Satellites and Other Virus-dependent Nucleic Acids

Definitions

Satellites are subviral agents which lack genes that could encode functions needed for replication. Thus for their multiplication they depend on the co-infection of a host cell with a helper virus. Satellite genomes have a substantial portion or all of their nucleotide sequences distinct from those of the genomes of their helper virus.

According to this definition, two major classes of satellites may be distinguished. **Satellite viruses** encode a structural protein that encapsidates their genome and so have nucleoprotein components distinct from those of their helper viruses. **Satellite nucleic acids** encode either non-structural proteins, or no proteins at all, and are encapsidated by the CP of helper viruses.

In addition to the true satellites, this chapter also describes subviral agents (nucleic acids) that depend upon viruses in a variety of ways. **Satellite-like nucleic acids** resemble satellites because they do not encode a replicase but differ because they encode a function necessary for the biological success of the associated virus. They can therefore be considered as components that remedy a deficiency in a defective virus. They have sometimes been classified as part of the genome of the virus they assist but they can also be dispensable because they are not always found in association with their helper virus. Examples include RNAs associated with groundnut rosette virus (genus *Umbravirus*) or with beet necrotic yellow vein virus (genus *Benyvirus*), that contribute to vector transmissibility and DNAs associated with begomoviruses (betasatellites) that encode a pathogenicity determinant.

A final group of agents described are nucleic acids capable of autonomous replication and which therefore are not strictly satellites although the term has sometimes been loosely applied to them. These agents are dependent on their helper viruses for various functions such as encapsidation, cell-to-cell and long-distance movement and vector transmission. Examples are the alphasatellites (DNAs that encode a replication initiator protein) or the RNAs associated with some poleroviruses that appear to encode a carmovirus-like RdRp.

The distinction between satellite nucleic acids, satellite-like nucleic acids and virus genomic components can be subtle and these agents are not always easy to categorize.

Distinguishing features

Satellites are genetically distinct from their helper virus with a nucleotide sequence that is substantially different from that of their helper virus. However, the genomes of most satellites have short sequences, often at the termini, that are identical to the genome of the helper virus. This is presumably linked to the dependence of nucleic acids of both satellite and helper virus on the same viral polymerase and host-encoded proteins for replication. Satellites are distinct from defective interfering (DI) RNAs or defective RNAs because such RNAs are derived from their "helper" virus genomes. Nevertheless, satellite viruses may form their own DI RNAs that specifically interfere with the satellite virus genomic RNA, as has been shown for satellite panicum mosaic virus. Recombination can occur between satellites and their helper viruses. For example, chimeric molecules can be formed from a satellite RNA associated with turnip crinkle virus (genus *Carmovirus*) and parts of the helper virus genome.

Satellites do not constitute a homogeneous taxonomic group and are not formally classified into species and higher taxa by ICTV. The descriptions in this section are meant only to provide a classification framework and a nomenclature to assist in the description and identification of satellites and other virus-dependent nucleic acids. The arrangement adopted is based largely on features of the genetic material of the satellites. The physicochemical and biological features of the helper virus and of the helper virus host are important secondary characters.

There appears to be no taxonomic correlation between the viruses that are associated with satellites. Satellites would appear to have arisen independently a number of times during virus evolution. A

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further complication is that some viruses are associated with more than one satellite and some satellites are supported by more than one species of helper virus. Satellites can even depend on both a second satellite and a helper virus for multiplication.

The first satellites characterized were mostly ssRNA satellites that use ssRNA plant viruses as helpers. It can be very difficult to distinguish between satellite RNA and viral genomic RNA (e. g., dsRNA satellites of fungus viruses) and it is very likely that other satellites, some with novel combinations of characters, remain to be discovered.

Categories of satellites

Satellite viruses:

1. **Chronic bee-paralysis virus-associated satellite virus**
2. **Satellites that resemble tobacco necrosis satellite virus**
3. **Nodavirus-associated satellite virus**
4. **Adenovirus-associated satellite virus (*Dependovirus*)**
5. **Mimivirus-associated satellite virus (Sputnik, virophage)**

Virus-dependent nucleic acids:

6. **Single stranded DNAs**
   - **6a. Alphasatellites (encoding a replication initiator protein)**
   - **6b. Betasatellites (encoding a pathogenicity determinant)**
7. **Double stranded RNAs**
8. **Single stranded RNAs**
   - **8a. Large linear single stranded satellite RNAs**
   - **8b. Small linear single stranded satellite and satellite-like RNAs**
   - **8c. Small circular single stranded satellite RNAs**
   - **8d. Hepadnavirus-associated satellite-like RNAs (*Deltavirus*)**
   - **8e. Polerovirus-associated RNAs**

Satellite Viruses

These satellites encode a structural protein to encapsidate their genomes. The satellite virus particles are antigenically, and usually morphologically, distinct from those of the helper virus. Five subgroups of satellite viruses are currently distinguished.

1. Chronic bee-paralysis associated satellite virus

Satellite virus particles are found in bees infected with the helper, chronic bee-paralysis virus (CBPV; a virus not yet classified). Particles are about 12 nm in diameter and serologically unrelated to those of CBPV. The satellite interferes with CBPV replication.

List of group members

Chronic bee-paralysis satellite virus	(CBPSV)

2. Satellites that resemble tobacco necrosis satellite virus

These satellite virus particles are found in plant hosts in association with taxonomically diverse helper viruses. The $T = 1$ isometric particles are about 17 nm in diameter. The capsid consists of 60 copies of a single protein of 17–24 kDa, which is encoded by the satellite virus genome (positive sense ssRNA). The genomes of some satellite viruses contain a second ORF.

List of group members

Satellite viruses associated with viruses in the family *Tombusviridae*

Maize white line mosaic satellite virus	[M55012]	(SMWLMV)

Panicum mosaic satellite virus	[M17182]	(SPMV)
Tobacco necrosis satellite virus	[V01468]	(STNV)
Satellite viruses associated with viruses in the family *Virgaviridae*		
Tobacco mosaic satellite virus	[M25782]	(STMV)

3. Nodavirus-associated satellite virus

Satellite virus particles are found in *Macrobrachium rosenbergii* (giant river prawn) infected with Macrobrachium rosenbergii nodavirus (MrNV; a virus not yet classified but clearly related to viruses in the family *Nodaviridae*). The XSV (extra small virus) satellite virus particles are about 15nm in diameter and serologically unrelated to those of MrNV. XSV is a positive-sense single-stranded RNA, about 800 bases in size, encoding a 17kDa capsid protein. The mixed infection of MrNV and XSV is implicated in white spot disease of prawns.

List of group members

Macrobrachium rosenbergii nodavirus XSV (extra small virus)	[AY247793]	(XSV)

4. Adenovirus-associated satellite virus (*Dependovirus*)

Adenovirus-associated (AAV) satellite virus particles are found in humans, domesticated animals, fowl and in tissue or cell cultures as co-infections with a helper virus. The single stranded 5kb DNA genome encodes three structural proteins (VP1, −2 and −3). The 26nm T = 1 particles have a 10:1:1 ratio of VP3:VP2:VP1. Smaller particles about 12nm in diameter only contain the 60 kDa VP3 protein. AAV satellite viruses are dependent on adenoviruses (or herpesviruses) for replication and cap functions. This group of satellites is anomalous, having been placed in a genus *Dependovirus* within the family *Parvoviridae*, although they meet all definitions for an authentic satellite virus. For more details see the section on genus *Dependovirus*.

List of group members

See tables for the genus *Dependovirus* in the *Parvoviridae* chapter.

5. Mimivirus-associated satellite virus (Sputnik, virophage)

Acanthamoeba polyphaga mimivirus (genus *Mimivirus*) is an extremely large (ca. 1.2Mbp) virus with a dsDNA genome that infects amoebae of the genus *Acanthamoeba*. A mimivirus strain (sometimes called mamavirus) isolated from *A. castellanii* supports a 50nm T = 27 satellite virus, referred to as Sputnik (= satellite in Russian). The satellite virus has a circular dsDNA genome of 18kbp that is predicted to code for about 22 proteins. Sputnik does not replicate in either host in the absence of the helper virus.

List of group members

Acanthamoeba castellanii mamavirus-associated satellite virus (Sputnik)	[EU606015]	(Sputnik; virophage)

Virus-dependent Nucleic Acids

This category includes a diverse range of DNA and RNA molecules that do not encode a capsid protein but are packaged in capsids encoded by their helper virus. Those that encode a function necessary for the biological success of the associated virus are described as "satellite-like".

6. Single stranded DNAs

6a. Alphasatellites

These molecules are not strictly satellites because they encode a rolling-circle replication initiator protein (known as the replication-associated protein [Rep]) with similarity to the master Rep encoding genomic components (DNA-R) of nanoviruses. They are capable of autonomous replication in host cells, have a stem-loop region containing the ubiquitous nonanucleotide TAA/GTATTAC, and depend on their helper viruses for encapsidation, movement in plants and insect transmission. Some are associated with viruses in the genus *Begomovirus* and are typically about 1.4 kb, half the size of their helper viruses. Others are associated with multipartite genome viruses of the family *Nanoviridae* and are approximately the same size (ca. 1 kb) as the genomic components of their helper viruses (but are not derived from them). The presence of alphasatellites in begomovirus and nanovirid infections may reduce symptom severity, suggesting interference akin to that seen with defective interfering DNAs. Recent results have shown that the Rep encoded by at least some alphasatellites associated with begomoviruses suppresses host defenses based on RNA interference.

List of group members

Begomovirus-associated alphasatellites		
Ageratum yellow vein alphasatellite	[AJ238493]	(AYVA)
Ageratum yellow vein India alphasatellite	[AJ512958]	(AYVIA)
Ageratum yellow vein Kenya alphasatellite	[AJ512960]	(AYVKA)
Ageratum yellow vein Pakistan alphasatellite	[AJ512949]	(AYVPKA)
Ageratum yellow vein Singapore alphasatellite	[AJ416153]	(AYVSGA)
Cotton leaf curl Dabwali alphasatellite	[AJ512957]	(CLCuDaA)
Cotton leaf curl Gezira alphasatellite	[FN554581]	(CLCuGeA)
Cotton leaf curl Multan alphasatellite	[GQ374450]	(CLCuMuA)
Cotton leaf curl Shadadpur alphasatellite	[AM711116]	(CLCuShA)
Duranta leaf curl alphasatellite	[FM179614]	(DuLCA)
Gossypium darwinii symptomless alphasatellite	[EU384606]	(GDarSLA)
Gossypium davidsonii symptomless alphasatellite	[EU384652]	(GDavSLA)
Gossypium mustilinum symptomless alphasatellite	[EU384662]	(GMusSLA)
Hibiscus leaf curl alphasatellite	[AJ579349]	(HLCuA)
Malvastrum yellow mosaic alphasatellite	[AM236763]	(MalYMA)
Malvastrum yellow mosaic Hainan alphasatellite	[AM236765]	(MalYMHnA)
Okra leaf curl alphasatellite	[AJ512954]	(OLCuA)
Okra leaf curl Barombi alphasatellite	[FM164739]	(OLCuBaA)
Okra leaf curl Burkina Faso alphasatellite	[FN554582]	(OLCuBFA)
Okra leaf curl Mali alphasatellite	[FN554580]	(OLCuMA)
Sida yellow vein Vietnam alphasatellite	[DQ641718]	(SiYVVA)
Tobacco curly shoot alphasatellite	[AJ579346]	(TbCSA)
Tomato leaf curl Pakistan alphasatellite	[FM164939]	(ToLCPKA)
Tomato yellow leaf curl China alphasatellite	[AJ579358]	(TYLCCNA)
Babu- and nanovirus-associated alphasatellites		
Banana bunchy top S1 alphasatellite	[AF216221]	(BBTS1A)
Banana bunchy top S2 alphasatellite	[L32167]	(BBTS2A)
Banana bunchy top S3 alphasatellite	[AF416471]	(BBTS3A)
Banana bunchy top W1 alphasatellite	[L32166]	(BBTW1A)
Banana bunchy top Y alphasatellite	[FJ389724]	(BBTS2A)
Faba bean necrotic yellows C1 alphasatellite	[X80879]	(FBNYC1A)
Faba bean necrotic yellows C11 alphasatellite	[AJ005968]	(FBNYC11A)
Faba bean necrotic yellows C7 alphasatellite	[AJ005964]	(FBNYC7A)
Faba bean necrotic yellows C9 alphasatellite	[AJ005966]	(FBNYC9A)
Milk vetch dwarf C1 alphasatellite	[AB000920]	(MDC1A)
Milk vetch dwarf C10 alphasatellite	[AB009047]	(MDC10A)
Milk vetch dwarf C2 alphasatellite	[AB000921]	(MVDC2A)
Milk vetch dwarf C3 alphasatellite	[AB000922]	(MDC3A)
Subterranean clover stunt C2 alphasatellite	[U16731]	(SCSC2A)
Subterranean clover stunt C6 alphasatellite	[U16735]	(SCSC6A)
Possible member		
Coconut foliar decay alphasatellite	[M29963]	(CFDA)

6b. Betasatellites

These are satellite-like circular ssDNA components, usually about 1.3 kb in size that are associated with viruses in the genus *Begomovirus*. Although initially identified only in association with monopartite begomoviruses, recently they have been increasingly identified in association with bipartite begomoviruses. All betasatellites have a stem-loop region containing the ubiquitous nonanucleotide TAATATTAC and an associated highly conserved sequence located immediately upstream (the function of which remains uncertain), a conserved ORF (termed βC1; encoding a protein that is a pathogenicity determinant and a suppressor of host defenses based on RNA interference), and an A-rich region that may reflect size adaptation for maintenance of the component by the helper begomovirus. The betasatellite DNAs readily recombine with the helper begomovirus genome and such recombinants may retain a biological activity similar to the parental betasatellite. Pairwise comparisons between sequences have shown that a sequence identity of about 78% is an appropriate demarcation threshold for distinguishing between betasatellites.

List of group members

Ageratum leaf curl Cameroon betasatellite	[FM164738]	(ALCCMB)
Ageratum yellow leaf curl betasatellite	[AJ316041]	(AYLCB)
Ageratum yellow vein betasatellite	[AJ252072]	(AYVB)
Ageratum yellow vein Sri Lanka betasatellite	[AJ542493]	(AYVSLB)
Alternanthera yellow vein betasatellite	[DQ641716]	(AlYVB)
Bean leaf curl China betasatellite	[AM260730]	(BeLCCNB)
Bhendi yellow vein betasatellite	[AJ308425]	(BYVB)
Cardiospemum yellow leaf curl betasatellite	[AM933578]	(CarYLCB)
Chilli leaf curl betasatellite	[AJ316032]	(ChLCB)
Cotton leaf curl Gezira betasatellite	[AJ316039]	(CLCuGeB)
Cotton leaf curl Multan betasatellite	[AJ292769]	(CLCuMuB)
Croton yellow vein mosaic betasatellite	[AM410551]	(CroYVMB)
Emilia yellow vein betasatellite	[FJ869906]	(EmYVB)
Erectites yellow mosaic betasatellite	[DQ641713]	(ErYMB)
Eupatorium yellow vein betasatellite	[AJ438938]	(EpYVB)
Honeysuckle yellow vein betasatellite	[AJ316040]	(HYVB)
Honeysuckle yellow vein Japan betasatellite	[AB236324]	(HYVJB)
Honeysuckle yellow vein Kochi betasatellite	[AB236326]	(HYVKoB)
Honeysuckle yellow vein mosaic betasatellite	[AB287442]	(HYVMB)
Honeysuckle yellow vein mosaic Hyogo betasatellite	[AB182263]	(HYVMHyB)
Honeysuckle yellow vein mosaic Nara betasatellite	[AB287443]	(HYVMNaB)
Kenaf leaf curl betasatellite	[AY705381]	(KLCuB)
Leucas zeylanica yellow vein betasatellite	[GQ421324]	(LeZYVB)
Lindernia anagallis yellow vein betasatellite	[DQ641715]	(LaYVB)
Ludwigia yellow vein betasatellite	[AJ965541]	(LuYVB)
Luffa leaf distortion betasatellite	[EU557374]	(LuLDB)
Malvastrum leaf curl betasatellite	[AM072289]	(MaLCB)
Malvastrum yellow vein betasatellite	[AJ971459]	(MaYVB)
Malvastrum yellow vein Yunnan betasatellite	[AJ786712]	(MaYVYnB)
Mesta yellow vein mosaic betasatellite	[EF614160]	(MeYVMB)
Okra leaf curl betasatellite	[AJ316029]	(OLCuB)
Papaya leaf curl betasatellite	[AY230138]	(PaLCuB)
Radish leaf curl betasatellite	[EF175734]	(RaLCB)
Sida leaf curl betasatellite	[AM050732]	(SiLCuB)
Sida yellow mosaic China betasatellite	[AM048833]	(SiYMCNB)
Sida yellow vein betasatellite	[AJ967003]	(SiYVB)
Sida yellow vein mosaic betasatellite	[EU188921]	(SiYVMB)
Sida yellow vein Vietnam betasatellite	[DQ641712]	(SiYVVB)
Siegesbeckia yellow vein betasatellite	[AM230643]	(SgYVB)
Siegesbeckia yellow vein Guangxi betasatellite	[AM238695]	(SgYVGxB)
Tobacco curly shoot betasatellite	[AJ421485]	(TbCSB)
Tobacco leaf curl betasatellite	[AJ316033]	(TbLCB)
Tomato leaf curl Bangalore betasatellite	[AY428768]	(ToLCBaB)
Tomato leaf curl Bangladesh betasatellite	[AJ542489]	(ToLCBB)
Tomato leaf curl betasatellite	[AJ316036]	(ToLCB)
Tomato leaf curl China betasatellite	[AJ704609]	(ToLCCNB)
Tomato leaf curl Java betasatellite	[AB100306]	(ToLCJaB)
Tomato leaf curl Joydebpur betasatellite	[AJ966244]	(ToLCJoB)
Tomato leaf curl Karnataka betasatellite	[AY754813]	(ToLCKaB)
Tomato leaf curl Laos betasatellite	[AJ542491]	(ToLCLB)

Tomato leaf curl Maharastra betasatellite	[AY838894]	(ToLCMaB)
Tomato leaf curl Patna betasatellite	[EU862324]	(ToLCPaB)
Tomato leaf curl Philippines betasatellite	[AB308071]	(ToLCPB)
Tomato leaf curl virus satellite	[U74627]	(ToLCV-sat)
Tomato yellow dwarf betasatellite	[AB294512]	(ToYDB)
Tomato yellow leaf curl China betasatellite	[AJ781297]	(TYLCCNB)
Tomato yellow leaf curl Thailand betasatellite	[AJ536621]	(TYLCTHB)
Tomato yellow leaf curl Vietnam betasatellite	[DQ641714]	(TYLCVB)
Tomato yellow leaf curl Yunnan betasatellite	[AJ421620]	(TYLCYnB)
Vernonia yellow vein betasatellite	[FN435836]	(VerYVB)
Zinnia leaf curl betasatellite	[AJ542499]	(ZLCuB)

7. Double stranded RNAs

Most satellites in this category are found in association with viruses in the families *Totiviridae* and *Partitiviridae*. The dsRNAs range in size from 0.5 to 1.8 kbp and are encapsidated using the helper virus capsid protein. These particles often also contain a positive sense single stranded copy of the dsRNA. The satellite dsRNAs associated with helper viruses in the genus *Totivirus* encode a secreted preprotoxin that is lethal to sensitive cells (virus-free or containing helper virus only). The presence of satellites in helper totivirus cultures imparts self-protection against the secreted toxin and confers ecological advantage by killing competing virus- or satellite-free fungi. The satellite dsRNAs associated with partitiviruses do not code for functional proteins and their biological significance is not known.

List of group members

Satellites associated with viruses in the family *Totiviridae*		
M satellites of Saccharomyces cerevisiae L-A virus		
M1	[U78817]	(ScV-M1)
M2	[X56987]	(ScV-M2)
M28		(ScV-M28)
M satellites of Ustilago maydis virus H		
M-P1	[M63149]	(UmV-P1)
M-P4	[L12226]	(UmV-P4)
M-P6	[P16948]	(UmV-P6)
Satellites of Trichomonas vaginalis T1 virus	[U15991]	(TVV-Sat*)
Possible member		
M satellite of Zygosaccharomyces balii virus	[AF515592]	(ZbV-M)
Satellites associated with viruses in the family *Partitiviridae*		
Satellite of Atkinsonella hypoxylon virus	[L39127]	(AhV-Seg3*)
Satellites of Discula destructiva virus 1		
dsRNA 3	[AF316994]	(DdV-Seg3)
dsRNA4	[AF316995]	(DdV-Seg4)
Satellite of Gremmeniella abietina virus MS1	[AY089995]	(GaVMS1-Seg3)
Satellite of Penicillium stoloniferum virus F	[AY738338]	(PsVF-Seg3)
Possible members		
Satellites of Amasya cherry disease-associated virus		
Satellite A	[AM085138]	(ACDAV-SatA)
Satellite B	[AM085139]	(ACDAV-SatB)
Satellites of cherry chlorotic rusty spot -associated virus		
Satellite A	[AM749118]	(CCRSAV-SatA)
Satellite B	[AM749119]	(CCRSAV-SatB)
Satellite C	[AM749120]	(CCRAV-SatC)
Satellites associated with viruses in the family *Reoviridae*		
Bombyx mori cypovirus 1 satellite RNA	[AB183384]	(BmCpV1-Sat)

*Abbreviations: Sat, satellite; Seg, segment.

8. Single stranded RNAs

8a. Large linear single stranded satellite RNAs

This category comprises satellites with genomes that are 0.8 to 1.5 kb in size and encode a non-structural protein that, at least in some cases, is essential for satellite RNA multiplication. Little sequence homology exists between the satellites and their helpers, some satellites can be exchanged among different helper viruses. These satellites rarely modify the disease induced in host plants by the helper virus. Most are associated with helper viruses in the family *Secoviridae*.

List of group members

Satellite RNAs associated with viruses in the family *Secoviridae*	
Arabis mosaic virus large satellite RNA	[D00664]
Beet ringspot virus satellite RNA (TBRV-S serotype satellite RNA)	
Blackcurrant reversion virus satellite RNA	[AF112119]
Chicory yellow mottle virus large satellite RNA	[D00686]
Grapevine Bulgarian latent virus satellite RNA	
Grapevine fanleaf virus satellite RNA	[D00442]
Myrobalan latent ringspot virus satellite RNA	
Strawberry latent ringspot virus satellite RNA	[X69826]
Tomato black ring virus satellite RNA (TBRV-G serotype satellite RNA)	[X00978]
Satellite RNAs associated with viruses in the family *Alphaflexiviridae*	
Bamboo mosaic virus satellite RNA	[L22762]
Possible member	
Beet necrotic yellow vein virus RNA5*	[D63759]

*Non-essential genome component that may be regarded as a satellite-like RNA. Beet necrotic yellow vein virus is a member of the genus *Benyvirus*.

8b. Small linear single stranded satellite and satellite-like RNAs

These satellites have a strictly linear genome of less than 0.7 kb that does not encode functional proteins. Some satellites can attenuate the symptoms induced by helper virus infection, whereas other satellites can exacerbate the symptoms.

List of group members

Satellite RNAs associated with viruses in the family *Tombusviridae*	
Artichoke mottled crinkle virus satellite RNA	
Black beet scorch virus satellite RNA	[AY394497]
Carnation Italian ringspot virus satellite RNA	
Cymbidium ringspot virus satellite RNA	[D00720]
Panicum mosaic virus satellite RNA	[M17182]
Pelargonium leaf curl virus satellite RNA	
Petunia asteroid mosaic virus satellite RNA	
Tobacco necrosis virus small satellite RNA	[E03054]
Tomato bushy stunt virus satellite RNA (several types)	[AF022787-8][FJ666076]
Satellite RNAs associated with viruses in the family *Bromoviridae*	
Cucumber mosaic virus satellite RNA (several types)	[X69136]
Peanut stunt virus satellite RNA	[Z98197]
Satellite RNAs associated with viruses in the genus *Umbravirus*†	
Carrot mottle mimic virus satellite RNA	[EU914919]
Groundnut rosette virus satellite RNA*	[Z29702]
Pea enation mosaic virus satellite RNA	[U03564]
Tobacco bushy top virus satellite RNA*	[AF510392]

*These may be regarded as a satellite-like RNAs as they appear to be essential components of a disease complex.
†These in turn depend upon viruses in the family *Luteoviridae* for their encapsidation and transmission.

8c. Small circular single stranded satellite RNAs

These satellites have genomes that are about 350 nt long. Both circular and linear forms of the genome are found in infected cells. In some cases (e.g. the satellite RNA associated with tobacco ringspot virus, genus *Nepovirus*), replication involves self-cleavage of circular progeny molecules by an RNA-catalyzed reaction.

List of group members

Satellite RNAs associated with viruses in the family *Secoviridae*	
Arabis mosaic virus small satellite RNA	[M21212]
Chicory yellow mottle virus satellite RNA	[D00721]
Tobacco ringspot virus satellite RNA	[M14879]

Satellite RNAs associated with viruses in the family *Luteoviridae*	
Cereal yellow dwarf virus-RPV satellite RNA	[M63666]
Satellite RNAs associated with viruses in the genus *Sobemovirus*	
Lucerne transient streak virus satellite RNA	[X01984]
Rice yellow mottle virus satellite	[AF039909]
Solanum nodiflorum mottle virus satellite RNA	[J02386]
Subterranean clover mottle virus satellite RNA (2 types)	[M33000][M33001]
Velvet tobacco mottle virus satellite RNA	[J02439]
Possible member	
Cherry small circular viroid-like RNA	[Y12833]

8d. Hepadnavirus-associated satellite-like RNAs (*Deltavirus*)

Hepatitis D virus (HDV, genus *Deltavirus*) has a single molecule of circular, negative sense 1.7 kb ssRNA that encodes a 24 kDa small protein (S-HDAg) and a 27 kDa large protein (L-HDAg). The ribonucleoprotein of HDV RNA and both HDAgs, are packaged within an envelope containing lipid and helper virus antigens. For complete replication and transmission, HDV also requires a host DNA dependent RNA polymerase II and HBsAg, a protein encoded by its helper virus, human hepatitis B virus (genus *Orthohepadnavirus*). HDV RNA is encapsidated in distinct virions by the HBsAg capsid protein of the helper virus. HDV is a serious human pathogen and has until now been classified as a virus, although it meets the definitions of a satellite-like RNA. For more details see the chapter on genus *Deltavirus*.

List of group members

See chapter for genus *Deltavirus*.

8e. Polerovirus-associated RNAs

These ssRNA genomes are about 2.8–3 kb long and have two major ORFs. It is likely that the second ORF, which contains the classic RdRp motifs of the carmovirus supergroup, is translated by readthrough of the ORF1 amber stop codon. Additional small ORFs have been identified in some members. The RNA is capable of autonomous replication but appears to depend on a virus of the genus *Polerovirus* as helper virus for aphid transmission by encapsidating this RNA with the polerovirus coat protein to form aphid-transmissible hybrid virions. Some members increase the severity of disease symptoms.

List of group members

Beet western yellows virus ST9-associated RNA	[L04281]	(BWYV ST9aRNA)
Carrot red leaf virus-associated RNA	[AF020617]	(CtRLVaRNA)
Tobacco vein distorting virus-associated RNA	[EF529625]	(TVDVaRNA)

Further reading

Journals and books

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