I, P
Filoviridae	NssRNA	+	Bacilliform, filamentous	1 - segment	~19	V
Paramyxoviridae	NssRNA	+	pleomorphic	1 - segment	13-18	V
Varicosavirus	NssRNA	-	rod-shaped	2 - segments	13	P
Orthomyxoviridae	NssRNA	+	pleomorphic	6-8 - segments	10-15	V
Bunyaviridae	NssRNA	+	spherical	3 - or +/- segments	11-19	V, P, I
Tenuivirus	NssRNA	-	filamentous	4-6 - or +/- segments	17-18	P, I
Ophiovirus	NssRNA	-	filamentous	3/4 - segments	11-12	P
Arenaviridae	NssRNA	+	spherical	2 +/- segments	11	V
Deltavirus	NssRNA	+	spherical	1 – circular	2	V
Leviviridae	ssRNA	-	isometric	1 + segment	3-4	B
Narnaviridae	ssRNA	-	RNP complex	1 + segment	2-3	F
Picornaviridae	ssRNA	-	isometric	1 + segment	7-9	V
Iflavirus	ssRNA	-	isometric	1 + segment	9-10	I
Dicistroviridae	ssRNA	-	isometric	1 + segment	9-10	I
Marnaviridae	SsRNA	-	isometric	1 + segment	9	Al
Sequiviridae	ssRNA	-	isometric	1 + segment	10-12	P
Sadwavirus	SsRNA	-	isometric	2 + segments	11-12	P
Cheravirus	SsRNA	-	isometric	2 + segments	10	P
Comoviridae	ssRNA	-	isometric	2 + segments	9-15	P
Potyviridae	ssRNA	-	filamentous	1 / 2 + segments	8-12	P
Caliciviridae	ssRNA	-	isometric	1 + segment	7-8	V
Hepevirus	ssRNA	-	isometric	1 + segment	7	V
Astroviridae	ssRNA	-	isometric	1 + segment	6-7	V
Nodaviridae	ssRNA	-	isometric	2 + segments	4-5	V, I
Tetraviridae	ssRNA	-	isometric	1 or 2 + segment	6-8	I
Sobemovirus	ssRNA	-	isometric	1 + segment	4-5	P
Luteoviridae	ssRNA	-	isometric	1 + segment	5-6	P
Umbravirus	ssRNA	-	RNP complex	1 + segment	4	P
Tombusviridae	ssRNA	-	isometric	1 / 2 + segments	4-5	P
Coronaviridae	ssRNA	+	spherical	1 + segment	28-31	V
Arteriviridae	ssRNA	+	spherical	1 + segment	13-16	V
Roniviridae	SsRNA	+	Bacilliform	1 + segment	26	I
Flaviviridae	ssRNA	+	spherical	1 + segment	10-12	V, I
Togaviridae	ssRNA	+	spherical	1 + segment	10-12	V, I
Tobamovirus	ssRNA	-	rod-shaped	1 + segment	6-7	P
Tobravirus	ssRNA	-	rod-shaped	2 + segments	9-11	P
Hordeivirus	ssRNA	-	rod-shaped	3 + segments	9-11	P
Furovirus	ssRNA	-	rod-shaped	2 + segments	10-11	P
Pomovirus	ssRNA	-	rod-shaped	3 + segments	~12	P
Pecluvirus	ssRNA	-	rod-shaped	2 + segments	10	P
Benyvirus	ssRNA	-	rod-shaped	4/5 + segments	13-16	P
Bromoviridae	ssRNA	-	Isometric, bacilliform	3 + segments	8-9	P
Ourmiavirus	ssRNA	-	bacilliform	3 + segments	5	P
Idaeovirus	ssRNA	-	isometric	2 + segments	8	P
Tymoviridae	ssRNA	-	isometric	1 + segment	6-8	P, I
Closteroviridae	ssRNA	-	filamentous	1/2 + segments	15-19	P
Flexiviridae	SsRNA	-	filamentous	1 + segment	6-9	P
Barnaviridae	ssRNA	-	bacilliform	1 + segment	4	F

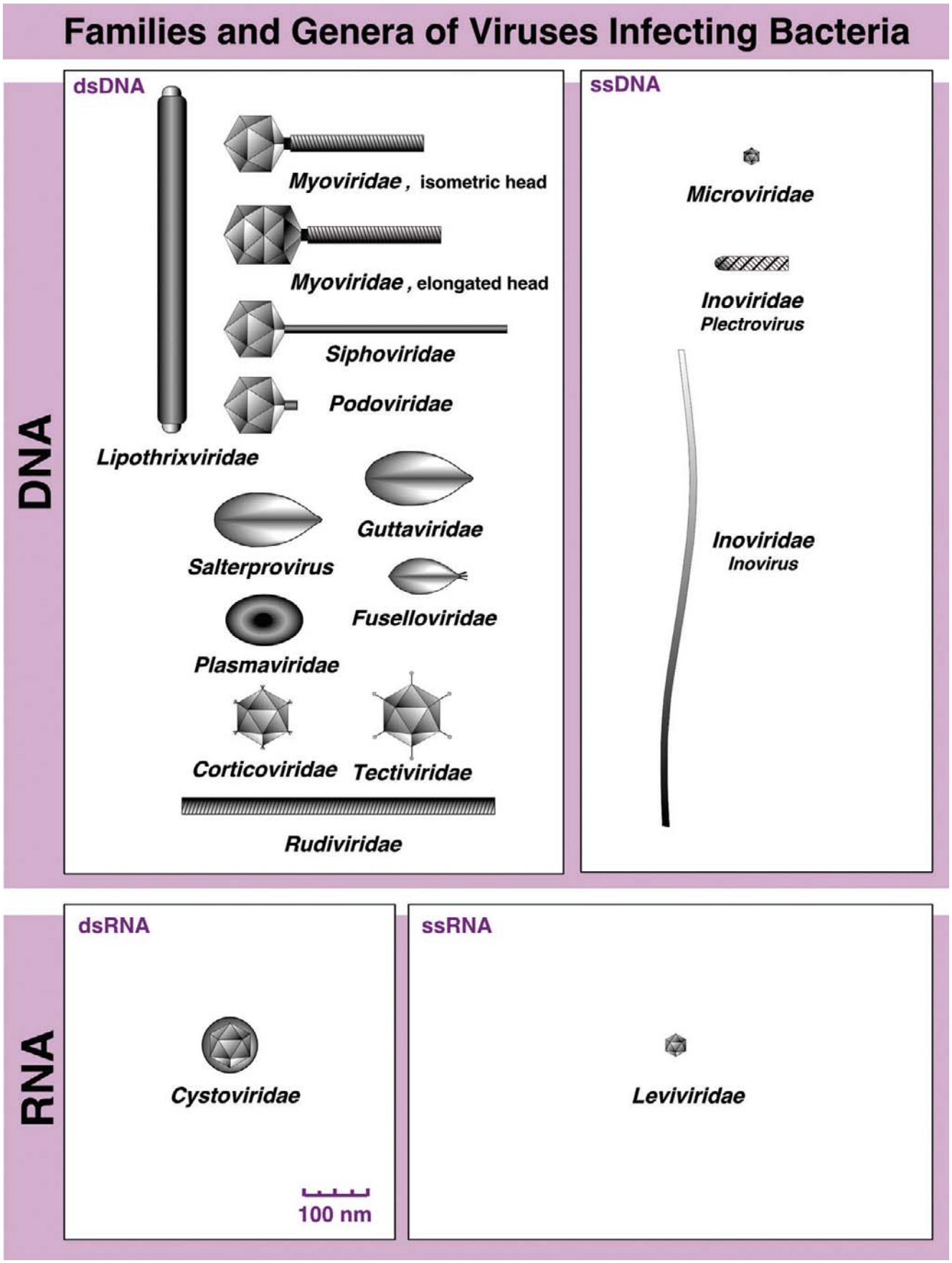
Abbreviations of the virus hosts

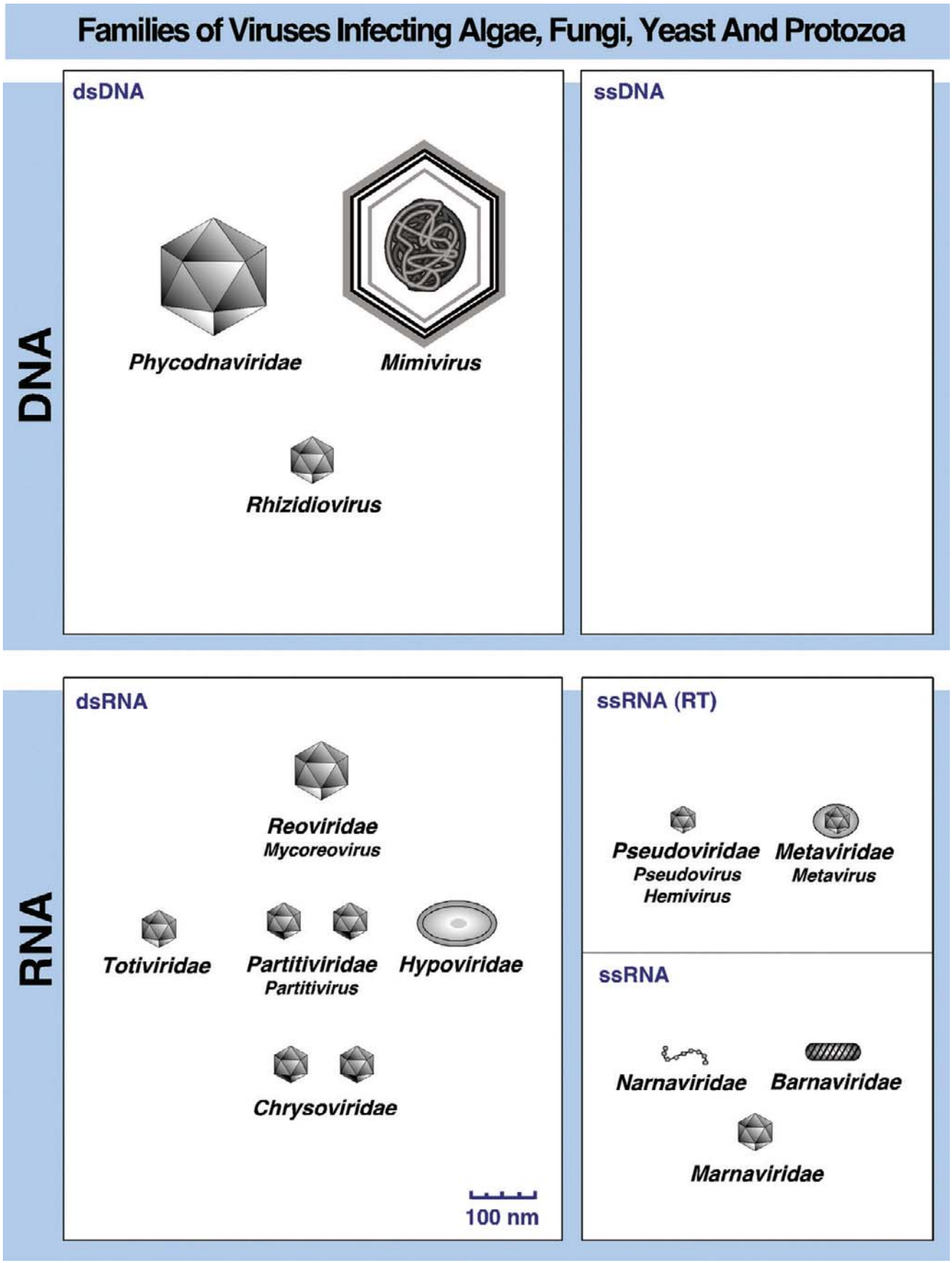
Algae	Al	Bacteria	B	Invertebrates	I	Protozoa	Pr
Archaea	Ar	Fungi	F	Plants	P	Vertebrates	V

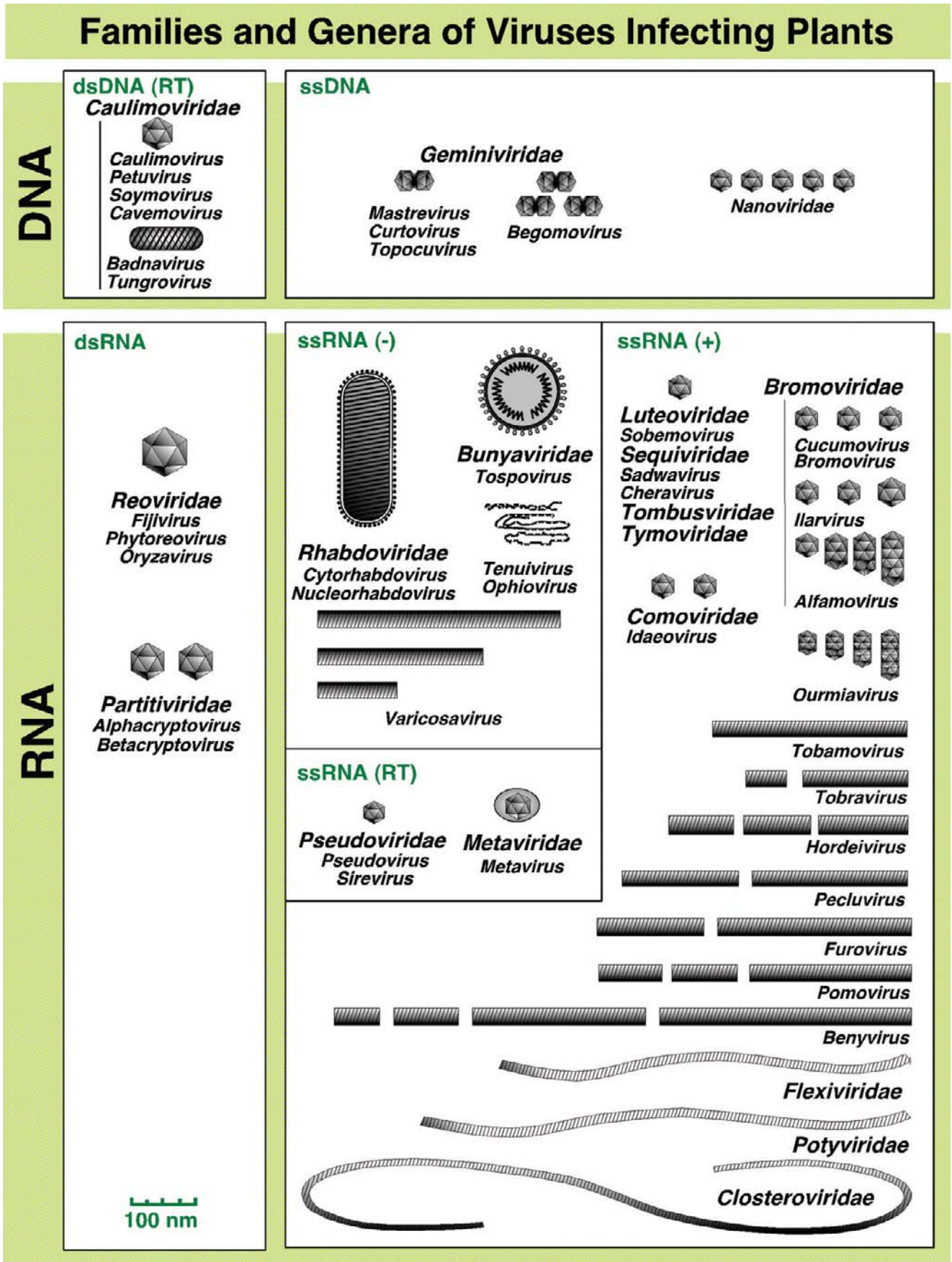

Families and Genera of Viruses Infecting Vertebrates
DNA
dsDNA
Asfarviridae
Poxviridae
Chordopoxvirinae
Iridoviridae
Ranavirus
Lymphocystivirus
Megalocytivirus
dsDNA (RT)
Hepadnaviridae
Herpesviridae
Polyomaviridae
Papillomaviridae
Adenoviridae
ssDNA
Circoviridae
Anellovirus
Parvoviridae
Parvovirinae
RNA
dsRNA
Reoviridae
Orthoreovirus
Orbivirus
Coltivirus
Rotavirus
Aquareovirus
Birnaviridae
Aquabirnavirus
Avibirnavirus
100 nm
ssRNA (-)
Orthomyxoviridae
Rhabdoviridae
Lyssavirus
Vesiculovirus
Ephemerovirus
Novirhabdovirus
Deltavirus
Paramyxoviridae
Bornaviridae
Arenaviridae
Filoviridae
ssRNA (RT)
Retroviridae
Bunyaviridae
Orthobunyavirus
Hantavirus
Nairovirus
Phlebovirus
ssRNA (+)
Caliciviridae
Hepevirus
Nodaviridae
Betanodavirus
Togaviridae
Picornaviridae
Astroviridae
Flaviviridae
Coronaviridae
Arteriviridae

Families and Genera of Viruses Infecting Invertebrates




Families and Genera of Viruses Infecting Bacteria
DNA
dsDNA
Myoviridae, isometric head
Myoviridae, elongated head
Siphoviridae
Podoviridae
Lipothrixviridae
Guttaviridae
Salterprovirus
Fuselloviridae
Plasmaviridae
Corticoviridae
Tectiviridae
Rudiviridae
ssDNA
Microviridae
Inoviridae
Plectrovirus
Inoviridae
Inovirus
RNA
dsRNA
Cystoviridae
100 nm
ssRNA
Leviviridae


Families of Viruses Infecting Algae, Fungi, Yeast And Protozoa
DNA
dsDNA
Phycodnaviridae
Mimivirus
Rhizidiovirus
ssDNA
RNA
dsRNA
Reoviridae
Mycoreovirus
Totiviridae
Partitiviridae
Partitivirus
Hypoviridae
Chrysoviridae
100 nm
ssRNA (RT)
Pseudoviridae
Pseudovirus
Hemivirus
Metaviridae
Metavirus
ssRNA
Narnaviridae
Barnaviridae
Marnaviridae


Families and Genera of Viruses Infecting Plants
DNA
dsDNA (RT)
Caulimoviridae
Caulimovirus
Petuvirus
Soymovirus
Cavemovirus
Badnavirus
Tungrovirus
ssDNA
Geminiviridae
Mastrevirus
Curtovirus
Topocuvirus
Begomovirus
Nanoviridae
RNA
dsRNA
Reoviridae
Fijivirus
Phytoreovirus
Oryzavirus
Partitiviridae
Alphacryptovirus
Betacryptovirus
100 nm
ssRNA (-)
Bunyaviridae
Tospovirus
Rhabdoviridae
Cytorhabdovirus
Nucleorhabdovirus
Tenuivirus
Ophiovirus
Varicosavirus
ssRNA (RT)
Pseudoviridae
Pseudovirus
Sirevirus
Metaviridae
Metavirus
ssRNA (+)
Luteoviridae
Sobemovirus
Sequiviridae
Sadwavirus
Cheravirus
Tombusviridae
Tymoviridae
Comoviridae
Idaeovirus
Bromoviridae
Cucumovirus
Bromovirus
Ilarvirus
Alfamovirus
Ourmiavirus
Tobamovirus
Tobravirus
Hordeivirus
Pecluvirus
Furovirus
Pomovirus
Benyvirus
Flexiviridae
Potyviridae
Closteroviridae

Virus Particle Structures

Palmenberg, A.C. and Sgro, J.-Y.

Color Plate Legends

These color plates depict the relative sizes and comparative virion structures of multiple types of viruses. The renderings are based on data from published atomic coordinates as determined by X-ray crystallography. The international online repository for 3D coordinates is the Protein Databank (www.rcsb.org/pdb/), maintained by the Research Collaboratory for Structural Bioinformatics (RCSB). The VIPER web site (mmtsb.scripps.edu/viper), maintains a parallel collection of PDB coordinates for icosahedral viruses and additionally offers a version of each data file permuted into the same relative 3D orientation (Reddy, V., Natarajan, P., Okerberg, B., Li, K., Damodaran, K., Morton, R., Brooks, C. and Johnson, J. (2001). *J. Virol.*, **75**, 11943-11947). VIPER also contains an excellent repository of instructional materials pertaining to icosahedral symmetry and viral structures. All images presented here, except for the filamentous viruses, used the standard VIPER orientation along the icosahedral 2-fold axis.

With the exception of Plate 3 as described below, these images were generated from their atomic coordinates using a novel radial depth-cue colorization technique and the program Rasmol (Sayle, R.A., Milner-White, E.J. (1995). RASMOL: biomolecular graphics for all. *Trends Biochem Sci.*, **20**, 374-376). First, the Temperature Factor column for every atom in a PDB coordinate file was edited to record a measure of the radial distance from the virion center. The files were rendered using the Rasmol spacefill menu, with specular and shadow options according to the Van de Waals radius of each atom. Color was assigned on a sliding scale by individual radial distances. The composite assembly and processing used Adobe Photoshop software with attention to relative scale, visual contrast and a uniform color pallet.

Plate 1: Picornaviruses

Bovine enterovirus 1: Picornaviridae; Enterovirus; Bovine enterovirus; strain VG-5-27.

Smyth, M., Tate, J., Hoey, E., Lyons, C., Martin, S. and Stuart, D. (1995). Implications for viral uncoating from the structure of bovine enterovirus. *Nat. Struct. Biol.*, **2**, 224-231. (PDB-ID: 1BEV)

Foot-and-mouth disease virus: Picornaviridae; Aphthovirus; Foot-and-mouth disease virus; strain disease virus.

Fry, E., Acharya, R. and Stuart, D. (1993). Methods used in the structure determination of foot-and-mouth disease virus. *Acta Crystallogr.* A, **49**, 45-55. (PDB-ID: 1BBT)

Human coxsackievirus B3: Picornaviridae; Enterovirus; Human enterovirus B; strain Nancy.

Muckelbauer, J.K., Kremer, M., Minor, I., Diana, G., Dutko, F.J., Groarke, J., Pevear, D.C., Rossmann, M.G. (1995). The structure of coxsackievirus B3 at 3.5 angstrom resolution. *Structure*, **3**, 653-667. (PDB-ID: 1COV)

Human echovirus 1: Picornaviridae; Enterovirus; Human enterovirus B; strain Farouk.

Filman, D.J., Wien, M.W., Cunningham, J.A., Bergelson, J.M. and Hogle, J.M. (1998). Structure determination of echovirus 1. *Acta Crystallogr.* D, **54**, 1261-1272. (PDB-ID: 1EV1)

Human echovirus 11: Picornaviridae; Enterovirus; Human enterovirus B; strain 207.
Stuart, A., Mckee, T., Williams, P., Harley, C., Shen, S., Stuart, D., Brown, T. and Lea, S. (2002). Determination of the structure of a decay accelerating factor-binding clinical isolate of echovirus 11 allows mapping of mutants with altered receptor requirements for infection. *J. Virol.,* **76**, 7694-7704. (PDB-ID: 1H8T)
Human poliovirus 1: Picornaviridae; Enterovirus; Poliovirus; strain Mahoney Type I.
Miller, S.T., Hogle, J.M. and Filman, D.J. (2003). Crystal structure of Mahoney strain of poliovirus at 2.2A Resolution. (PDB-ID: 1HXS)
Human rhinovirus 16: Picornaviridae; Rhinovirus; Human rhinovirus A; strain (NA).
Hadfield, A.T., Lee, W.M., Zhao, R., Oliveira, M.A., Minor, I., Rueckert, R.R. and Rossmann, M.G. (1997). The refined structure of human rhinovirus 16 at 2.15 A resolution: implications for the viral life cycle. *Structure,* **5**, 427-441. (PDB-ID: 1AYM)
Mengo virus: Picornaviridae, Cardiovirus; Encephalomyocarditis virus; strain M.
Krishnaswamy, S. and Rossmann, M.G. (1990). Structural refinement and analysis of Mengo virus. *J. Mol. Biol.,* **211**, 803-844. (PDB-ID: 2MEV)
Theiler's murine encephalomyelitis virus: Picornaviridae; Cardiovirus; Theilovirus; strain BeAn.
Luo, M., He, C., Toth, K.S., Zhang, C.X. and Lipton, H.L. (1992). Three-dimensional structure of Theiler murine encephalomyelitis virus (BeAn strain). *Proc. Natl. Acad. Sci. USA*, **89**, 2409-2413. (PDB-ID: 1TMF) A10-61.

PLATE 2: COMPARATIVE STRUCTURES

Adeno-associated virus 2: *Parvoviridae; Dependovirus*; *Adeno-associated virus 2*; strain (recombinant).
Xie, Q., Bu, W., Bhatia, S., Hare, J., Somasundaram, T., Azzi, A. and Chapman, M.S. (2002). Atomic structure of adeno-associated virus (Aav-2), a vector for human therapy. *Proc. Nat. Acad. Sci. USA,* **99**, 10405-10410. (PDB-ID: 1LP3)
Bean pod mottle virus: *Comoviridae; Comovirus*; *Bean pod mottle virus*; strain Kentucky G7.
Chen, Z.G., Stauffacher, C., Li, Y., Schmidt, T., Bomu, W., Kamer, G., Shanks, M., Lomonossoff, G. and Johnson, J.E. (1989). Protein-RNA interactions in an icosahedral virus at 3.0 A resolution. *Science,* **245**, 154-159. (PDB-ID: 1BMV)
Bluetongue virus 1, Core: *Reoviridae; Orbivirus*; *Bluetongue virus* (VP3 core protein); serotype 1, South Africa.
Grimes, J.M., Burroughs, J.N., Gouet, P., Diprose, J.M., Malby, R., Zientara, S., Mertens, P.P. and Stuart, D.I. (1998). The atomic structure of the bluetongue virus core. *Nature*, **395**, 470-478. (PDB-ID: 2BTV)
Brome mosaic virus: *Bromoviridae; Bromovirus*; *Brome mosaic virus*; strain (NA).
Lucas, R.W., Larson, S.B. and McPherson, A. (2002). The crystallographic structure of brome mosaic virus. *J. Mol. Biol.,* **317**, 95-108. (PDB-ID: 1JS9)
Carnation mottle virus; *Tombusviridae; Carmovirus*; *Carnation mottle virus*; strain (NA).
Morgunova, E.Yu., Dauter, Z., Fry, E., Stuart, D.I., Stel'mashchuk, V.Ya., Mikhailov, A.M., Wilson, K.S. and Vainshtein, B.K. (1994). The atomic structure of carnation mottle virus capsid protein. *FEBS Lett.,* **338**, 267-271. (PDB-ID: 1OPO)
Cricket paralysis virus 1: *Dicistroviridae; Cripavirus*; *Cricket paralysis virus 1*; strain (NA).
Tate, J., Liljas, L., Scotti, P., Christian, P., Lin, T. and Johnson, J.E. (1999). The crystal structure of cricket paralysis virus: the first view of a new virus family. *Nat. Struct. Biol.,* **8**, 765-774. (PDB-ID: 1B35)
Canine parvovirus: *Parvoviridae; Parvovirus*; *Canine parvovirus*; strain D Cornell 320 (recombinant empty capsid).
Wu, H. and Rossmann, M.G. (1993). The canine parvovirus empty capsid structure. *J. Mol. Biol.,* **233**, 231-244. (PDB-ID: 2CAS)
Cucumber mosaic virus: *Bromoviridae; cucumovirus*; *cucumber mosaic virus*; strain Fny.
Smith, T.J., Chase, E., Schmidt, T. and Perry, K. (2000). The structure of cucumber mosaic virus and comparison to cowpea chlorotic mottle virus. *J. Virol.,* **74**, 7578-7586. (PDB-ID: 1F15)
Enterobacteria phage fd: *Inoviridae; Inovirus*; *Enterobacteria phage fd*;

Marvin, D.A. (1990). Model-building studies of *Inovirus*: genetic variations on a geometric theme. *Int. J. Biol. Macromol.,* **12**, 125-138. (PDB-ID: 1IFD)

Enterobacteria phage MS2: *Leviviradae; Levivirus*; *Enterobacteria phage MS2*, strain (NA).

Golmohammadi, R., Valegard, K., Fridborg, K. and Liljas, L. (1993). The refined structure of bacteriophage MS2 at 2.8 A resolution. *J. Mol. Biol.*, **234**, 620-639. (PDB-ID: 2MS2)

Enterobacteria phage QBeta: *Leviviridae; Allolevivirus*; *Enterobacteria phage Q-beta*; strain (NA).

Golmohammadi, R., Fridborg, K., Bundule, M., Valegard, K. and Liljas, L. (1996). The crystal structure of bacteriophage Q-beta at 3.5 A resolution. *Structure*, **4**, 543-554. (PDB-ID: 1QBE)

Enterobacteria phage PhiX174: *Microviridae; Microvirus*; *Enterobacteria phage phi-X174*, strain (NA).

McKenna, R., Xia, D., Willingmann, P., Ilag, L.L., Krishnaswamy, S., Rossmann, M.G., Olson, N.H., Baker, T.S. and Incardona, N.L. (1992). Atomic structure of single-stranded DNA bacteriophage phiX174 and its functional implications. *Nature*, **355**, 137-143. (PDB-ID: 2BPA)

Enterobacteria phage PhiX174+scaffold: *Microviridae; Microvirus*; *Enterobacteria phage phi-X174*; with scaffold.

Dokland, T., McKenna, R., Ilag, L.L., Bowman, B.R., Incardona, N.L., Fane, B.A. and Rossmann, M.G. (1997). Structure of a viral procapsid with molecular scaffolding. *Nature,* **389**, 308-313. (PDB-ID: 1AL0)

Galleria mellonella densovirus: *Parvoviridae; Densovirus*; *Galleria mellonella densovirus*; strain (NA).

Simpson, A.A., Chipman, P.R., Baker, T.S., Tijssen, P. and Rossmann, M.G. (1998). The structure of an insect parvovirus (Galleria mellonella densovirus) at 3.7 A resolution. *Structure*, **6**, 1355-1367. (PDB-ID: 1DNV)

Hepatitis B virus: *Hepadnaviridae; Orthohepadnavirus*; *Hepatitis B virus*; strain ayw.

Wynne, S.A., Crowther, R.A. and Leslie, A.G.W. (1999). The crystal structure of the human hepatitis B virus capsid. *Molecular Cell*, **3**, 771-780. (PDB-ID: 1QGT)

Human papillomavirus 16: *Papillomaviridae; Papillomavirus*; *Human papillomavirus 16*, strain (recombinant L1 protein).

Modis, Y., Trus, B.L. and Harrison, S.C. (2002). Atomic model of the papillomavirus capsid. *EMBO J.*, **21**, 4754-4762. (PDB-ID: 1L0T)

Mammalian orthoreovirus 3 - Core: *Reoviridae; Orthoreovirus*; *Mammalian orthoreovirus* type 3 (LMD1, LMD2, sigma2 core proteins), strain Dearing.

Reinisch, K.M., Nibert, M.L. and Harrison, S.C. (2000). Structure of the reovirus core at 3.6 A resolution. *Nature*, **404**, 960-967. (PDB-ID: 1EJ6)

Nodamura virus: *Nodaviridae; Alphanodavirus*; *Nodamura virus*, strain (NA).

Zlotnick, A., Natarajan, P., Munshi, S. and Johnson, J.E. (1997). Resolution of space-group ambiguity and the structure determination of Nodamura virus to 3.3 angstrom resolution from pseudo-R32 (monoclinic) crystals. *Acta Crystallogr.,* **53**, 738-746. (PDB-ID: 1NOV)

Norwalk virus: *Caliciviridae; Norovirus*; *Norwalk virus*; strain (recombinant capsid).

Prasad, B.V.V., Hardy, M.E., Dokland, T., Bella, J., Rossmann, M.G. and Estes, M.K. (1999). X-ray crystallographic structure of Norwalk virus capsid. *Science,* **286**, 287-290. (PDB-ID: 1IHM)

Nudaurelia capensis omega virus: *Tetraviridae; Omegatetravirus*; *Nudaurelia capensis omega virus*; strain (NA).

Munshi, S., Liljas, L., Cavarelli, J., Bomu, W., McKinney, B., Reddy, V. and Johnson, J.E. (1996). The 2.8 A structure of a T=4 animal virus and its implications for membrane translocation of RNA. *J. Mol. Biol.,* **261**, 1-10. (PDB-ID: NA, coordinates available from VIPER)

Rice dwarf virus: *Reoviridae; Phytoreovirus*; *Rice dwarf virus*; strain Akita.

Nakagawa, A., Miyazaki, N., Taka, J., Naitow, H., Ogawa, A., Fujimoto, Z., Mizuno, H., Higashi, T., Watanabe, Y., Omura, T., Cheng, R.H. and Tsukihara, T. (2003). The Atomic structure of rice dwarf virus. *Structure*, **11**, 1227-1238. (PDB-ID: 1UF2)

Simian virus 40: *Polyomaviridae; polyomavirus*; *simian virus 40*; strain (NA).

Stehle, T., Gamblin, S.J., Yan, Y. and Harrison, S.C. (1996). The structure of simian virus 40 refined at 3.1 A resolution. *Structure*, **4,** 165-182. (PDB-ID: 1SVA)

Southern bean mosaic virus: *Sobemovirus*; *Southern bean mosaic virus*; strain (NA).

Silva, A.M. and Rossmann, M.G. (1987). The refinement of southern bean mosaic virus at 2.9 A resolution. *J. Mol. Biol.,* **197**, 69-87. (PDB-ID: 4SBV)

Swine vesicular disease virus: *Picornaviridae; Enterovirus*; *Human enterovirus B*; strain UKG/27/72.
Fry, E.E., Knowles, N.J., Newman, J.W.I., Wilsden, G., Rao, Z., King, A.M.Q. and Stuart, D.I. (2003). Crystal structure of swine vesicular disease virus and implications for host adaptation. *J. Virol.*, **77**, 5475-5486. (PDB-ID: 1OOP)
Tobacco mosaic virus; *Tobamovirus*; *Tobacco mosaic virus*; strain vulgare;
Namba, K., Pattanayek, R. and Stubbs, G. (1989). Visualization of protein-nucleic acid interactions in a virus. Refined structure of intact tobacco mosaic virus at 2.9 A resolution by X-ray fiber diffraction. *J. Mol. Biol.*, **208**, 307-325. (PDB-ID: 2TMV)
Tobacco necrosis satellite virus; Satellite viruses; subgroup 2; strain (NA).
Jones, T.A. and Liljas, L. (1984). Structure of satellite tobacco necrosis virus after crystallographic refinement at 2.5 A resolution. *J. Mol. Biol.*, **177**, 735-767. (PDB-ID: 2STV)
Tobacco necrosis virus; *Tombusviridae; Necrovirus; Tobacco necrosis virus*; strain A.
Oda, Y., Saeki, K., Takahashi, Y., Maeda, T., Naitow, H., Tsukihara, T. and Fukuyama, K. (2000). Crystal structure of tobacco necrosis virus at 2.25 A resolution. *J. Mol. Biol.*, **300**, 153-169. (PDB-ID: 1C8N)
Tomato bushy stunt virus; *Tombusviridae; Tombusvirus, Tomato bushy stunt virus*; strain BS-3.
Olson, A.J., Bricogne, G. and Harrison, S.C. (1983). Structure of tomato busy stunt virus IV. The virus particle at 2.9 A resolution. *J. Mol. Biol.*, **171**, 61-93. (PDB-ID: 2TBV)
Turnip yellow mosaic virus: *Tymoviridae; Tymovirus*; *Turnip yellow mosaic virus*; strain (NA).
Canady, M.A., Larson, S.B., Day, J., McPherson, A. (1996). Crystal structure of turnip yellow mosaic virus. *Nat. Struct. Biol.*, **3**, 771-781. (PDB-ID: 1AUY)

PLATE 3: LARGEST AND SMALLEST VIRAL STRUCTURES. NUCLEIC ACID REVEALED WITHIN PARIACOTO VIRUS.

Both images are rendered to the same relative size scale.

Top: **Paramecium bursaria Chlorella virus 1:** *Phycodnaviridae; Chlorovirus*, *Paramecium bursaria Chlorella virus 1*; strain (NA), quasi-atomic model.
Nandhagopal, N., Simpson, A., Gurnon, J.R., Yan, X., Baker, T.S., Graves, M.V., van Etten, J.L. and Rossmann, M.G. (002). The structure and evolution of the major capsid protein of a large, lipid containing, DNA virus. *Proc. Nat. Acad. Sci. USA*, **99**, 14758-14763. (PDB-ID: 1M4X)
Tobacco necrosis satellite virus; Satellite viruses; subgroup 2; strain (NA).
Jones, T.A. and Liljas, L. (1984). Structure of satellite tobacco necrosis virus after crystallographic refinement at 2.5 A resolution. *J. Mol. Biol.*, **177**, 735-767. (PDB-ID: 2STV)

Inset: axial and side views of one trimeric protein unit from Chlorella. Images were created with MOLSCRIPT software (P.J. Kraulism. (1991). MOLSCRIPT: a program to produce both detailed and schematic plots of protein structures. *J. Appl. Cryst.*, **24**, 946-950) then rendered with Raster3D (Merritt, E.A. and Bacon, D.J. (1997). Raster3D: photorealistic molecular graphics. *Meth. Enzymol.*, **277**, 505-524)

Bottom: Left: radial depth-cue molecular surface of a particle of *Pariacoto virus*, split to reveal the dodecahedral arrangement of a portion of the RNA. Right: same image rotated 90º. Both images were rendered using GRASP software. (Nicholls A, Sharp K.A. and Honig B. (1991). Protein folding and association: insights from the interfacial and thermodynamic properties of hydrocarbons. *Proteins*, **11**, 281-296)

Pariacoto virus: *Nodaviridae; Alphanodavirus*; *Pariacoto virus*; strain (NA).
Tang, L., Johnson, K.N., Ball, L.A., Lin, T., Yeager, M. and Johnson, J.E. 2001. The structure of Pariacoto virus reveals a dodecahedral cage of duplex RNA. *Nat. Struct. Biol.*, **8**, 77-83. (PDB-ID: 1F8V)

Order of Presentation of Virus Taxonomic Descriptions

Taxonomic descriptions in this Report are organized and presented in clusters. The first level of organization is an informal grouping according to genome composition and structure (dsDNA, ssDNA, etc.) and the second level is according to taxonomic rank; i.e., order or family, if there is no order, or genus, if there is no family assignment. In general, descriptions of taxa that appear to share some level of similarity are placed close to each other.

At the end of each virus description is a list of species. The species names are in green italic script. The names of isolates within a species follow the species name and are indented and in black roman script. Isolate names are aligned with relevant accession numbers (between square brackets in the center column) and a recommended abbreviation (between parenthesis in the rightmost column). Some lists contain extra information such as details of vector and/or host. In some genera, species are clustered into groups or serogroups, while in others the isolates within a species are clustered. These clusters are not formal taxonomic groupings. When a species has been re-named recently, the former name (= synonym) is added in parentheses.

ORDER Family	Subfamily	Genus	Type Species	Host	Page
The DNA Viruses **The dsDNA Viruses**					
CAUDOVIRALES					35
Myoviridae		"T4-like viruses"	*Enterobacteria phage T4*	B	43
		"P1-like viruses"	*Enterobacteria phage P1*	B	47
		"P2-like viruses"	*Enterobacteria phage P2*	B	48
		"Mu-like viruses"	*Enterobacteria phage Mu*	B	50
		"SP01-like viruses"	*Bacillus phage SP01*	B	51
		"ϕH-like viruses"	*Halobacterium phage ϕH*	Ar	52
Siphoviridae		"λ-like viruses"	*Enterobacteria phage λ*	B	57
		"T1-like viruses"	*Enterobacteria phage T1*	B	59
		"T5-like viruses"	*Enterobacteria phage T5*	B	60
		"L5-like viruses"	*Mycobacterium phage L5*	B	61
		"c2-like viruses"	*Lactococcus phage c2*	B	63
		"ψM1-like viruses"	*Methanobacterium phage ψM1*	Ar	64
		"ϕC31-like viruses"	*Streptomyces phage ϕC31*	B	65
		"N15-like viruses"	*Enterobacteria phage N15*	B	66
Podoviridae		"T7-like viruses"	*Enterobacteria phage T7*	B	71
		"P22-like viruses"	*Enterobacteria phage P22*	B	73
		"ϕ29-like viruses"	*Bacillus phage ϕ29*	B	75
		"N4-like viruses"	*Enterobacteria phage N4*	B	76
Tectiviridae		*Tectivirus*	*Enterobacteria phage PRD1*	B	81
Corticoviridae		*Corticovirus*	*Pseudoalteromonas phage PM2*	B	87
Plasmaviridae		*Plasmavirus*	*Acholeplasma phage L2*	B	91
Lipothrixviridae		*Alphalipothrixvirus*	*Thermoproteus tenax virus 1*	Ar	95
		Betalipothrixvirus	*Sulfolobus islandicus filamentous virus*	Ar	98
		Gammalipothrixvirus	*Acidianus filamentous virus 1*	Ar	100
Rudiviridae		*Rudivirus*	*Sulfolobus islandicus rod-shaped virus 2*	Ar	103
Fuselloviridae		*Fusellovirus*	*Sulfolobus spindle-shaped virus 1*	Ar	107
		Salterprovirus	*His1 virus*	Ar	111
Guttaviridae		*Guttavirus*	*Sulfolobus newzealandicus droplet-shaped virus*	Ar	115
Poxviridae					117
	Chordopoxvirinae				122
		Orthopoxvirus	*Vaccinia virus*	V	122
		Parapoxvirus	*Orf virus*	V	123
		Avipoxvirus	*Fowlpox virus*	V	124
		Capripoxvirus	*Sheeppox virus*	V	125
		Leporipoxvirus	*Myxoma virus*	V	126
		Suipoxvirus	*Swinepox virus*	V	127
		Molluscipoxvirus	*Molluscum contagiosum virus*	V	127
		Yatapoxvirus	*Yaba monkey tumor virus*	V	128
	Entomopoxvirinae				129
		Alphaentomopoxvirus	*Melolontha melolontha entomopoxvirus*	I	129
		Betaentomopoxvirus	*Amsacta moorei entomopoxvirus 'L'*	I	130
		Gammaentomopoxvirus	*Chironomus luridus entomopoxvirus*	I	131
Asfarviridae		*Asfivirus*	*African swine fever virus*	V, I	135
Iridoviridae		*Iridovirus*	*Invertebrate iridescent virus 6*	I	145
		Chloriridovirus	*Invertebrate iridescent virus 3*	I	153
		Ranavirus	*Frog virus 3*	V	154
		Lymphocystivirus	*Lymphocystis disease virus 1*	V	156
		Megalocytivirus	*Infectious spleen and kidney necrosis virus*	V	158

ORDER Family	Subfamily	Genus	Type Species	Host	Page
Phycodnaviridae		*Chlorovirus*	*Paramecium bursaria Chlorella virus 1*	Al	163
		Coccolithovirus	*Emiliania huxleyi virus 86*	Al	168
		Prasinovirus	*Micromonas pusilla virus SP1*	Al	169
		Prymnesiovirus	*Chrysochromulina brevifilum virus PW1*	Al	170
		Phaeovirus	*Ectocarpus siliculosus virus 1*	Al	171
		Raphidovirus	*Heterosigma akashiwo virus 01*	Al	172
Baculoviridae		*Nucleopolyhedrovirus*	*Autographa californica multiple nucleopolyhedrovirus*	I	177
		Granulovirus	*Cydia pomonella granulovirus*	I	183
Nimaviridae		*Whispovirus*	*White spot syndrome virus 1*	I	187
Herpesviridae					193
	Alphaherpesvirinae				199
		Simplexvirus	*Human herpesvirus 1*	V	199
		Varicellovirus	*Human herpesvirus 3*	V	200
		Mardivirus	*Gallid herpesvirus 2*	V	201
		Iltovirus	*Gallid herpesvirus 1*	V	202
	Betaherpesvirinae				203
		Cytomegalovirus	*Human herpesvirus 5*	V	203
		Muromegalovirus	*Murid herpesvirus 1*	V	204
		Roseolovirus	*Human herpesvirus 6*	V	204
	Gammaherpesvirinae				205
		Lymphocryptovirus	*Human herpesvirus 4*	V	205
		Rhadinovirus	*Saimiriine herpesvirus 2*	V	206
		Ictalurivirus	*Ictalurid herpesvirus 1*	V	208
Adenoviridae		*Mastadenovirus*	*Human adenovirus C*	V	213
		Aviadenovirus	*Fowl adenovirus A*	V	221
		Atadenovirus	*Ovine adenovirus D*	V	223
		Siadenovirus	*Frog adenovirus*	V	225
		Rhizidiovirus	*Rhizidiomyces virus*	F	229
Polyomaviridae		*Polyomavirus*	*Simian virus 40*	V	231
Papillomaviridae		*Alphapapillomavirus*	*Human papillomavirus 32*	V	239
		Betapapillomavirus	*Human papillomavirus 5*	V	245
		Gammapapillomavirus	*Human papillomavirus 4*	V	246
		Deltapapillomavirus	*European elk papillomavirus*	V	247
		Epsilonpapillomavirus	*Bovine papillomavirus 5*	V	247
		Zetapapillomavirus	*Equine papillomavirus 1*	V	247
		Etapapillomavirus	*Fringilla coelebs papillomavirus*	V	248
		Thetapapillomavirus	*Psittacus erithacus timneh papillomavirus*	V	248
		Iotapapillomavirus	*Mastomys natalensis papillomavirus*	V	249
		Kappapapillomavirus	*Cottontail rabbit papillomavirus*	V	249
		Lambdapapillomavirus	*Canine oral papillomavirus*	V	249
		Mupapillomavirus	*Human papillomavirus 1*	V	250
		Nupapillomavirus	*Human papillomavirus 41*	V	250
		Xipapillomavirus	*Bovine papillomavirus 3*	V	251
		Omikronpapillomavirus	*Phocoena spinipinnis papillomavirus*	V	251
		Pipapillomavirus	*Hamster oral papillomavirus*	V	251
Polydnaviridae		*Bracovirus*	*Cotesia melanoscela bracovirus*	I	255
		Ichnovirus	*Campoletis sonorensis ichnovirus*	I	261
Ascoviridae		*Ascovirus*	*Spodoptera frugiperda ascovirus 1a*	I	269
		Mimivirus	*Acanthamoeba polyphaga mimivirus*	Pr, V	275

ORDER Family	Subfamily	Genus	Type Species	Host	Page
The RNA Viruses **The dsRNA Viruses**					
Cystoviridae		*Cystovirus*	*Pseudomonas phage ϕ6*	B	443
Reoviridae					447
		Orthoreovirus	*Mammalian orthoreovirus*	V	455
		Orbivirus	*Bluetongue virus*	V, I	466
		Rotavirus	*Rotavirus A*	V	484
		Coltivirus	*Colorado tick fever virus*	V, I	497
		Seadornavirus	*Banna virus*	V	504
		Aquareovirus	*Aquareovirus A*	V	511
		Idnoreovirus	*Idnoreovirus 1*	I	517
		Cypovirus	*Cypovirus 1*	I	522
		Fijivirus	*Fiji disease virus*	P, I	534
		Phytoreovirus	*Wound tumor virus*	P, I	543
		Oryzavirus	*Rice ragged stunt virus*	P, I	550
		Mycoreovirus	*Mycoreovirus 1*	F	556
Birnaviridae					561
		Aquabirnavirus	*Infectious pancreatic necrosis virus*	V	565
		Avibirnavirus	*Infectious bursal disease virus*	V	566
		Entomobirnavirus	*Drosophila X virus*	I	567
Totiviridae					571
		Totivirus	*Saccharomyces cerevisiae virus L-A*	F	572
		Giardiavirus	*Giardia lamblia virus*	Pr	575
		Leishmaniavirus	*Leishmania RNA virus 1-1*	Pr	577
Partitiviridae					581
		Partitivirus	*Atkinsonella hypoxylon virus*	F	582
		Alphacryptovirus	*White clover cryptic virus 1*	P	585
		Betacryptovirus	*White clover cryptic virus 2*	P	587
Chrysoviridae		*Chrysovirus*	*Penicillium chrysogenum virus*	F	591
Hypoviridae		*Hypovirus*	*Cryphonectria hypovirus 1*	F	597
		Endornavirus	*Vicia faba endornavirus*	P	603

ORDER Family	Subfamily	Genus	Type Species	Host	Page
The Negative Stranded ssRNA Viruses					
MONONEGAVIRALES					609
Bornaviridae					615
		Bornavirus	*Borna disease virus*	V	615
Rhabdoviridae					623
		Vesiculovirus	*Vesicular stomatitis Indiana virus*	V, I	629
		Lyssavirus	*Rabies virus*	V	630
		Ephemerovirus	*Bovine ephemeral fever virus*	V, I	633
		Novirhabdovirus	*Infectious hematopoietic necrosis virus*	V	635
		Cytorhabdovirus	*Lettuce necrotic yellows virus*	P, I	637
		Nucleorhabdovirus	*Potato yellow dwarf virus*	P, I	638
Filoviridae					645
		Marburgvirus	*Lake Victoria marburgvirus*	V	650
		Ebolavirus	*Zaire ebolavirus*	V	651
Paramyxoviridae					651
	Paramyxovirinae				659
		Rubulavirus	*Mumps virus*	V	659
		Avulavirus	*Newcastle disease virus*	V	661
		Respirovirus	*Sendai virus*	V	662
		Henipavirus	*Hendra virus*	V	663
		Morbillivirus	*Measles virus*	V	663
	Pneumovirinae				665
		Pneumovirus	*Human respiratory syncytial virus*	V	665
		Metapneumovirus	*Avian metapneumovirus*	V	666
		Varicosavirus	*Lettuce big-vein associated virus*	P	669
		Ophiovirus	*Citrus psorosis virus*	P	673
Orthomyxoviridae					681
		Influenzavirus A	*Influenza A virus*	V	685
		Influenzavirus B	*Influenza B virus*	V	687
		Influenzavirus C	*Influenza C virus*	V	688
		Thogotovirus	*Thogoto virus*	V, I	689
		Isavirus	*Infectious salmon anemia virus*	V	691
Bunyaviridae					695
		Orthobunyavirus	*Bunyamwera virus*	V, I	699
		Hantavirus	*Hantaan virus*	V	704
		Nairovirus	*Dugbe virus*	V, I	707
		Phlebovirus	*Rift Valley fever virus*	V, I	709
		Tospovirus	*Tomato spotted wilt virus*	P, I	712
		Tenuivirus	*Rice stripe virus*	P, I	717
Arenaviridae		*Arenavirus*	*Lymphocytic choriomeningitis virus*	V	725
		Deltavirus	*Hepatitis delta virus*	V	735

ORDER Family	Subfamily	Genus	Type Species	Host	Page
The Positive Stranded ssRNA Viruses					
Leviviridae					741
		Levivirus	*Enterobacteria phage MS2*	B	743
		Allolevivirus	*Enterobacteria phage Qβ*	B	745
Narnaviridae					751
		Narnavirus	*Saccharomyces 20S narnavirus*	F	751
		Mitovirus	*Cryphonectria mitovirus 1*	F	753
Picornaviridae					757
		Enterovirus	*Poliovirus*	V	760
		Rhinovirus	*Human rhinovirus A*	V	764
		Cardiovirus	*Encephalomyocarditis virus*	V	767
		Aphthovirus	*Foot-and-mouth disease virus*	V	768
		Hepatovirus	*Hepatitis A virus*	V	770
		Parechovirus	*Human parechovirus*	V	771
		Erbovirus	*Equine rhinitis B virus*	V	772
		Kobuvirus	*Aichi virus*	V	773
		Teschovirus	*Porcine teschovirus*	V	774
		Iflavirus	*Infectious flacherie virus*	I	779
Dicistroviridae		*Cripavirus*	*Cricket paralysis virus*	I	783
Marnaviridae		*Marnavirus*	*Heterosigma akashiwo RNA virus*	F	789
Sequiviridae					793
		Sequivirus	*Parsnip yellow fleck virus*	P	794
		Waikavirus	*Rice tungro spherical virus*	P	795
		Sadwavirus	*Satsuma dwarf virus*	P	799
		Cheravirus	*Cherry rasp leaf virus*	P	803
Comoviridae					807
		Comovirus	*Cowpea mosaic virus*	P	810
		Fabavirus	*Broad bean wilt virus 1*	P	812
		Nepovirus	*Tobacco ringspot virus*	P	813
Potyviridae					819
		Potyvirus	*Potato virus Y*	P	821
		Ipomovirus	*Sweet potato mild mottle virus*	P	829
		Macluravirus	*Maclura mosaic virus*	P	831
		Rymovirus	*Ryegrass mosaic virus*	P	833
		Tritimovirus	*Wheat streak mosaic virus*	P	834
		Bymovirus	*Barley yellow mosaic virus*	P	837
Caliciviridae					843
		Lagovirus	*Rabbit hemorrhagic disease virus*	V	846
		Norovirus	*Norwalk virus*	V	847
		Sapovirus	*Sapporo virus*	V	848
		Vesivirus	*Vesicular exanthema of swine virus*	V	848
		Hepevirus	*Hepatitis E virus*	V	853
Astroviridae					859
		Avastrovirus	*Turkey astrovirus*	V	861
		Mamastrovirus	*Human astrovirus*	V	861

ORDER Family	Subfamily	Genus	Type Species	Host	Page
Nodaviridae		*Alphanodavirus*	*Nodamura virus*	I	865
		Betanodavirus	*Striped jack nervous necrosis virus*	V	869
Tetraviridae		*Betatetravirus*	*Nudaurelia capensis β virus*	I	873
		Omegatetravirus	*Nudaurelia capensis ω virus*	I	877
		Sobemovirus	*Southern bean mosaic virus*	P	885
Luteoviridae					891
		Luteovirus	*Barley yellow dwarf virus - PAV*	P	895
		Polerovirus	*Potato leafroll virus*	P	896
		Enamovirus	*Pea enation mosaic virus-1*	P	897
		Umbravirus	*Carrot mottle virus*	P	901
Tombusviridae					907
		Dianthovirus	*Carnation ringspot virus*	P	911
		Tombusvirus	*Tomato bushy stunt virus*	P	914
		Aureusvirus	*Pothos latent virus*	P	918
		Avenavirus	*Oat chlorotic stunt virus*	P	920
		Carmovirus	*Carnation mottle virus*	P	922
		Necrovirus	*Tobacco necrosis virus A*	P	926
		Panicovirus	*Panicum mosaic virus*	P	929
		Machlomovirus	*Maize chlorotic mottle virus*	P	932
NIDOVIRALES					937
Coronaviridae					947
		Coronavirus	*Infectious bronchitis virus*	V	947
		Torovirus	*Equine torovirus*	V	956
Arteriviridae					965
		Arterivirus	*Equine arteritis virus*	V	965
Roniviridae					975
		Okavirus	*Gill-associated virus*	I	975
Flaviviridae					981
		Flavivirus	*Yellow fever virus*	V, I	981
		Pestivirus	*Bovine viral diarrhea virus 1*	V	988
		Hepacivirus	*Hepatitis C virus*	V	993
Togaviridae		*Alphavirus*	*Sindbis virus*	V, I	999
		Rubivirus	*Rubella virus*	V	1006
		Tobamovirus	*Tobacco mosaic virus*	P	1009
		Tobravirus	*Tobacco rattle virus*	P	1015
		Hordeivirus	*Barley stripe mosaic virus*	P	1021
		Furovirus	*Soil-borne wheat mosaic virus*	P	1027
		Pomovirus	*Potato mop-top virus*	P	1033
		Pecluvirus	*Peanut clump virus*	P	1039
		Benyvirus	*Beet necrotic yellow vein virus*	P	1043
Bromoviridae					1049
		Alfamovirus	*Alfalfa mosaic virus*	P	1051
		Bromovirus	*Brome mosaic virus*	P	1052
		Cucumovirus	*Cucumber mosaic virus*	P	1053
		Ilarvirus	*Tobacco streak virus*	P	1055
		Oleavirus	*Olive latent virus 2*	P	1057

Abbreviations of the virus hosts

Algae	Al	Bacteria	B	Invertebrates	I	Protozoa	Pr
Archaea	Ar	Fungi	F	Plants	P	Vertebrates	V

The Double Stranded DNA Viruses

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ORDER CAUDOVIRALES

TAXONOMIC STRUCTURE OF THE ORDER

Order	***Caudovirales***
Family	***Myoviridae***
Genus	"T4-like viruses"
Genus	"P1-like viruses"
Genus	"P2-like viruses"
Genus	"Mu-like viruses"
Genus	"SPO1-like viruses"
Genus	"ϕH-like viruses"
Family	***Siphoviridae***
Genus	"λ-like viruses"
Genus	"T1-like viruses"
Genus	"T5-like viruses"
Genus	"L5-like viruses"
Genus	"c2-like viruses"
Genus	"ΨM1-like viruses"
Genus	"ϕC31-like viruses"
Genus	"N15-like viruses"
Family	***Podoviridae***
Genus	"T7-like viruses"
Genus	"P22-like viruses"
Genus	"ϕ29-like viruses"
Genus	"N4-like viruses"

GENERAL

The order consists of the three families of tailed bacterial viruses infecting Bacteria and Archaea: *Myoviridae* (long contractile tails), *Siphoviridae* (long non-contractile tails), and *Podoviridae* (short non-contractile tails). Tailed bacterial viruses are an extremely large group with highly diverse virion, genome, and replication properties. Over 4,500 descriptions have been published (accounting for 96% of reported bacterial viruses): 24% in the family *Myoviridae*, 62% in the family *Siphoviridae*, and 14% in the family *Podoviridae* (as of November 2001). However, data on virion structure, genome organization, and replication properties are available for only a small number of well-studied species. Their great evolutionary age, large population sizes, and extensive horizontal gene transfer between bacterial cells and viruses have erased or obscured many phylogenetic relationships amongst the tailed viruses. However, enough common features survive to indicate their fundamental relatedness. Therefore, formal taxonomic names are used for *Caudovirales* at the order and family level, but only vernacular names at the genus level.

VIRION PROPERTIES

MORPHOLOGY

The virion has no envelope and consists of two parts, the head and the tail. The head is a protein shell and contains a single linear dsDNA molecule, and the tail is a protein tube whose distal end binds the surface receptors on susceptible bacterial cells. DNA travels through the tail tube during delivery (often called "injection") into the cell being infected. Heads have icosahedral symmetry or elongated derivatives thereof (with known triangulation numbers of T=4, 7, 13, 16 and 52). Capsomers are seldom visible: heads usually appear smooth and thin-walled (2-3 nm). When they are visible, morphological features (capsomeres) on the surface of the head commonly form 72 capsomers (T=7; 420

protein subunits), but known capsomer numbers vary from 42 to 522. Isometric heads are typically 45-170 nm in diameter. Elongated heads derive from icosahedra by addition of equatorial belts of capsomers and can be up to 230 nm long. DNA forms a tightly packed coil (without bound proteins) inside the head. Tail shafts have six-fold or (rarely) three-fold symmetry, and are helical or stacks of disks of subunits from 3 and 825 nm in length. They usually have base plates, spikes, or terminal fibers at the distal end. Some viruses have collars at the head-tail junction, head or collar appendages, transverse tail disks, or other attachments.

PHYSICOCHEMICAL AND PHYSICAL PROPERTIES

Virion Mr is 20 to 600 x 10^6; S_{20w} values are 200 to >1200S. Both upper limits may be underestimates, since these properties have not been determined for the largest tailed viruses. Buoyant density in CsCl is typically ~1.5 g/cm^3. Most tailed viruses are stable at pH 5-9; a few are stable at pH 2 or pH 11. Heat sensitivity is variable, but many virions are inactivated by heating at 55-75°C for 30 min. Tailed viruses are rather resistant to UV irradiation. Heat and UV inactivation generally follow first-order kinetics. Most tailed phages are stable to chloroform. Inactivation by nonionic detergents is variable and concentration dependent. Some virions are sensitive to osmotic shock, and many are sensitive to Mg^{++} chelators.

NUCLEIC ACID

Virions contain one molecule of linear dsDNA. Genome sizes are 18 to 500 kbp, corresponding to Mr values of 11-300 x 10^6. DNA content is 45-55% of the virions. G+C contents are 27-72% and usually resemble those of host DNA. Some viral DNAs contain modified nucleotides which partially or completely replace normal nucleotides (*e.g.*, 5-hydroxymethylcytosine instead of cytosine), and/or are glycosylated or otherwise modified.

PROTEINS

The number of different virion structural proteins ranges from 7-49. Typical head shells are made up of 60T molecules of a single main building block CP and 12 molecules of portal protein through which DNA enters and leaves, but they can also contain varied numbers of proteins that plug the portal hole, proteins to which tails bind, proteins that bind to the outside of the CP shell (decoration proteins) and other proteins whose roles are not known. Non-contractile tails are made of one major shaft or tube protein and contractile tails have a second major protein, the sheath protein, that forms a cylinder around the central tube. Tails also have small numbers of varied specific proteins at both ends. Those at the end distal from the head form a structure called the tail tip (*Siphovirus*) or baseplate (*Myovirus*) to which the tail fibers are attached. The tail fibers bind to the first-contact receptors on the surface of susceptible cells. Fibers or baseplates may include proteins with endoglycosidase or peptidoglycan hydrolase activity that aid in gaining access to the cell surface and entry of DNA into the cell. Most virions carry proteins that are injected with the DNA, such as transcription factors, RNA polymerase and others with poorly understood functions.

LIPIDS

No well-characterized virions contain lipid.

CARBOHYDRATES

Glycoproteins, glycolipids, hexosamine, and a polysaccharide have been reported in certain virions but these are not well-characterized.

Genome Organization and Replication

Genome Organization

The linear dsDNA genomes encode from 27 to over 600 genes that are highly clustered according to function and tend to be arranged in large operons. Complete functional genomic maps are very diverse and available for only a relatively small number of tailed viruses. Virion DNAs may be circularly permuted and/or terminally redundant, have single-stranded gaps, or have covalently-bound terminal proteins. The ends of these linear molecules can be blunt or have complementary protruding 5'- or 3'-ends (the "cohesive" or "sticky" ends, which can base pair to circularize the molecule). Prophages of temperate tailed viruses are either integrated into the host genome or replicate as circular or linear plasmids; these linear plasmids have covalently-closed hairpin telomeres.

Replication

In typical lytic infections, after entering the host cell, viral DNA may either circularize or remain linear. All tailed viruses encode proteins that direct the replication apparatus to the replication origin, but this apparatus may be entirely host derived, partly virus encoded, or entirely virus encoded. DNA replication is semi-conservative, may be either bidirectional or unidirectional, and usually results in the formation of concatemers (multiple genomes joined head-to-tail) by recombination between phage DNAs or by rolling circle replication. Progeny viral DNA is generated during virion assembly by cleavage from this concatemeric DNA: (i) at unique sites to produce identical DNA molecules with either *cos* sites or blunt-ended, terminally redundant termini, (ii) at *pac* sites to produce circularly permuted, terminal redundant DNAs, or (iii) by a headful mechanism to produce terminally redundant, circularly permuted DNAs. A few viruses use terminal proteins to prime DNA replication and package progeny viral DNA (ϕ29 and its relatives) or replicate DNA by a duplicative transposition mechanism (Mu and its relatives). Gene expression is largely time-ordered and groups of genes are sequentially expressed. "Early genes" are expressed first and are largely involved in host cell modification and viral DNA replication. "Late genes" specify virion structural proteins and lysis proteins. The larger tailed viruses have gene expression cascades that are more complex than this simple scenario. Transcription often requires host RNA polymerase, but many tailed viruses encode RNA polymerases or transcription factors that affect the host RNA polymerase. Translational control is poorly understood and no generalizations are possible at the present state of knowledge.

Virion Assembly and DNA Packaging

Assembly of virions from newly made proteins and replicated DNA is complex and generally includes separate pathways for heads, tails and tail fibers. Coat protein shells, called procapsids or proheads, are assembled first, and DNA is inserted into these preformed proteinaceous containers. Assembly of procapsids is poorly understood, but often utilizes an internal scaffolding protein which helps CP assemble correctly and is then released from the shell after its construction. In many, but not all, tailed viruses, proteolytic cleavages (by host or virus-encoded proteases) of some proteins accompany assembly. Virus-specific DNA is recognized for packaging into procapsids by the terminase protein. One end of the DNA is then threaded through the procapsid's portal structure, and DNA is pumped into the head by an ATP hydrolysis-driven motor that is probably made up of the two terminase subunits and portal protein. Unless unit length DNA molecules are the substrate for packaging (such as with ϕ29), when the head is full of DNA a "headful sensing device" recognizes this fact and causes the terminase to cleave the DNA to release the full head from the unpackaged remainder of the DNA concatemer. The terminase subunits are usually released from the virion after DNA is packaged. Filled heads then join to tails and tail fibers to form progeny virions. Some viruses form intracellular arrays, and many produce aberrant structures (polyheads, polytails, giant,

multi-tailed, or misshapen particles). Progeny viruses are liberated by lysis of the host cell. Cell lysis is caused by phage-encoded peptidoglycan hydrolases; but lysis timing is controlled by holins, phage encoded inner membrane proteins that allow the hydrolases to escape from the cytoplasm.

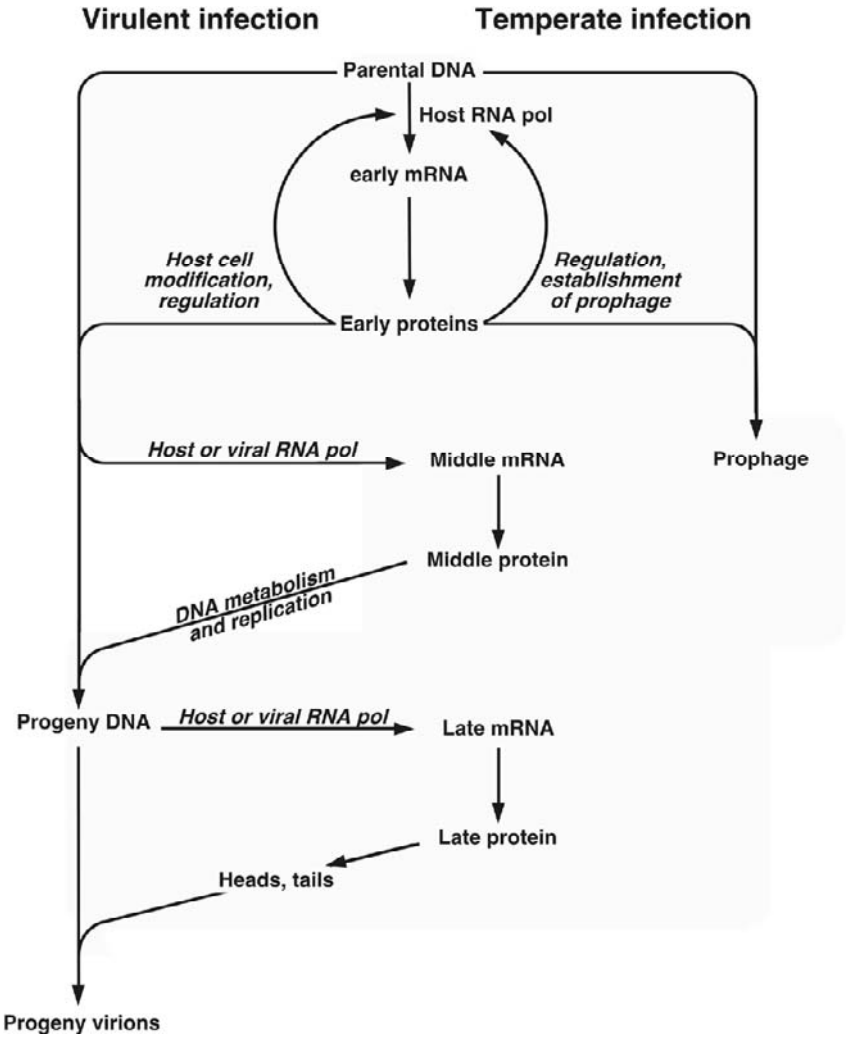

Figure 1: Flow chart of tailed phage replication. The chart depicts the replication of "typical" virulent phages such as Enterobacteria phage T4 (T4), Enterobacteria phage T7 (T7), and the temperate phages.

Antigenic Properties

Viruses are antigenically complex and efficient immunogens, inducing the formation of neutralizing and complement-fixing antigens. The existence of group antigens is likely within species or genera.

Biological Properties

Infection

Tailed-viruses are lytic or temperate. Lytic infection results in production of progeny viruses and destruction of the host. Phages adsorb tail-first to specific protein or lipoprotein host cell receptors, which are located on the outer cell surface. In a few cases, not represented by the genera described here, the primary adsorption sites are capsules, flagella, or pili. Upon adsorption to the outside of the cell, virions undergo complex and often poorly understood rearrangements which release the DNA to enter the cell through

the tail. Cell walls are often locally digested by a virion-associated peptidoglycan hydrolase and viral DNA enters the cytoplasm by as yet unknown mechanisms. In some cases DNA entry is stepwise and transcription of the first DNA to enter is required for entry of the rest of the DNA. Empty virions remain outside the infected bacterium, however most viruses inject specific proteins with the DNA. Temperate viruses can, upon infection, either enter a lytic growth cycle (above) or establish a lysogenic state (below). Physiological factors in the cell can affect the decision between these two pathways.

Latency

All three tailed virus families include genera or species of temperate viruses. Viral genomes in lysogenized cells are called "prophages". Prophages are either integrated into host cell chromosomes or persist as extrachromosomal elements (plasmids). Integration is usually mediated by recombinases called integrases. The most common are in the tyrosine-active site class and some are in the serine-active site class. For the Mu-like viruses, integration is accomplished by transposases. Integrated prophages typically express only a very small fraction of their genes. The genes that are expressed from the prophage are called "lysogenic conversion" genes, and their products usually alter the properties of the bacterial host. Among these genes is the prophage repressor gene, whose product binds operators in the prophage to keep the lytic cascade of gene expression from initiating. Plasmid prophages typically express many of their early genes, some of which are involved in replication of the plasmid (which can be circular or linear). Prophages can often be induced to initiate a lytic growth cycle; DNA damaging agents such as ultraviolet light or mitomycin C cause many prophages to induce.

Host Range

Tailed viruses have been found in over 140 prokaryote genera representing most branches of the Bacterial and Archaeal phylogenetic trees. The host specificity of these viruses can vary widely; some can infect multiple closely related genera, but perhaps more common (especially in the host family *Enterobacteriacea*, where the most varieties have been studied) are viruses that are specific for particular isolates or groups of isolates of closely related host species.

Transmission in Nature

Virions are typically carried and transmitted in aqueous environments, although a few are stable to drying. Virus genomes can be carried as prophages inside host bacteria. Such lysogenic bacteria can induce to release virions, either spontaneously or in response to specific environmental signals.

Geographic Distribution

Tailed phages are the most abundant type of organism on Earth; the current best estimates are 10^{31} particles in our biosphere. If all these phages were laid end to end the line would extend for 2×10^{8} light years. Data from genome sequence analyses implies that these viruses can move around the globe on a time scale that is short relative to the rate at which they accumulate mutations. They have a worldwide distribution and presumably share the habitats of their hosts. An important habitat is inside lysogenic bacteria as prophages.

Phylogenetic Relationships within the Order and the Perils of Mosaicism

The recent availability of high-throughput DNA sequencing has led to a dramatic increase in the number of complete genome sequences that are available for members of the *Caudovirales*. This has led in turn to a similarly dramatic change in our understanding of the phylogenetic relationships among members of the order. The new data substantially enrich our appreciation of the genetic structure of the global *Caudovirales* population and

of the evolutionary mechanisms within that order; the new data also substantially complicate considerations of how best to represent these viruses in a taxonomy.

The hallmark of the genomes of these viruses is that they are genetic mosaics, a property that becomes apparent only when two or more genome sequences are compared. The modules of sequence that constitute the mosaic are typically individual genes, but they can also be parts of genes corresponding to protein domains, or small groups of genes such as prohead assembly genes. The mosaicism is evidently the result of non-homologous recombination during the evolution of these viruses. The novel juxtapositions of sequence produced in this way are spread through the population and reassorted with each other by means of homologous recombination. Regardless of mechanism, the overall result is as if each phage had constituted its genome by picking modules from a menu, choosing one module from each of perhaps fifty columns, each of which has alternative choices.

A consequence of the mosaic relationships among the genomes of these viruses is that if we ask how closely two viruses are related to each other — as we might do in trying to reconstruct their phylogeny or in deciding on a taxonomy — the answer will be radically different depending on which module we base our comparison on. Thus, we could look, for example, at the sequences of the major capsid proteins from a group of phages and derive a self-consistent hierarchical phylogeny, ostensibly representing the evolutionary history of the capsid genes, but if we were to construct a similar phylogeny for a different genetic module from the same group of phages, say the C-terminal domain of the integrase proteins, we would get another self-consistent phylogeny which was however completely incongruent with the phylogeny of the capsid proteins. A formal representation of such relationships is shown in figure 2.

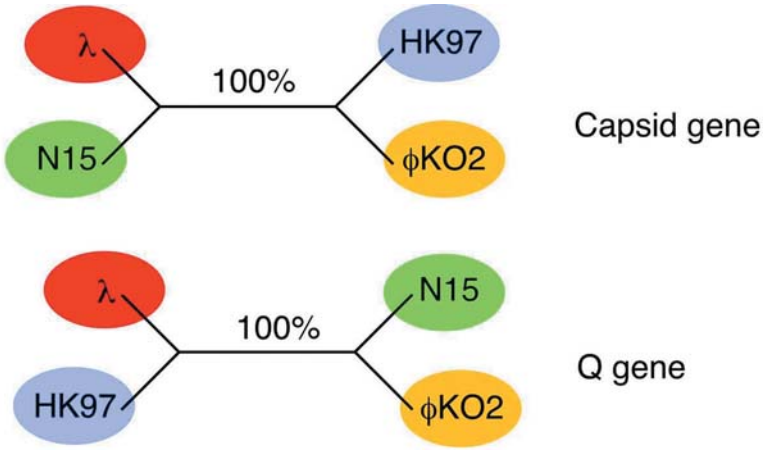

Figure 2: Phylogenetic trees showing the relationships among two different genes from four phages. Enterobacteria phage λ, Enterobacteria phage HK97 and Enterobacteria phage N15 infect *E. coli*; Klebsiella phage ϕKO2 is a phage of *Klebsiella oxytoca*. The trees are incongruent owing to mosaicism in the genomes of the phages.

A logical consequence of such mosaic relationships is that it is not possible to construct a hierarchical phylogeny for the viruses that does not misrepresent the phylogenies of some (often many) of the component genetic modules. In fact, given the degree of mosaicism in the order *Caudovirales*, any attempt at a hierarchical whole virus phylogeny will necessarily misrepresent a majority of the component modules. This is true whether the phylogeny is based on the relationships among members of a single module type (say DNA polymerases) or on some sort of average or blending of all the modules.

The question for virus taxonomists then becomes, how should we construct a taxonomy to represent these biological properties of the phage population? In the current ICTV

taxonomy, represented here, the division of the order *Caudovirales* into three families is based solely on tail morphology: *Siphoviridae* have long non-contractile tails, *Myoviridae* have long contractile tails, and *Podoviridae* have short tails. As might be expected from the discussion above, this hierarchical division of phages on the basis of one character leads to many examples of inappropriate divisions of other characters. One well known and easily illustrated example of this is shown in figure 3, comparing phages λ and P22. These two phages are considered by most phage biologists to be closely related, because they share genome organization (including regulation and layout of transcription and functional order of genes), temperate lifestyle, a number of similarities of gene sequences, and they can form viable hybrids. Despite these similarities, they are classified into different families (*Siphoviridae* and *Podoviridae* for λ and P22, respectively) based on their differences in tail morphology. An argument could be made as to whether or not the similarities between these two phages are enough that they should be classified in the same family, but it is in any case clear that P22 is much closer to λ than it is to most other members of the family *Podoviridae*, such as phages T7 and N4, which have essentially no similarity to λ in sequence, genome organization, or lifestyle. The critical issue is in fact not to decide how different two phages need to be to be assigned to different families, but rather whether it is a useful exercise to try to represent a population in which the individuals are related to each other in a "reticulate" or "multi-dimensional" fashion by using a purely hierarchical taxonomy that is doomed to misrepresent the majority of those biological relationships?

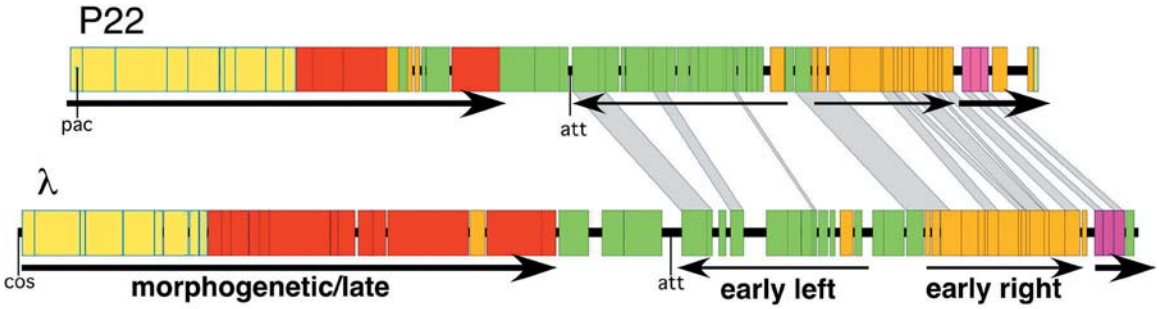

Figure 3: The mosaic relationship between the genomes of phages P22 and λ. The circular maps are opened for linear display between the lysis and head genes. The genes in each genome are represented by rectangles; white - transcribed right to left, gray - transcribed left to right. P22 genes that have sequence similarity to λ genes are connected by light gray trapezoids. The thin arrows represent transcription of the early operons and thick arrows transcription of the late operons. The circular phage genomes are opened at their attachment (att) sites for insertion of the prophage into the host chromosome in lysogens. DNA packaging initiation sites (called pac and cos in P22 and λ, respectively) are also indicated below the maps.

This discussion recapitulates a long-running controversy in the field of taxonomy over whether it is of paramount importance for a taxonomy to accurately reflect the biological relationships of the classified organisms or whether it is sufficiently useful to get organisms assigned a place in a recognized taxonomy that an occasional (or even frequent) misrepresentation of biological relationships is of little consequence. These issues are particularly sharply focused for the order *Caudovirales* due to the fact that the mosaicism is so extensive and the consequent misrepresentations so pervasive. Because of this, the ICTV considers the taxonomy of this group to be provisional, and this is the reason that the names of the genera are in a non-official vernacular format. Discussions are ongoing, both within the ICTV and in the virology community at large, and there may well be significant changes to the *Caudovirales* taxonomy in the future in response to our new understanding of the biology.

SIMILARITY WITH OTHER TAXA

Tailed bacterial viruses resemble members of the family *Tectiviridae* by the presence of a dedicated structure for DNA injection, but differ from them by the permanent nature of their tails and lack of a lipid bilayer. Tailed viruses resemble viruses belonging to the family *Herpesviridae* in morphogenesis (use of scaffolding proteins, packaging of DNA into preformed shells, maturation of procapsids by proteolytic cleavage, and capsid conformational change) and overall strategy of replication. In addition, temperate tailed phages and members of the family *Herpesviridae* are able to establish latent infections.

DERIVATION OF NAMES

Caudo: from Latin *cauda*, "tail".
Myo: from Greek *my*, *myos*, "muscle", referring to the contractile tail.
Sipho: from Greek *siphon*, "tube", referring to the long tail.
Podo: from Greek *pous*, *podos*, "foot", referring to the short tail.

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FAMILY MYOVIRIDAE

TAXONOMIC STRUCTURE OF THE FAMILY

Family	*Myoviridae*
Genus	**"T4-like viruses"**
Genus	**"P1-like viruses"**
Genus	**"P2-like viruses"**
Genus	**"Mu-like viruses"**
Genus	**"SPO1-like viruses"**
Genus	**"ϕH-like viruses"**

DISTINGUISHING FEATURES

Tails are contractile, more or less rigid, long and relatively thick (80-455 x 16-20 nm). They consist of a central core built of stacked rings of 6 subunits and surrounded by a helical contractile sheath, which is separated from the head by a neck. During contraction, sheath subunits slide over each other and the sheath becomes shorter and thicker. This brings the tail core in contact with the bacterial plasma membrane and is an essential stage of infection. Heads and tails are assembled in separate pathways. With respect to other tailed phages, myoviruses often have larger heads and higher particle weights and DNA contents, and seem to be more sensitive to freezing and thawing and to osmotic shock. Genera are differentiated by genome organization, mechanisms of DNA replication, and packaging, and the presence or absence of unusual bases and DNA polymerases.

GENUS "T4-LIKE VIRUSES"

Type Species *Enterobacteria phage T4*

DISTINGUISHING FEATURES

Virions have elongated heads and tails with long, kinked fibers. Genomes are circularly permuted and terminally redundant, and typically code for hydroxymethylcytosine synthesizing enzymes and type B DNA polymerase. The genetic map is circular and the DNA is packaged by a headful mechanism.

VIRION PROPERTIES

MORPHOLOGY

Phage heads are prolate icosahedra (elongated pentagonal bipyramidal antiprisms), measure ~111 x 78 nm, and consist of 152 capsomers (T=13, elongated). Tails measure 113 x 16 nm and have a collar, base plate, 6 short spikes and 6 long fibers.

PHYSICOCHEMICAL AND PHYSICAL PROPERTIES

Virion Mr is ~210 x 10^6, buoyant density in CsCl is 1.50 g/cm^3, and S_{20w} ~1030S. Infectivity is ether and chloroform resistant.

NUCLEIC ACID

Genomes have a Mr ~120 x 10^6, corresponding to 48% of the particle weight. DNA contains 5-hydroxymethylcytosine (HMC) instead of cytosine (these nucleotides are glycosylated), a G+C content of 35%, and is circularly permuted and terminally redundant. The Enterobacteria phage T4 (T4) genome has been fully sequenced (168,903 bp).

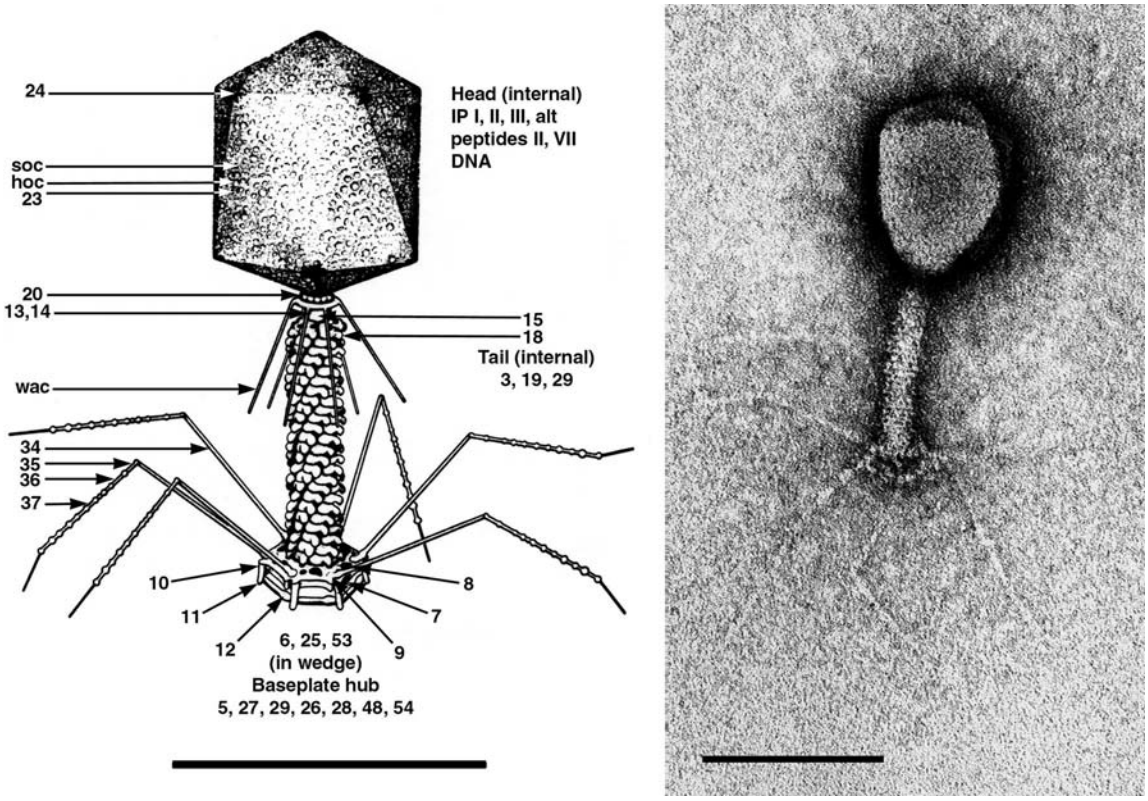

Figure 1: (Left) Diagram of Enterobacteria phage T4 (T4) showing detailed location of structural proteins. Head vertices consist of cleaved gp24. Gp20 is located at the head tail connector. Collar and whiskers appear to be made of the same protein, gp*wac*. Sheath subunits (gp18) fit into holes in the base plate and short tail proteins (gp12) are shown in the quiescent state. The complex base is assembled from a central plug and six wedges. Tail fibers consist of three proteins. (From Eiserling, F.A. (1983). *Bacteriophage T4*, (C.K., Mathews, E.M., Kutter, G., Mosig and P.B., Berget, eds). American Society for Microbiology, Washington, DC. Reproduced with permission). (Right) Negative contrast electron micrograph of T4 particle stained with uranyl acetate. The bars represent 100 nm.

PROTEINS

T4 particles contain at least 49 polypeptides (8-155 kDa), including 1,600-2,000 copies of the major CP (43 kDa) and 3 proteins located inside the head. Various enzymes are present or encoded, *e.g*. type B (*E. coli* Pol II) DNA polymerase, numerous nucleotide metabolism enzymes and lysozyme. Amino acid sequences for T4 proteins are available.

LIPIDS

None known.

CARBOHYDRATES

Glucose is covalently linked to HMC in phage DNA.

GENOME ORGANIZATION AND REPLICATION

The genetic map is circular and comprises ~300 genes. Morphopoietic genes generally cluster together, but this is not universally true, suggesting extensive translocation of genes during evolution. The genome is circularly permuted and has 1-3% terminal redundancy. After infection, the host chromosome breaks down and viral DNA replicates as a concatemer, generating forked replicative intermediates from multiple origins of replication. Transcription is regulated in part by phage-induced modification of host bacterial RNA polymerase and proceeds in three waves (early, middle, late). Heads, tails, and tail fibers are assembled in 3 separate pathways. Unique DNA molecules are packaged by a headful mechanism. Virions are assembled at the cell periphery. Aberrant head structures (polyheads and isometric heads) are frequent.

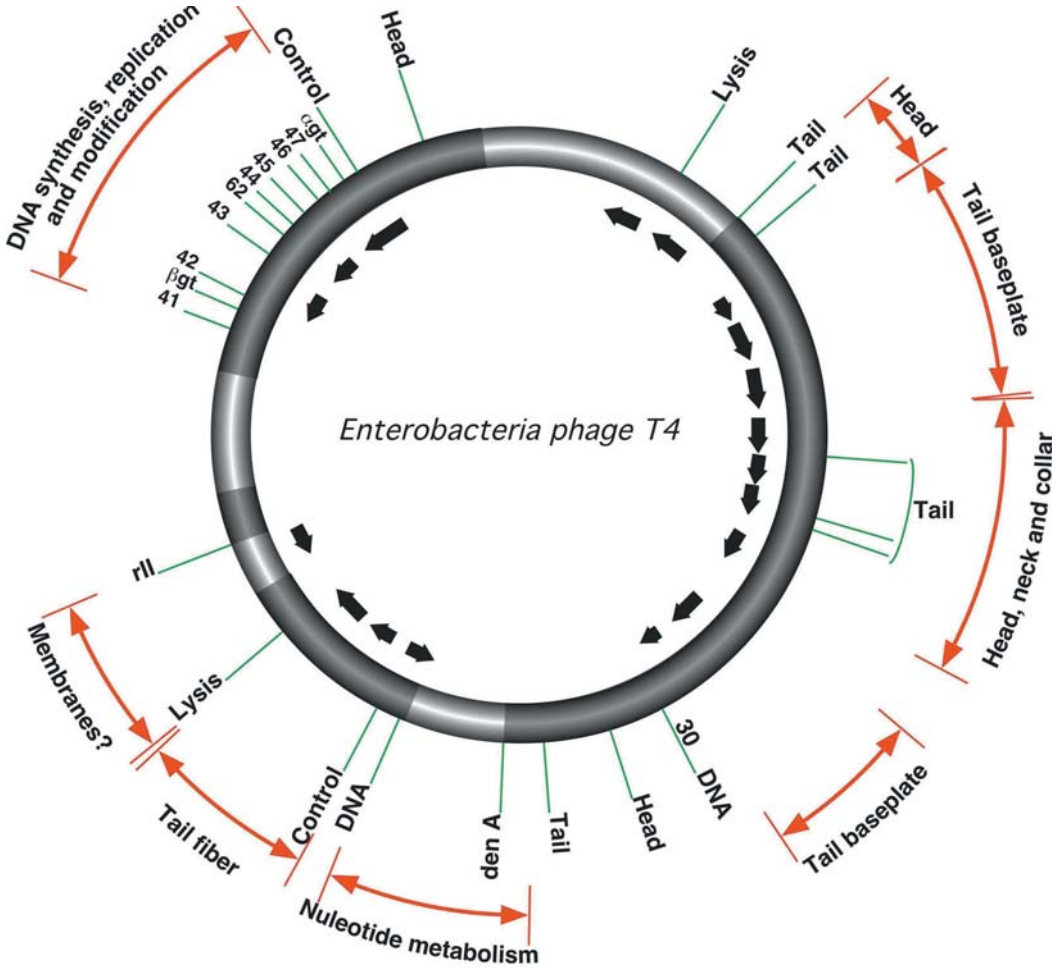

Figure 2: Simplified genetic map of Enterobacteria phage T4 (T4) showing clustering of genes with related functions, location of essential genes (solid bars), and direction and origin of transcripts (arrows). (From Freifelder, D. (ed)(1983). *Molecular Biology*. Science Books International, Boston, and Van Nostrand Reynolds, New York, p 614. With permission).

ANTIGENIC PROPERTIES

A group antigen and antigens defining 8 subgroups have been identified by complement fixation

BIOLOGICAL PROPERTIES

Phages are virulent, and infect enteric and related bacteria (γ3-subgroup of Gram-negative proteobacteria). Their distribution is worldwide.

LIST OF SPECIES DEMARCATION CRITERIA IN THE GENUS

Species differ in host range, capsid length, serological properties, and, insofar as known, DNA homology and amino acid sequences. Capsid length is 137 nm for Aeromonas phage Aeh1 (Aeh1) and Vibrio phage nt-1 (nt-1) and 111 nm for a number of other species. Phage T4 and Enterobacteria phage SV14 (Sv14) are in different hybridization groups.

LIST OF SPECIES IN THE GENUS

Species names are in green italic script; strain names and synonyms are in black roman script; tentative species names are in blue roman script. Sequence accession numbers, and assigned abbreviations ( ) are also listed.

SPECIES IN THE GENUS

Acinetobacter phage 133		
Acinetobacter phage 133		(133)
Aeromonas phage 40RR2.8t		
Aeromonas phage 40RR2.8t		(40RR2.8t)
(Aeromonas phage 40R)		(40R)
Aeromonas phage 65		
Aeromonas phage 65		(65)
Aeromonas phage Aeh1		
Aeromonas phage Aeh1		(Aeh1)
Enterobacteria phage SV14		
Enterobacteria phage D2A		(D2A)
Enterobacteria phage D8		(D8)
Enterobacteria phage SV14		(SV14)
Enterobacteria phage T4		
Enterobacteria phage C16		(C16)
Enterobacteria phage F10		(F10)
Enterobacteria phage Fsα		(Fsα)
Enterobacteria phage PST		(PST)
Enterobacteria phage SKII		(SKII)
Enterobacteria phage SKV		(SKV)
Enterobacteria phage SKX		(SKX)
Enterobacteria phage SV3		(SV3)
Enterobacteria phage T2		(T2)
Enterobacteria phage T4	[A158101]	(T4)
Enterobacteria phage T6		(T6)
Pseudomonas phage 42		
Pseudomonas phage 42		(42)
Vibrio phage nt-1		
Vibrio phage KVP20		(KVP20)
Vibrio phage KVP40		(KVP40)
Vibrio phage nt-1		(nt-1)

TENTATIVE SPECIES IN THE GENUS

Acinetobacter phage E4	(E4)
Acinetobacter phage E5	(E5)
Aeromonas phage 1	(Aer1)
Aeromonas phage 25	(25)
Aeromonas phage 31	(31)
Enterobacteria phage 1 (Phage aeI)	(aeI)
Enterobacteria phage 11F	(11F)
Enterobacteria phage 3	(3)
Enterobacteria phage 3T+	(3T+)
Enterobacteria phage 50	(50)
Enterobacteria phage 5845	(5845)
Enterobacteria phage 66F	(66F)
Enterobacteria phage 8893	(8893)
Enterobacteria phage 9/0	(9/0)
Enterobacteria phage α1	(α1)
Enterobacteria phage DdVI	(DdV1)
Enterobacteria phage F7	(F7)
Enterobacteria phage Kl3	(K13)
Enterobacteria phage RB42	(RB42)
Enterobacteria phage RB43	(RB43)

Enterobacteria phage RB49		(RB49)
Enterobacteria phage RB69	[AY303349]	(RB69)
Enterobacteria phage SMB		(SMB)
Enterobacteria phage SMP2		(SMP2)

GENUS "P1-LIKE VIRUSES"

Type Species ***Enterobacteria phage P1***

DISTINGUISHING FEATURES

Virions produce head size variants. DNA is circularly permuted and terminally redundant, and is packaged from a *pac* site. The genetic map is linear, and phages can carry out generalized transduction. Prophages persist as plasmids.

VIRION PROPERTIES

MORPHOLOGY

Virions have icosahedral heads ~85 nm in diameter and produce head size variants (~47-65 nm). Tails measure 228 x 18 nm in Enterobacteria phage P1 (P1) and vary in length from 170-240 nm in other members of the genus (i.e., Enterobacteria phage P1D (P1D) and Aeromonas phage 43 (43)). Tails have base plates and six 90 nm-long kinked fibers. Particles with contracted tails aggregate side-by-side by means of exposed tail cores.

PHYSICOCHEMICAL AND PHYSICAL PROPERTIES

Phage P1 virion buoyant density is 1.48 g/cm^3.

NUCLEIC ACID

Genomes are ~100 kbp and have a G+C content of 46%.

PROTEINS

Virions contain 24-28 constitutive proteins (10-220 kDa), including a major coat protein of 44 kDa.

LIPIDS

None known.

CARBOHYDRATES

None known.

GENOME ORGANIZATION AND REPLICATION

The genetic map is linear and includes ~100 genes; related functions are often distributed over several genome regions. Prophage DNA is circular. The genome is circularly permuted and terminally redundant (8-12%), and includes a recombinational hot spot (*lox-cre*). The genome also has an invertible tail fiber segment of ~4 kbp (C-loop) that is homologous to the G-loop of Enterobacteria phage Mu (Mu). Virion DNA circularizes after injection. Replication starts at a single site and has a phase of Θ replication and then a phase of σ structures, suggesting a rolling-circle mechanism. Progeny DNA is cut from concatemers at a *pac* site.

ANTIGENIC PROPERTIES

Phages P1, P2, and Mu share tail fiber antigens.

BIOLOGICAL PROPERTIES

Phages are temperate, can carry out generalized transduction, and infect enteric and related Gram-negative bacteria. Prophages are maintained as plasmids (1-2 copies per cell) or integrate (rarely) at specific sites into the bacterial chromosome. Prophages are

weakly UV inducible. The invertible C-loop codes for two sets of tail fiber genes and provides a means of extending host range.

List of Species Demarcation Criteria in the Genus

Species differ in host range and tail length (phage P1, 228 nm; phage P1D, 240 nm; and phage 43, 170 nm).

List of Species in the Genus

Species names are in green italic script; strain names and synonyms are in black roman script; tentative species names are in blue roman script. Sequence accession numbers, and assigned abbreviations ( ) are also listed.

Species in the Genus

Aeromonas phage 43
- Aeromonas phage 43 (43)

Enterobacteria phage P1
- Enterobacteria phage P1 (P1)
- Enterobacteria phage P1D (P1D)
- Enterobacteria phage P7 (P7)

Tentative Species in the Genus

- Acetobacter phage pKG-2 (pKG-2)
- Acetobacter phage pKG-3 (pKG-3)
- Enterobacteria phage D6 (D6)
- Enterobacteria phage ϕW39 (ϕW39)
- Enterobacteria phage j2 (j2)
- Pseudomonas phage PP8 (PP8)
- Vibrio phage ϕVP25 (ϕVP253)
- Vibrio phage P147 (P147)

Genus "P2-like viruses"

Type Species *Enterobacteria phage P2*

Distinguishing Features

Virion DNA has cohesive ends. Transcription of virion structural genes is divergent.

Virion Properties

Morphology

Phage heads are icosahedral, measure ~60 nm in diameter, and consist of 72 capsomers (60 hexamers and 12 pentamers; T=7). Tails measure 135 x 18 nm and have a collar and 6 short kinked fibers.

Physicochemical and Physical Properties

Virion Mr is 58 x 10^6; buoyant density in CsC1 is 1.43 g/cm^3; and S_{20W} is 283S.

Nucleic Acid

Genomes are ~34 kbp, are ~48% of particle weight, and have a G+C content of 52%. The genomes of P2 and the related phages (HP1, HP2, 186, ϕCTX, Fels-2 and K139) have been sequenced.

Proteins

Virions contain at least 13 structural proteins (20-94 kDa), including 420 copies of the major CP (39 kDa). Amino acid sequences of the proteins of phages with completely sequenced genomes are available at GenBank and EMBL.

LIPIDS
None known.

CARBOHYDRATES
None known.

GENOME ORGANIZATION AND REPLICATION

The genetic map is linear and non-permuted, has *cos* sites, and includes ~40 genes. Transcription starts in the right half of the genome, has two phases (early and late), and depends on host RNA polymerase. Replication starts at a single site, is unidirectional, and follows a modified rolling-circle mechanism. DNA is cut from concatemers at specific sites during packaging into proheads.

ANTIGENIC PROPERTIES

Virions of phages P2, P1 (Genus "P1-like viruses"), and Mu (Genus "Mu-like viruses") share tail fiber antigens.

BIOLOGICAL PROPERTIES

Phages are temperate, adsorb to the cell wall, and infect enteric and related Gram-negative bacteria. Prophages may integrate at ~10 specific sites of the bacterial chromosome and are not UV-inducible. P2 acts as a "helper" for defective Enterobacteria phage P4 (P4) in by providing head and tail genes for P4 propagation.

LIST OF SPECIES DEMARCATION CRITERIA IN THE GENUS

Species differ in host range and DNA homology.

LIST OF SPECIES IN THE GENUS

Species names are in green italic script; strain names and synonyms are in black roman script; tentative species names are in blue roman script. Sequence accession numbers, and assigned abbreviations ( ) are also listed.

SPECIES IN THE GENUS

Enterobacteria phage P2		
Enterobacteria phage P2	[AF063097]	(P2)
Haemophilus phage HP1		(HP1)
Haemophilus phage HP1	[U24159]	(HP1)
Haemophilus phage S2		(S2)

TENTATIVE SPECIES IN THE GENUS

Aeromonas phage 29		(29)
Aeromonas phage 37		(37)
Agrobacterium phage PIIBNV6		(PIIBNV6)
Caulobacter phage ΦCr24		(ΦCr24)
Enterobacteria phage 186	[U32222]	(186)
Enterobacteria phage 299		(299)
Enterobacteria phage Beccles		(Beccles)
Enterobacteria phage Pk2		(Pk2)
Enterobacteria phage Wϕ		(Wϕ)
Haemophilus phage HP2	[AY027935]	(HP2)
Pasteurella phage AU		(AU)
Pseudomonas phage ϕCTX	[AB008550]	(ϕCTX)
Pseudomonas phage PsP3		(PsP3)
Rhizobium phage ϕgal-1/R		(ϕgal-1/R)
Rhizobium phage WT1		(WT1)
Salmonella phage Fels-2		(Fels-2)
Vibrio phage X29		(X29)
Vibrio phage K139	[AF125163]	(K139)

GENUS "MU-LIKE VIRUSES"

Type Species *Enterobacteria phage Mu*

DISTINGUISHING FEATURES

The viral genome contains two terminal, variable sequences of host DNA. It is able to integrate at virtually any site of the host chromosome and generate a wide range of mutations due to its unique mode of DNA replication (replicative transposition). Integration is required for establishment of lysogeny and DNA replication during lytic development.

VIRION PROPERTIES

MORPHOLOGY

Virions have icosahedral heads ~60 nm in diameter, contractile tails ~120 x 18 nm, a baseplate, and 6 short fibers.

PHYSICOCHEMICAL AND PHYSICAL PROPERTIES

Virion buoyant density in CsC1 is 1.49 g/cm^3.

NUCLEIC ACID

The phage Mu genome is ~36-40 kbp, corresponding to ~40% of particle weight, has a G+C content of 50-51%, and has been completely sequenced.

PROTEINS

Particles have 12 structural proteins (20-76 kDa), including the major coat protein (33 kDa).

LIPIDS

None known.

CARBOHYDRATES

None known

GENOME ORGANIZATION AND REPLICATION

The phage Mu genetic map is linear and includes 55 genes. Related functions cluster together. The genome is non-permuted and heterogeneous, consisting of 36,717 bp of phage-specific DNA flanked at both ends by 0.5-3 kbp of covalently bound segments of host DNA. It contains an invertible segment of ~3 kbp (the G-loop) that is homologous to the invertible C-segment of Enterobacteria phage P1 (P1) DNA. Infecting DNA undergoes either lytic or lysogenic development. Both modes require (random) integration of phage DNA into host DNA, mediated by a phage-encoded transposase. Transcription starts at the left end of the genome and depends on host RNA polymerase. Replication may start at either end of the genome, is semi-conservative, and occurs during transposition into new integration sites. Phage heads package integrated, non-concatemeric phage DNA and adjacent host DNA by an atypical headful mechanism. Progeny phage DNA is cut out of the host DNA 100-200 bp away from a phage-coded *pac* site.

ANTIGENIC RELATIONSHIPS

Enterobacteria phages Mu, D108, P1, and P2 have some common tail fiber antigens.

BIOLOGICAL PROPERTIES

Viruses are temperate and can carry out generalized transduction, and infect enteric and (possibly) other related Gram-negative bacteria. The invertible G-loop codes for two sets of tail fibers which provides a means of extending host range. Prophages are not inducible by UV light.

LIST OF SPECIES DEMARCATION CRITERIA IN THE GENUS

Not applicable.

LIST OF SPECIES IN THE GENUS

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SPECIES IN THE GENUS

Enterobacteria phage Mu

Enterobacteria phage D108		(D108)
Enterobacteria phage Mu	[AF083977]	(Mu)
(Enterobacteria phage Mu-1)		

TENTATIVE SPECIES IN THE GENUS

Pseudomonas phage B3	(B3)
Pseudomonas phage B39	(B39)
Pseudomonas phage D3112	(D3112)
Pseudomonas phage PM69	(PM69)
Vibrio phage VcA3	(VcA3)

GENUS "SPO1-LIKE VIRUSES"

Type Species ***Bacillus phage SPO1***

NOTE ON NOMENCLATURE

The "O" in the name SPO1 derives from Osaka, where the phage was isolated. It is therefore properly the letter "O" (oh) and not the numeral "0" (zero). However, in the published literature and earlier versions of this taxonomy, the names "SPO1" and SP01" are used interchangeably to refer to the same virus. As a consequence, database searches for SPO1 should always be done with both forms of the name.

DISTINGUISHING FEATURES

Members of this genus are large lytic phages. Heads show conspicuous capsomers. DNA is terminally redundant (but not circularly permuted), contains 5-hydroxymethyluracil, and codes for a type A (*E. coli* Pol I) DNA polymerase.

VIRION PROPERTIES

MORPHOLOGY

Virions have isometric, icosahedral heads of ~94 nm in diameter with conspicuous capsomers. Contractile tails measure 150 x 18 nm and have a small collar and a 60 nm wide baseplate.

PHYSICOCHEMICAL AND PHYSICAL PROPERTIES

SPO1 virion Mr is ~180 x 10^6; buoyant density in CsC1 is 1.54 g/cm^3; and S_{20w} is 794S.

NUCLEIC ACID

Genomes are ~140-160 kbp and those that have been measured have a G+C content of 42%. Thymine is replaced by 5-hydroxymethyluracil in SPO1 DNA.

PROTEINS

Virions contain ~53 proteins (16 in the head and 28 in the tail and baseplate). Type A DNA polymerase is encoded in the phage genome.

LIPIDS

None known.

CARBOHYDRATES
None known.

GENOME ORGANIZATION AND REPLICATION

The genetic map is linear and may contain as many as 200 genes. Related functions cluster together. The genome has a terminally redundancy of ~12 kbp, but is not circularly permuted. After infection, host syntheses are shut off and replication starts at two SPO1 DNA sites. Phage-encoded sigma factors are used to modify and appropriate host RNA polymerase for phage syntheses.

BIOLOGICAL PROPERTIES

Phages are virulent and so far have been characterized only from *Bacillus* and *Lactobacillus*. Distribution is worldwide.

LIST OF SPECIES DEMARCATION CRITERIA IN THE GENUS

Not applicable.

LIST OF SPECIES IN THE GENUS

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SPECIES IN THE GENUS

Bacillus phage SPO1

Bacillus phage SPO1	(SPO1)
Bacillus phage SP8	(SP8)
Bacillus phage SP82	(SP82)

TENTATIVE SPECIES IN THE GENUS

Bacillus phage AR1	(AR1)
Bacillus phage GS1	(GS1)
Bacillus phage I9	(I9)
Bacillus phage NLP-1	(NLP-1)
Bacillus phage SP5	(SP5)
Bacillus phage SW	(SW)
Bacillus phage ϕe	(ϕe)
Bacillus phage ϕ25	(ϕ25)
Bacillus phage 2C	(2C)
Lactobacillus phage 222a	(222a)

GENUS "ϕH-LIKE VIRUSES"

Type Species ***Halobacterium phage ϕH***

DISTINGUISHING FEATURES

The host is an archaeon. Phage DNA has a *pac* site, and is circularly permuted and terminally redundant.

VIRION PROPERTIES

MORPHOLOGY
Virions have isometric heads 64 nm in diameter, tails of 170 x 18 nm, and short tail fibers.

PHYSICOCHEMICAL AND PHYSICAL PROPERTIES
Not known.

NUCLEIC ACID
Genomes are ~59 kbp in size and have a G+C content of 64%. Cytosine is replaced by 5-methylcytosine.

PROTEINS
Virions have three major proteins (20, 45, and 70 kDa) and 10 minor components.

LIPIDS
None known.

CARBOHYDRATES
None known.

GENOME ORGANIZATION AND REPLICATION

Genomes are partially circularly permuted and ~3% terminally redundant and have a *pac* site. Halobacterium phage ϕH (ϕH) DNA is markedly variable. All DNAs harbor one or more insertion elements, and also include ordinary deletion and insertion variants. Early transcription is regulated by viral antisense mRNA. Replication results in formation of concatemers. Cutting of concatemers at *pac* sites is inaccurate and produces DNA molecules with imprecisely defined ends.

ANTIGENIC PROPERTIES

Not known.

BIOLOGICAL PROPERTIES

Phages are temperate, specific for halobacteria, and require the presence of 3.5 M NaCl. Prophages persist as plasmids and are not UV-inducible.

LIST OF SPECIES DEMARCATION CRITERIA IN THE GENUS

Not applicable.

LIST OF SPECIES IN THE GENUS

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SPECIES IN THE GENUS

Halobacterium phage ϕH

Halobacterium phage ϕH (ϕH)

TENTATIVE SPECIES IN THE GENUS

Halobacterium phage Hs1 (Hs1)

LIST OF UNASSIGNED VIRUSES IN THE FAMILY

Acinetobacter phage A3/2 (A3/2)
Acinetobacter phage A10/45 (A10/45)
Acinetobacter phage BS46 (BS46)
Acinetobacter phage E14 (E14)
Actinomycetes phage SK1 (SK1)
Actinomycetes phage 108/016 (108/016)
Aeromonas phage Aeh2 (Aeh2)
Aeromonas phage 51 (51)
Aeromonas phage 59.1 (59.1)
Alcaligenes phage A6 (A6)
Bacillus phage Bace-11 (Bace-11)
Bacillus phage CP-54 (CP-54)
Bacillus phage G (G)

Bacillus phage MP13		(MP13)
Bacillus phage PBS1		(PBS1)
Bacillus phage SP3		(SP3)
Bacillus phage SP10		(SP10)
Bacillus phage SP15		(SP15)
Bacillus phage SP50		(SP50)
Bacillus phage Spy-2		(Spy-2)
Bacillus phage Spy-3		(Spy-3)
Bacillus phage SST		(SST)
Clostridium phage HM3		(HM3)
Clostridium phage CEβ		(CEβ)
Coryneform phage A19		(A19)
Cyanobacteria phage AS-1		(AS-1)
Cyanobacteria phage N1		(N1)
Cyanobacteria phage S-6(L)		(S-6(L))
Enterobacteria phage FC3-9		(FC3-9)
Enterobacteria phage Kl9		(Kl9)
Enterobacteria phage ΦP27	[AJ298298]	(ΦP27)
Enterobacteria phage 01		(01)
Enterobacteria phage ViI		(ViI)
Enterobacteria phage ϕ92		(ϕ92)
Enterobacteria phage 121		(121)
Enterobacteria phage 16-19		(16-19)
Enterobacteria phage 9266		(9266)
Halorubrum phage HF2	[AF222060]	(HF2)
Lactobacillus phage fri		(fri)
Lactobacillus phage hv		(hv)
Lactobacillus phage hw		(hw)
Listeria phage A511		(A511)
Listeria phage 4211		(4211)
Mollicutes phage Br1		(Br1)
Mycobacterium phage I3		(I3)
Mycobacterium phage Bxz1	[AY129337]	(Bxz1)
Pseudomonas phage PB-1		(PB-1)
Pseudomonas phage PS17		(PS17)
Pseudomonas phage ϕKZ	[AF399011]	(ϕKZ)
Pseudomonas phage ϕW-14		(ϕW-14)
Pseudomonas phage 12S		(12S)
Rhizobium phage CM1		(CM1)
Rhizobium phage CT4		(CT4)
Rhizobium phage m		(m)
Shigella phage SfV	[AF339141]	(SfV)
Xanthomonas phage XP5		(XP5)
Vibrio phage kappa		(kappa)
Vibrio phage 06N-22P		(06N-22P)
Vibrio phage VP1		(VP1)
Vibrio phage II		(II)

PHYLOGENETIC RELATIONSHIPS WITHIN THE FAMILY

Not available.

SIMILARITY WITH OTHER TAXA

See *Caudovirales* chapter.

DERIVATION OF NAMES

Myo: from Greek *my*, *myos*, "muscle", referring to the contractile tail.

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