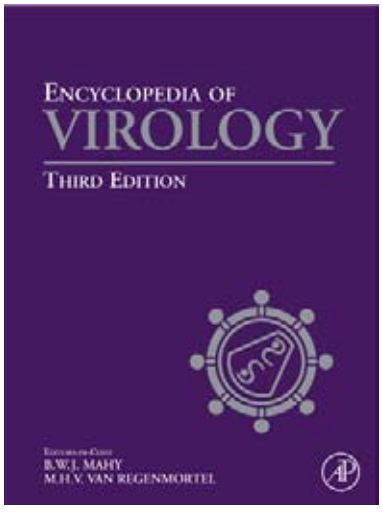

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Algal Viruses

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Glossary

Algal viruses Viruses infecting eukaryotic algae.
HaRNAV A positive-sense single-stranded RNA virus infecting the bloom-forming microalga *Heterosigma akashiwo* (Raphidophyceae).
VLPs Virus-like particles that are identified by transmission electron microscopy.

Introduction

With the realization during the last two decades that viruses are highly abundant in various aquatic environments (both marine and freshwater), interest in aquatic viruses significantly increased. Viruses are now recognized as important biological agents not only regulating population dynamics, succession, and diversity of the host organisms in marine systems, but also influencing the functioning of aquatic food webs and biogeochemical cycling (energy and matter fluxes). Organisms within the microbial food web can become infected by viruses, including eukaryotic algae, cyanobacteria, and heterotrophic protists. Indeed, viruses or virus-like particles (VLPs) have been found in more than 60 algal species for 12 recognized classes of eukaryotic algae; to date, about 40 algal viruses have been isolated and characterized (**Table 1**). Although their classification and nomenclature has been improved on, only two algal virus families are officially established to date: *Phycodnaviridae* and *Marnaviridae*. The family *Phycodnaviridae* comprises large genome-sized double-stranded DNA (dsDNA) viruses infecting eukaryotic algae, and the family *Marnaviridae* was just recently established based on the analysis of a positive-sense single-stranded RNA (ssRNA) virus infecting a raphidophyte *Heterosigma akashiwo*.

Most recently, four algal viruses were discovered that do not belong to the above two virus families – RsRNAV, HcRNAV, MpRV and CsNIV; they are infectious to the single-celled marine phytoplankton species *Rhizosolenia setigera*, *Heterocapsa circularisquama*, *Micromonas pusilla*, and *Chaetoceros salsugineum*, respectively. In this article, we summarize the characteristics of these algal viruses, and discuss their putative classification.

ssRNA Viruses Infecting Eukaryotic Algae

RsRNAV

Rhizosolenia setigera RNA virus (RsRNAV) is the first diatom-infecting virus that was isolated and characterized. It is a positive-sense ssRNA virus infecting the bloom-forming diatom *R. setigera*. Viral replication occurs within the host cytoplasm, the virus particle is icosahedral, lacking a tail, and 32 nm in diameter (**Figure 1**).

The RsRNAV genome is a 3′ polyadenylated linear RNA lacking a cap structure at the 5′ terminus. Although the genome size was initially estimated to be 11.2 kbp using denaturing gel electrophoresis, full genome sequencing later revealed that the genome is 8877 nt in length, excluding the polyA tail (DDBJ accession number: AB243297). This may be due to the additional length of the 3′ poly(A) tail or the addition of a viral genome-linked protein (VPg). Further analysis is required to explain this disagreement in genome length estimates. RsRNAV genome has two open reading frames (ORFs): ORF-1 coding for a putative polyprotein containing the RNA helicase domain and the RNA-dependent RNA polymera (RdRp) domain, and ORF-2 encoding at least three major

Table 1 Viruses infecting eukaryotic algae

Virus	*Host*	*Size (nm)*	*Genome type*	*Genome size (kbp)*
Viruses infecting unicellular algae				
BtV	*Aureococcus anophagefferens*	140	dsDNA	
CbV	*Chrysochromlina brevifilum*	145–170	dsDNA	
CdDNAV[a]	*Chaetoceros debilis*	30	ssDNA (fragmented?)	
CeV	*Chrysochromlina ericina*	160	dsDNA	510
CgNIV[a]	*Chaetoceros* cf. *gracilis*	30	ssDNA (?)	3–4
Chlorella virus (e.g., ATCV-1, -2)	*Chlorella* SAG 3.83 (symbiont of *Acanthocystis turfacea*)	140–190	dsDNA	288
Chlorella virus (e.g., PBCV-1, NY-2A, AR158)	*Chlorella* NC64A (symbiont of *Paramecium bursaria*)	190	dsDNA	331–369
Chlorella virus (e.g., MT325, FR483)	*Chlorella* Pbi (symbiont of *Paramecium bursaria*)	140–150	dsDNA	314–321
Chlorella virus (e.g., HVCV)	*Chlorella*-like alga (symbiont of *Hidra viridis*)	170–180	dsDNA	200
CnRNAV[a]	*Chaetoceros neogracilis*	31	ssRNA	
CsNIV	*Chaetoceros salsugineum*	38	(ss + ds)DNA	6
CspNIV	*Chaetoceros* cf. *gracilis*	25		
CsRNAV[a]	*Chaetoceros socialis*	~30	RNA (?)	
EhV	*Emiliania huxleyi*	170–200	dsDNA	410–415
HaNIV[a]	*Heterosigma akashiwo*	30	ssDNA	
HaV	*Heterosigma akashiwo*	202	dsDNA	294
HaRNAV	*Heterosigma akashiwo*	25	ssRNA	9.1
HcRNAV	*Heterocapsa circularisquama*	30	ssRNA	4.4
HcV	*Heterocapsa circularisquama*	197	dsDNA	356
MpRV (originally MpRNAV-01B)	*Micromonas pusilla*	50–60	dsRNA	24.6
MpV (e.g., MpV-PL1, PB7)	*Micromonas pusilla*	115	dsDNA	200
MpV[a] (e.g., MpV-02T,-03T)	*Micromonas pusilla*	~110–120	dsDNA	191–217
MpV[a] (e.g., MpV-01T, 15T)	*Micromonas pusilla*	~70–90		
PgV Group I	*Phaeocystis globosa*	150	dsDNA	466 ± 4
PgV Group II	*Phaeocystis globosa*	100	dsDNA	177 ± 3
PgV-102P	*Phaeocystis globosa*	98	dsDNA	176
PoV	*Pyramimonas orientalis*	180–220	dsDNA	560
PpV	*Phaeocystis pouchetii*	130–160	dsDNA	485
RsRNAV	*Rhizosolenia setigera*	32	ssRNA	11.2
Viruses infecting multicellular algae				
EsV	*Ectocarpus siliculosus*	130–150	dsDNA	336
EfasV	*Ectocarpus fasciculatus*	135–140	dsDNA	340
FlexV	*Feldmannia simplex*	120–150	dsDNA	170
FirrV	*Feldmannia irregularis*	140–170	dsDNA	180
FsV	*Feldmannia* sp.	150	dsDNA	170
HincV	*Hincksia hinckiae*	140–170	dsDNA	220
MclaV	*Myriotrichia clavaeformis*	170–180	dsDNA	340
PlitV	*Pilayella littoralis*	161	dsDNA	280

[a]Y Tomaru, Y Eissler, Y Shirai, CPD Brussaard, JE Lawrence, personal communication.

capsid proteins (MCPs) with molecular mass of 41.5, 41.0, and 29.5 kDa (**Figure 2**). Although a significant similarity in amino acid sequences of the nonstructural and structural proteins between RsRNAV and HaRNAV was found by BLAST search, these viruses differ in the number of ORFs (two and one, respectively) and AU content (63.7% and 53.1%, respectively); hence, RsRNAV was concluded not to be a member of the family *Marnaviridae*. Phylogenetic analysis of the amino acid sequences of the RNA helicase and RdRp domains suggests that RsRNAV belongs to a new previously unrecognized virus group (**Figure 3**). Smaller unidentified RNA molecules ranging in size of 0.6, 1.2, and 1.5 kbp were occasionally included in RsRNAV virions; one possibility is that they are subgenomic RNAs.

RsRNAV has a high degree of strain specificity. One-step growth experiment using an exponentially growing host culture showed 3.1×10^3 infectious units are released from an infected host cell within 48 h post infection. When a stationary phase culture was used as host for the one-step growth experiment, the burst size decreased to 1.0×10^3 infections units per cell. This shows that viral propagation

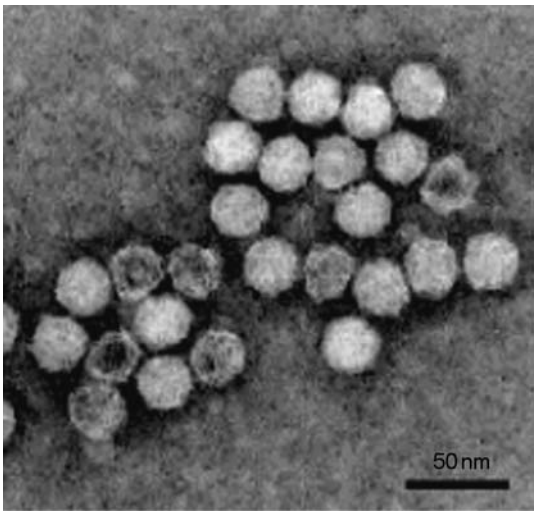

Figure 1 Negatively stained RsRNAV particles. Reprinted from Nagasaki K, Tomaru Y, Katanozaka N, *et al*. (2004) Isolation and characterization of a novel single-stranded RNA virus infecting the bloom-forming diatom *Rhizosolenia setigera*. *Applied and Environmental Microbiology* 70: 704–711, with permission from American Society for Microbiology.

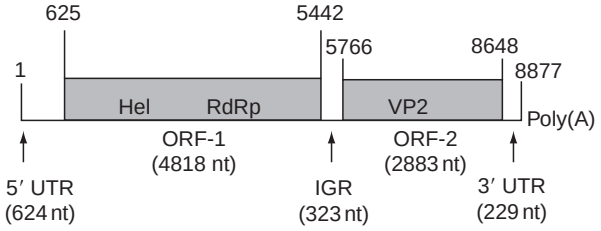

Figure 2 Schematic genome structure of RsRNAV. Numbers indicate base positions from the 5′ terminus in the nucleotide sequence. Hel, RNA helicase domain; RdRp, RNA-dependent RNA polymerase domain; UTR, untranslated region; IGR, intergenic region. Reprinted from Shirai Y, Takao Y, Mizumoto H, *et al*. (2006) Genomic and phylogenetic analysis of a single-stranded RNA virus infecting Rhizosolenia setigera (Stramenopiles: Bacillariophyceae). *Journal of the Marine Biological Association of the United Kingdom* 86: 475–483, with permission from The Marine Biological Association of the UK.

is considerably affected by the physiological condition of the host cells. Although the entry mechanism of RsRNAV into the host cell is unknown, the host's frustule pores (ellipses; 91 nm × 73 nm) are considered to be a possible route of infection.

HcRNAV

Heterocapsa circularisquama RNA virus (HcRNAV) is a positive-sense ssRNA virus infecting the bivalve-killing bloom-forming dinoflagellate *H. circularisquama*. This virus is icosahedral, ~30 nm in diameter, and propagates in the host cytoplasm often forming a crystalline array (**Figure 4**). Its genome is linear positive-sense ssRNA ~4.4 kbp long, lacking 5′ cap structure and 3′ polyA tail, and has a strong stem–loop structure at the 3′ end (**Figure 5**).

HcRNAV clones can be divided into two ecotypes (types UA and CY) based on their intraspecies host specificity patterns. Each type shows its own strain-specific infectivity that is complementary to each other; that is, the *H. circularisquama* strains sensitive to HcRNAV type UA were resistant to HcRNAV type CY, and vice versa, showing that HcRNAV is not species specific, but strain specific. These two HcRNAV ecotypes can coexist in natural water. Typical HcRNAV clones of type UA and CY (HcRNAV34 and 109, respectively) were fully sequenced (DDBJ accession numbers: AB218608 and AB218609, respectively); they are ~97% identical at the nucleotide sequence level. Each genome has two ORFs (**Figure 5**). ORF-1 encodes a putative polyprotein having at least the serine protease domain and the RdRp domain, but no RNA helicase domain was identified. A specific 15 nt deletion was found in about half of the tested virus clones. This, however, is not involved in determining the intraspecies host specificity. ORF-2 coding for the single MCP is unlikely a polyprotein gene because of the molecular mass directly estimated by sodium dodecyl sulfate (SDS) polyacrylamide gel electrophoresis is in good agreement with the value predicted by the deduced amino acid sequence of ORF-2. Between the two virus clones tested, the stem–loop structures at the 3′ end are different in stem length and loop size; this may affect the replication efficiency.

Similarity analysis for the deduced amino acid sequences of ORF-1 revealed that HcRNAV is evolutionarily quite distant from any of the land and aquatic viruses that have been genetically studied. This is also supported by a phylogenetic analysis of the RdRp amino acid sequence (**Figure 3**(b)). Although HcRNAV shares some characteristics with the typical marnavirus HaRNAV in infectivity (lytic to marine eukaryotic microalgae) and genome structure (a linear positive-sense ssRNA), they still differ in the number of ORFs (two and one, respectively) and 3′ polyadenylation of the genome RNA (polyadenylated and nonpolyadenylated, respectively). Hence, HcRNAV is not a member of the family *Marnaviridae*.

Genomic comparison revealed complementary host ranges of the two HcRNAV ecotypes (UA and CY: mentioned above) which may be related to the amino acid substitution patterns in ORF-2, the MCP-encoding gene. In addition, the tertiary structure of the MCPs predicted by using computer modeling indicated many of the amino acid substitutions were located in regions on the outside of the viral capsid proteins exposed to the ambient water environments. This suggests that the intraspecies host specificity of HcRNAV is determined by small structural differences of the viral surface that may affect its binding affinity to the host cell and the uncoating process. The results of the transfection experiment also supported this idea: (1) the intraspecies host specificity of HcRNAV

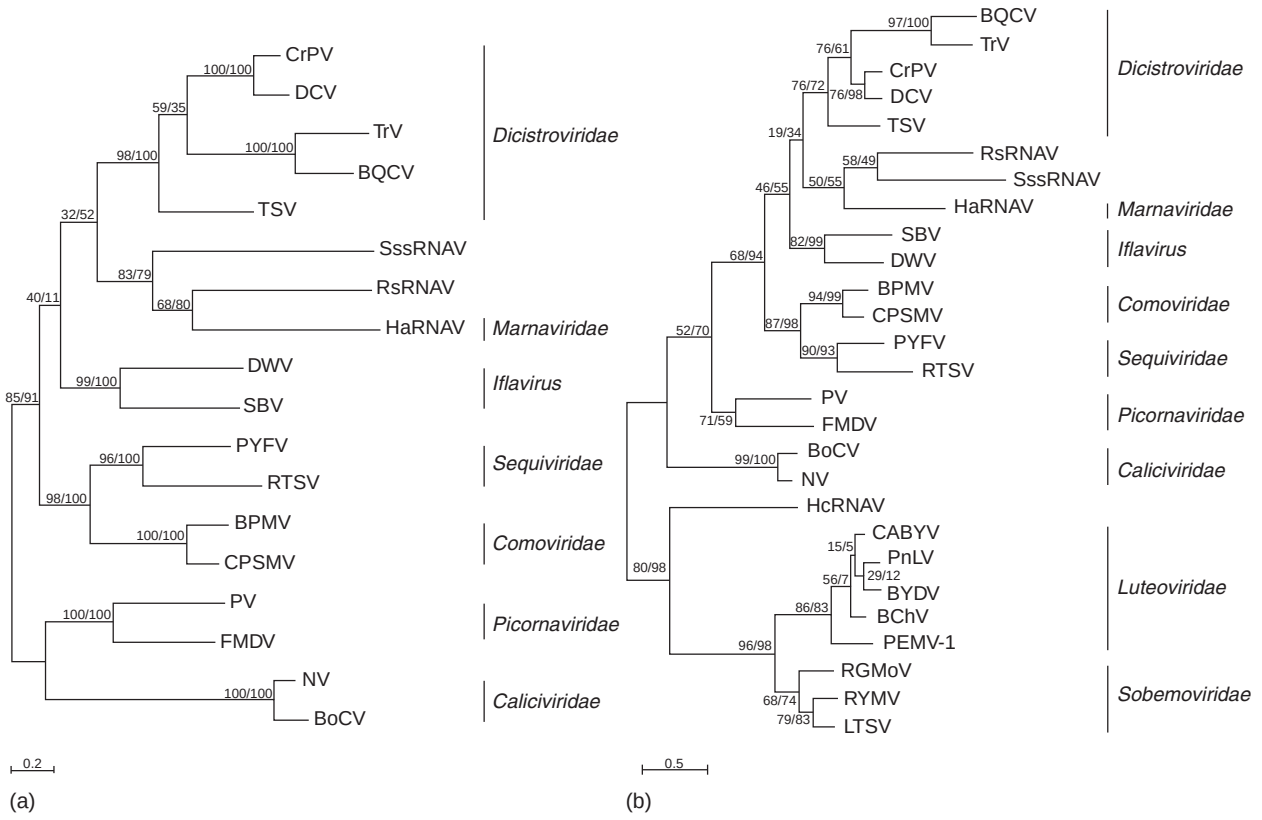

Figure 3 Maximum likelihood (ML) trees calculated from confidently aligned regions of amino acid sequences of concatenated amino acid sequences of RNA helicase domain and RNA-dependent RNA polymerase (RdRp) domain (a), and of RdRp whole domain (b). ML bootstrap values (%) from 100 samples are shown at the nodes followed by bootstrap values based on neighbor-joining analysis (%) from 100 samples. The ML distance scale bars are shown. Amino acid sequences used for comparison in the analyses are as follows with the organism's scientific names, with abbreviations in parentheses if necessary, and the database accession numbers (referring to the US National Center for Biotechnology Information (NCBI) unless otherwise stated): beet chlorosis virus (BChV), AAK49964; bovine enteric calicivirus (BoCV), AJ011099; bean pod mottle virus (BPMV), NC__003496; black queen cell virus (BQCV), NC__003784; barley yellow dwarf virus (BYDV), BAA01054; cucurbit aphid-borne yellows virus (CABYV), CAA54251; cowpea severe mosaic virus (CPSMV), M83830; cricket paralysis virus (CrPV), NC__003924; drosophila C virus (DCV), NC__001834; deformed wing virus (DWV), NC__004830; foot-and-mouth disease virus (FMDV), P03306; heterosigma akashiwo RNA virus (HaRNAV), NC__005281; heterocapsa circularisquama RNA virus 109 (HcRNAV), DDBJ accession number: AB218609; lucerne transient streak virus (LTSV), NP__736596; Norwalk virus (NV), M87661; pea enation mosaic virus 1 (PEMV-1), AAA72297; poinsettia latent virus (PnLV), CAI34771; human poliovirus 1 Mahoney (PV), V01149; parsnip yellow fleck virus (PYFV), D14066; ryegrass mottle virus (RGMoV), NP__736587; rhizosolenia setigera RNA virus (RsRNAV), DDBJ accession number: AB243297; rice turgo spherical virus (RTSV), AAA66056; rice yellow mottle virus (RYMV), CAE81345; sacbrood virus (SBV), NC__002066; schizochytrium single-stranded RNA virus (SssRNAV), BAE47143; triatoma virus (TrV), NC__003783; taura syndrome virus (TSV), NC__003005. Reprinted with minor modification from Shirai Y, Takao Y, Mizumoto H, *et al*. (2006) Genomic and phylogenetic analysis of a single-stranded RNA virus infecting Rhizosolenia setigera (Stramenopiles: Bacillariophyceae). *Journal of the Marine Biological Association of the United Kingdom* 86: 475–483, with permission from The Marine Biological Association of the UK.

is determined by the upstream events of virus infection; (2) the host intracellular condition is permissive for HcRNAV replication even in incompatible host–virus combinations.

By the cross-reactivity test, *H. circularisquama* clones are also divided into two ecotypes according to the sensitivity spectra to the two HcRNAV ecotypes; however, the two host ecotypes are indistinguishable when comparing their morphology or the sequences of the internal spacer regions of the ribosomal RNA genes. These two host ecotypes coexist in natural water. Thus, there are at least two distinct (and independent) host/virus systems between *H. circularisquama* and HcRNAV; that is, multiple ecotypes of host and virus coexist within natural blooms of *H. circularisquama* and their combinations are regulated with exquisite molecular mechanisms.

dsRNA Viruses Infecting Eukaryotic Algae

MpRV

The micromonas pusilla reovirus (MpRV, originally abbreviated as MpRNAV) is a dsRNA virus infecting the cosmopolitan picoprasinophyte *M. pusilla* (**Figure 6**).

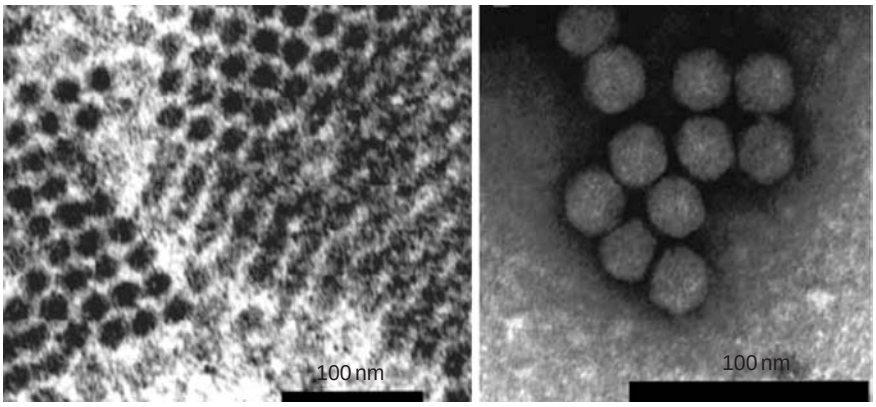

Figure 4 Transmission electron micrographs of intracellular crystalline array formation of HcRNAV (a) and negatively stained HcRNAV particles (b). Reprinted from Tomaru Y, Katanozaka N, Nishida K, *et al*. (2004) Isolation and characterization of two distinct types of HcRNAV, a single-stranded RNA virus infecting the bivalve-killing microalga Heterocapsa circularisquama. *Aquatic Microbial Ecology* 34: 207–218, with permission from Inter-Research Publication.

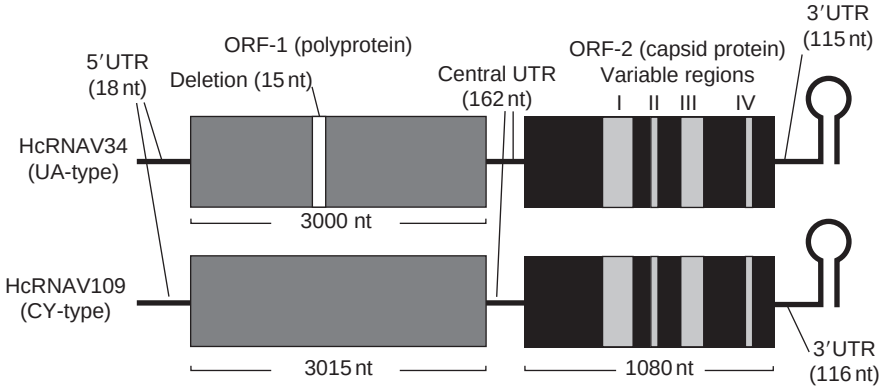

Figure 5 Schematic genome structure of HcRNAV34 and HcRNAV109. Note that the variable regions in ORF-2 are remarkably different between these two virus clones. Reprinted from Nagasaki K, Shirai Y, Takao Y, *et al*. (2005) Comparison of genome sequences of single-stranded RNA viruses infecting the bivalve-killing dinoflagellate *Heterocapsa circularisquama*. *Applied and Environmental Microbiology* 71: 8888–8894, with permission from American Society for Microbiology.

This is the first algal virus having a dsRNA genome that was isolated and characterized. The virus can coexist with a large genome-sized dsDNA virus infecting the same *M. pusilla* strain. It has a narrow host range, a latent period of 36 h (based on a one-step lytic virus growth cycle and transmission electron microscopy (TEM) enumeration of the virus particles), and sensitivity to temperatures $>35\,^{\circ}C$. Its genome is composed of 11 segments ranging between 741 and 5792 bp in length, with a total size of 25563 bp (**Figure 7** and **Table 2**). The polysegmented dsRNA genome of MpRV identified it as a member of the family *Reoviridae*, which was confirmed by sequence analysis, morphological and physiochemical properties. The size of intact virus particles (90–95 nm) is, however, large. The subcore particles size of 50 nm and its smooth surface indicate that MpRV belongs to non-turreted *Reoviridae*.

Comparison of the genome sequence of MpRV to those of characterized members of the family *Reoviridae* indicated that MpRV could not be classified within any of the existing genera of the family (including *Rotavirus* and *Aquareovirus* that both contain viruses with 11-segmented dsRNA genomes). The maximum amino acid identity with other *Reoviridae* proteins was 21%, which is compatible with differences existing between distinct genera.

Within the phylogenetic tree built with reovirus RdRp sequences, the branch of MpRV dissects the tree, separating the group of turreted and nonturreted viruses (**Figure 8**). As *M. pusilla* is evolutionarily older than the hosts of other members of the family *Reoviridae*, the topology of the tree suggests that the branch of MpRV could be ancestral. An interesting feature is the unusual length of segment 1, encoding a protein of 200 kDa (VP1). The many repeats within this sequence suggest that VP1 may have arisen from amino acid fragment duplication, followed by diversification of the sequence. The mechanism and the constraints, which have driven such an evolution, are not clear, although

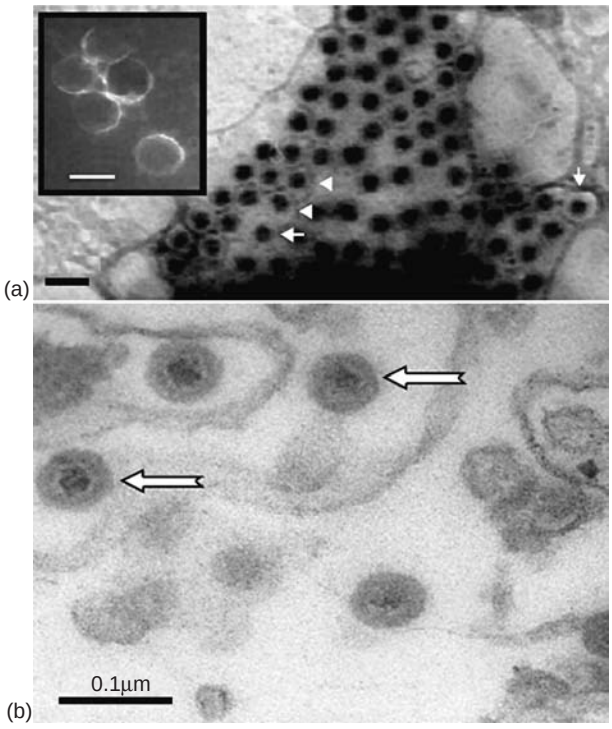

Figure 6 (a) Electron micrographs of MpRV. Particles pelleted from the clarified lysate of infected *M. pusilla*. Some particles (indicated by arrowheads) have a larger diameter. At the upper left corner (inset), core particles treated with 1.5 M $CaCl_2$ are shown to have a smooth outline (turrets are absent). Scale = 100 nm (main image); 50 nm (inset). (b) A TEM image of thin-sectioned *M. pusilla* cells infected with MpRV. The arrows point at intracellular virus particles consisting of a thick outer layer and a smaller electron-dense inner core. (a) Reprinted from Attoui H, Jaafar FM, Belhouchet M, *et al*. (2006) *Micromonas pusilla* reovirus: A new member of the family *Reoviridae* assigned to a novel proposed genus (*Mimoreovirus*). *Journal of General Virology* 87: 1375–1383, from the Society for General Microbiology. (b) Reprinted from Brussaard CP, Noordeloos AA, Sandaa RA, *et al*. (2004) Discovery of a dsRNA virus infecting the marine photosynthetic protist *Micromonas pusilla*. *Virology* 319: 280–291, with permission from Elsevier.

very recently a model of stem–loop formation (based on the crystal structure of the polymerase of a mammalian orthoreovirus) was proposed for explaining such duplications.

The structural proteins in the purified particles were analyzed and a protein having a molecular weight of approximately 200 kDa was identified in relatively intact particles. This size is compatible with the VP1 which should represent an additional coat protein layer. It is noteworthy that the sequence of VP1 bears many glycosylation sites and matched the envelope proteins of many bacteria and viruses.

Based on particle morphology and sequence analysis, MpRV was classified as the representative of a new genus within the family *Reoviridae*, for which the name *Mimoreovirus* has been proposed.

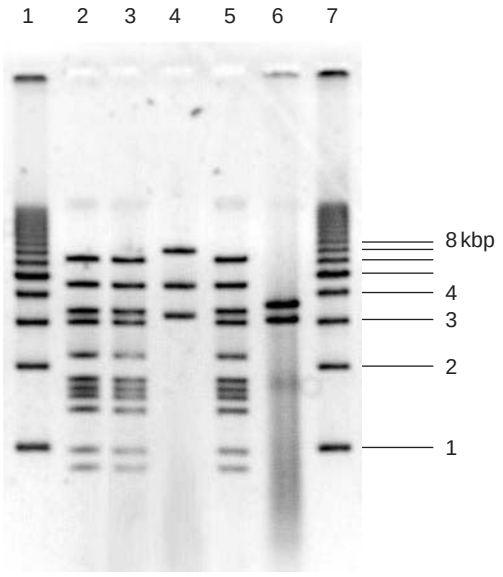

Figure 7 Total nucleic acid patterns of MpRV (lanes 2, 3, and 5). Molecular size standards: 1 kbp dsDNA Molecular Ruler (lanes 1 and 7), dsRNA bacteriophage Phi-6 (lane 4; segments of 6374, 4074, 2948 bp), and dsRNA Infectious Bursal Disease Virus IBDV-V4 (lane 6; segments of 3260 and 2827 bp). Precise lengths of the 11 dsRNA segments are shown in **Table 2**. Reprinted from Brussaard CP, Noordeloos AA, Sandaa RA, *et al*. (2004) Discovery of a dsRNA virus infecting the marine photosynthetic protist *Micromonas pusilla*. *Virology* 319: 280–291, with permission from Elsevier.

Table 2 Lengths of the dsRNA segments 1–11 of MpRV

Segment	*Segment length (bp)*
1	5792
2	4175
3	3129
4	2833
5	2027
6	1687
7	1556
8	1449
9	1296
10	878
11	741
Total	25 563

Adapted from Attoui H, Jaafar FM, Belhouchet M, *et al*. (2006) *Micromonas pusilla* reovirus: A new member of the family *Reoviridae* assigned to a novel proposed genus (*Mimoreovirus*). *Journal of General Virology* 87: 1375–1383, from the Society for General Microbiology.

ssDNA Viruses Infecting Eukaryotic Algae

CsNIV

Chaetoceros salsugineum nuclear inclusion virus (CsNIV) infects the small-sized (2.0–9.5 μm wide) diatom *C. salsugineum*, which forms short or long straight chains.

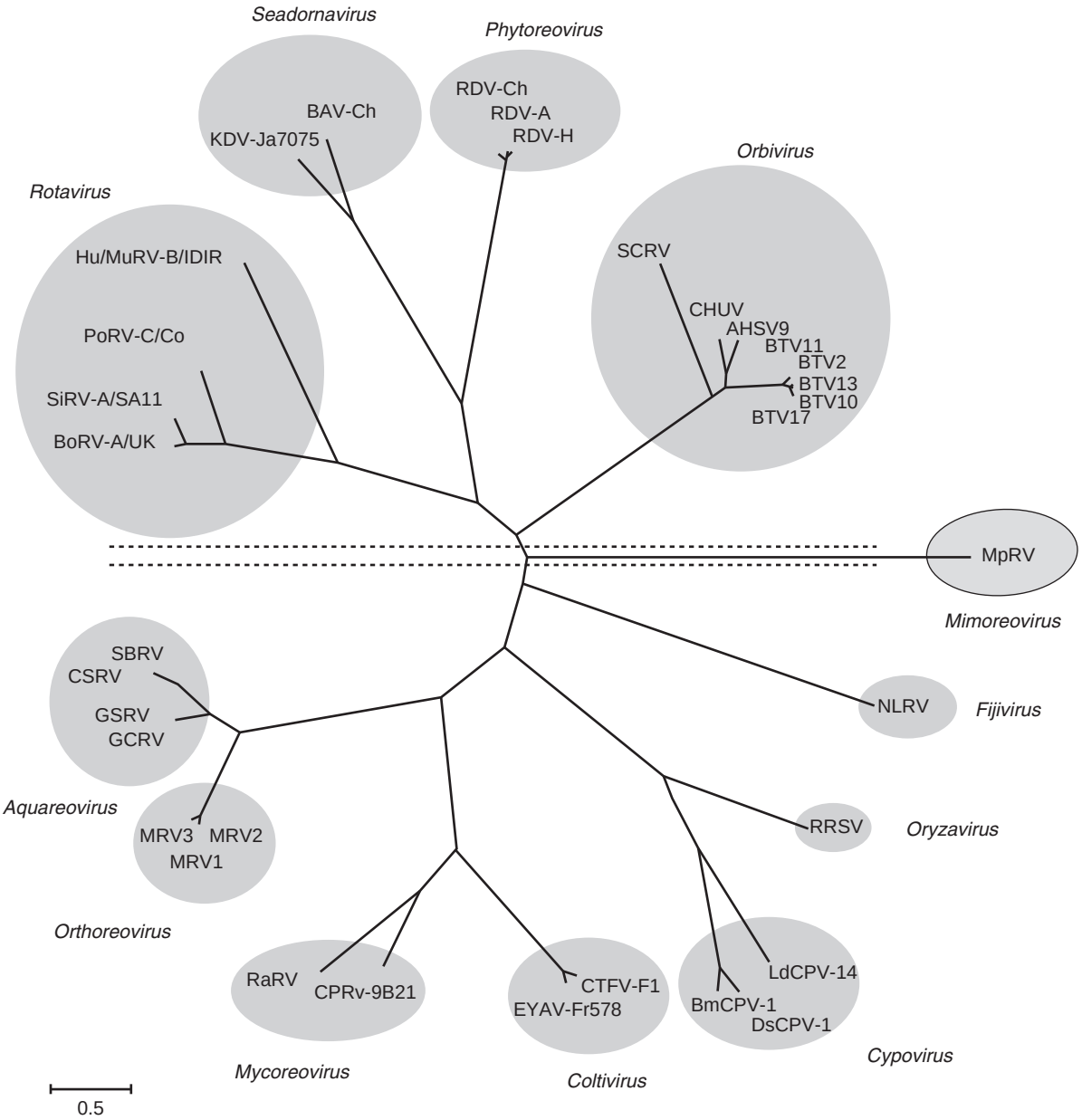

Figure 8 Phylogenetic relationships of MpRV to other members of the family *Reoviridae* based on the sequence of the putative RdRp. Neighbor-joining phylogenetic tree built with available polymerase sequences (using the Poisson-correction or gamma-distribution algorithms) for representative members of 11 genera of the family *Reoviridae*. Scale bar represents the number of substitutions per site. Reprinted from Attoui H, Jaafar FM, Belhouchet M, *et al*. (2006) Micromonas pusilla reovirus: A new member of the family Reoviridae assigned to a novel proposed genus (Mimoreovirus). *Journal of General Virology* 87: 1375–1383, with permission from the Society for General Microbiology.

Its bloom occurs in brackish lakes and estuarine waters. CsNIV is a ~38 nm icosahedral virus that replicates within the host nucleus (**Figure 9**). The genome structure is unlike that of other viruses that have been described to date; that is, it consists of a single molecule of covalently closed circular ssDNA (6000 nt (previously reported as 6005 nt)) as well as a segment of linear ssDNA (997 nt); the linear segment is complementary to a portion of the closed circle creating a partially double-stranded genome (**Figure 10**) (DDBJ accession number: AB193315). Sequence analysis revealed, within one of the six ORFs identified in the genome, only a low similarity to the replicase of circoviruses that have a covalently closed circular ssDNA genome. One-step growth experiment showed that ~330 infectious units are released from an infected cell within 24 h; however, considering that

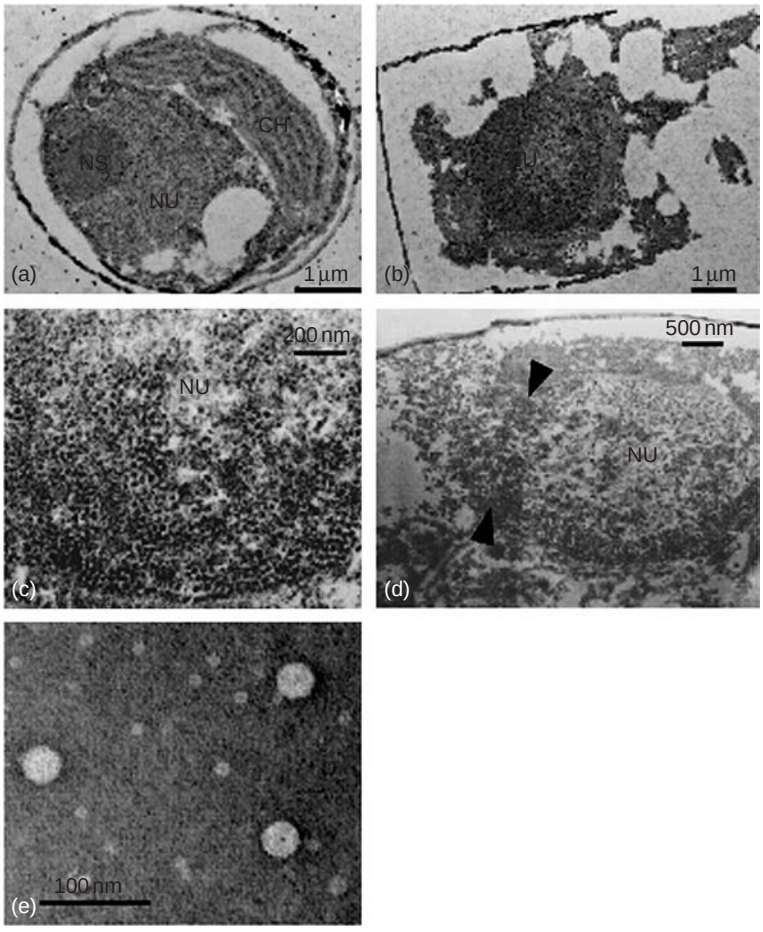

Figure 9 Transmission electron micrographs of *Chaetoceros salsugineum*. (a) Thin section of a healthy cell; (b) thin section of a cell 24 h after inoculation with CsNIV; (c) close-up view of intranuclear CsNIV particles in (b); (d) thin section of a CsNIV-infected cell in which the nuclear envelope was partially ruptured (arrowheads); (e) negatively stained CsNIV particles in the culture lysate. CH, a chloroplast; NU, a nucleus; NS, a nucleolus. Reprinted from Nagasaki K, Tomaru Y, Takao Y, *et al*. (2005) Previously unknown virus infects marine diatom. *Applied and Environmental Microbiology* 71: 3528–3535, with permission from American Society for Microbiology.

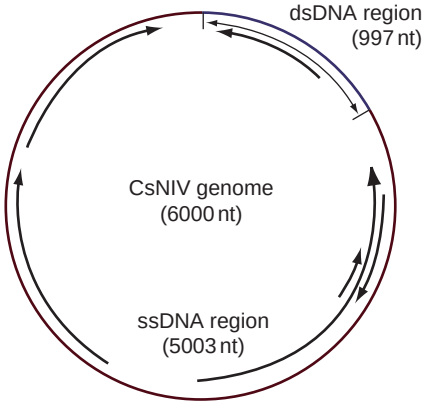

Figure 10 Schematic genome structure of CsNIV. Bold arrows indicate putative ORFs. Adapted from Nagasaki K, Tomaru Y, Takao Y, *et al*. (2005) Previously unknown virus infects marine diatom. *Applied and Environmental Microbiology* 71: 3528–3535, with permission from American Society for Microbiology.

several hundreds of virus particles were included even in a thin section for TEM observation, the resulting burst size is assumed to be underestimated. This may reflect aggregation of virions or dominance of defective particles.

Implications

Phytoplankton is important in maintaining oxygen levels in the atmosphere and sustaining the primary nutritional production of the aquatic environment. Its ecological dynamics is affected at different levels by various factors: physical factors (e.g., temperature, salinity, and irradiation), chemical factors (e.g., nutrients and metals), and biological factors (e.g., grazing, virus infection, and algicidal effects of bacteria). Among them, viruses are considered significant mortality agents, resulting in cell loss comparable

to grazing and/or sedimentation. Whether algae sink out, are grazed upon, or die due to viral-induced cell lysis has different implication for the flow of matter and energy in the aquatic ecosystems. Viral-mediated mortality will force the food web toward a more regenerative system as a result of enhanced production of dissolved organic matter.

Viral control of the algal host's population occurs for *M. pusilla*, a eukaryotic marine phytoplankter that is globally abundant but almost never forms massive blooms. *M. pusilla* belongs to the Prasinophyceae, a class of phytoplankton that is considered to have given rise to green algae and land plants. The dsRNA virus MpRV described earlier in this chapter has been found to coexist with large genome-sized dsDNA viruses, of which some infect the same clone of *M. pusilla*. The various different virus model systems infecting *M. pusilla* that are available in culture permit to investigate virus competition, intraspecies diversity, co-evolution, and genetic flux in more detail.

A good example of viral control on a finer scale, that is, the clonal composition of the algal host population, is the relationship between HcRNAV and its host *H. circularisquama*. Occurrence of *H. circularisquama* blooms in natural waters is accompanied by increased abundance of HcRNAV. Its abundance in the water column rapidly decreases following the termination of host blooms, but the viruses that are supplied to the sediment show only a very gradual decrease. Dynamics of the type UA viruses and the type CY viruses having complementary host ranges are different, supporting the idea that there are two independent host/virus systems between *H. circularisquama* and HcRNAV. Changes in abundance of each HcRNAV ecotype are considered to reflect the fluctuation of its suitable host ecotype *in situ*. By comparing the dynamics of HcRNAV and *H. circularisquama*, the amount of HcRNAV accumulated in the sediment just prior to the host's blooming season is suggested to be a significant factor in determining the size or term length of *H. circularisquama* blooms; that is, when concentration of HcRNAV is high in sediments, occurrence of dense *H. circularisquama* blooms appears suppressed. HcRNAV infection seems, thus, to affect the population dynamics of *H. circularisquama* not only in quantity (biomass) but also quality (clonal composition).

In contrast, ecological implication of viruses infecting diatoms has not been sufficiently understood. Considering that diatoms are one of the most widespread plant groups on earth, the impact viruses have on the diatom's population dynamics should be more intensively studied.

In this article, algal viruses having ssRNA, dsRNA, or ssDNA genomes are described. Given the large variety of algae and the diversity of viruses isolated and characterized to date, marine and freshwaters provide a treasury of undiscovered viruses.

See also: Marnaviruses; Phycodnaviruses.

Further Reading

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