

# Viroid

**Viroids** are small single-stranded, circular RNAs that are infectious pathogens.<sup>[1][2]</sup> Unlike viruses, they have no protein coating. All known viroids are inhabitants of angiosperms (flowering plants),<sup>[3]</sup> and most cause diseases, whose respective economic importance to humans varies widely.<sup>[4]</sup> A recent metatranscriptomics study suggests that the host diversity of viroids and viroid-like elements is broader than previously thought and is not limited to plants, encompassing even the prokaryotes.<sup>[5]</sup>

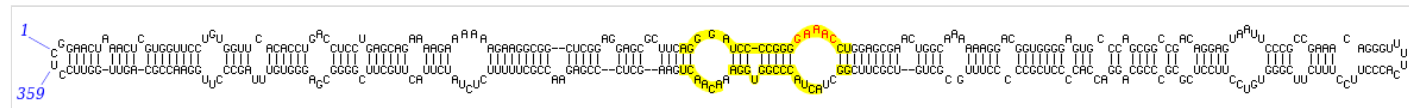
The first discoveries of viroids in the 1970s triggered the historically third major extension of the biosphere—to include smaller lifelike entities—after the discoveries in 1675 by Antonie van Leeuwenhoek (of the "subvisible" microorganisms) and in 1892–1898 by Dmitri Iosifovich Ivanovsky and Martinus Beijerinck (of the "submicroscopic" viruses). The unique properties of viroids have been recognized by the International Committee on Taxonomy of Viruses, in creating a new order of subviral agents.<sup>[6]</sup>

The first recognized viroid, the pathogenic agent of the potato spindle tuber disease, was discovered, initially molecularly characterized, and named by Theodor Otto Diener, plant pathologist at the U.S Department of Agriculture's Research Center in Beltsville, Maryland, in 1971.<sup>[7][8]</sup> This viroid is now called potato spindle tuber viroid, abbreviated PSTVd. The Citrus exocortis viroid (CEVd) was discovered soon thereafter, and together understanding of PSTVd and CEVd shaped the concept of the viroid.<sup>[9]</sup>

Although viroids are composed of nucleic acid, they do not code for any protein.<sup>[10][11]</sup> The viroid's replication mechanism uses RNA polymerase II, a host cell enzyme normally associated with synthesis of messenger RNA from DNA, which instead catalyzes "rolling circle" synthesis of new RNA using the viroid's RNA as a template. Viroids are often ribozymes, having catalytic properties that allow self-cleavage and ligation of unit-size genomes from larger replication intermediates.<sup>[12]</sup>

Diener initially hypothesized in 1989 that viroids may represent "living relics" from the widely assumed, ancient, and non-cellular RNA world, and others have followed this conjecture.<sup>[13][14]</sup> Following the discovery of retrozymes, it has been proposed that viroids and other viroid-like elements may derive from this newly found class of retrotransposon.<sup>[15][16][17]</sup>

## Taxonomy




Putative secondary structure of the PSTVd viroid. The highlighted nucleotides are found in most other viroids.

As of 2024:<sup>[9][18]</sup>

- Family Pospiviroidae: relies on host Rnase III<sup>[5]</sup>
  - Genus Pospiviroid; type species: Pospiviroid fusituberis (former name Potato spindle tuber viroid<sup>[19]</sup>); 356–361 nucleotides(nt)<sup>[20]</sup>
    - Pospiviroid chloronani (former name Tomato chlorotic dwarf viroid<sup>[21]</sup>); (TCDVd); accession AF162131, genome length 360nt
    - Mexican papita viroid; (MPVd); accession L78454, genome length 360nt

### Viroids



#### Virus classification

*Informal group:* Subviral agents

*Informal group:* **Viroids**

#### Families

- Pospiviroidae
- Avsunviroidae

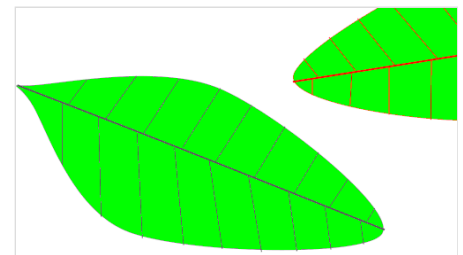
- *Pospiviroid machoplantae* (former name *Tomato planta macho viroid*<sup>[22]</sup>); (TPMVd); accession K00817, genome length 360nt
- *Pospiviroid exocortiscitri* (former name *Citrus exocortis viroid*<sup>[23]</sup>); 368–467 nt<sup>[20]</sup>
- *Pospiviroid impedichrysanthemi* (former name *Chrysanthemum stunt viroid*<sup>[24]</sup>); (CSVd); accession V01107, genome length 356nt
- *Pospiviroid apicimpeditum* (former name *Tomato apical stunt viroid*<sup>[25]</sup>); (TASVd); accession K00818, genome length 360nt
- *Pospiviroid alphairesinis* (former name *Iresine 1 viroid*<sup>[26]</sup>); (IrVd-1); accession X95734, genome length 370nt
- *Pospiviroid latenscolumneae* (former name *Columnnea latent viroid*<sup>[27]</sup>); (CLVd); accession X15663, genome length 370nt
- *Pospiviroid latensportulacae* (former name *Pospiviroid plvd*<sup>[28]</sup>)
- *Pospiviroid parvicapsici* (former name *Pepper chat fruit viroid*<sup>[29]</sup>)
- Genus *Hostuviroid*; type species: *Hostuviroid impedi humuli* (former name *Hop stunt viroid*<sup>[30]</sup>); 294–303 nt<sup>[20]</sup>
  - *Hostuviroid latensdahliae* (former name *Dahlia latent viroid*<sup>[31]</sup>)
- Genus *Cocadviroid*; type species: *Cocadviroid cadangi* (former name *Coconut cadang-cadang viroid*<sup>[32]</sup>); 246–247 nt<sup>[20]</sup>
  - *Cocadviroid tinangajae* (former name *Coconut tinangaja viroid*<sup>[33]</sup>); (CTiVd); accession M20731, genome length 254nt
  - *Cocadviroid latenshumuli* (former name *Hop latent viroid*<sup>[34]</sup>); (HLVd); accession X07397, genome length 256nt
  - *Cocadviroid rimocitri* (former names *Citrus bark cracking viroid*, *Citrus IV viroid*<sup>[35]</sup>); (CVd-IV); accession X14638, genome length 284nt
- Genus *Apscaviroid*; type species: *Apscaviroid cicatricimali* (former name *Apple scar skin viroid*<sup>[36]</sup>); 329–334 nt<sup>[20]</sup>
  - *Citrus III viroid*; (CVd-III); accession AF184147, genome length 294nt
  - *Apscaviroid fossulamali* (former name *Apple dimple fruit viroid*<sup>[37]</sup>); (ADFVd); accession X99487, genome length 306nt
  - *Apscaviroid alphaflavivitis* (former name *Grapevine yellow speckle viroid 1*<sup>[38]</sup>); (GVYSd-1); accession X06904, genome length 367nt
  - *Apscaviroid betaflavivitis* (former name *Grapevine yellow speckle viroid 2*<sup>[39]</sup>); (GVYSd-2); accession J04348, genome length 363nt
  - *Apscaviroid curvifoliumcitri* (former name *Citrus bent leaf viroid*<sup>[40]</sup>); (CBLVd); accession M74065, genome length 318nt
  - *Apscaviroid pustulapyri* (former name *Pear blister canker viroid*<sup>[41]</sup>); (PBCVd); accession D12823, genome length 315nt
  - *Apscaviroid austravitis* (former name *Australian grapevine viroid*<sup>[42]</sup>); (AGVd); accession X17101, genome length 369nt
  - *Apscaviroid maculamali* (former name *Apscaviroid aclsvd*<sup>[43]</sup>)
  - *Apscaviroid etacitri* (former name *Apscaviroid cvd-VII*<sup>[44]</sup>)
  - *Apscaviroid dendrobii* (former name *Apscaviroid dvd*<sup>[45]</sup>)
  - *Apscaviroid latensvitis* (former name *Apscaviroid glvd*<sup>[46]</sup>)
  - *Apscaviroid litchis* (former name *Apscaviroid lvd*<sup>[47]</sup>)
  - *Apscaviroid latenspruni* (former name *Apscaviroid plvd*<sup>[48]</sup>)
  - *Apscaviroid diospyri* (former name *Apscaviroid pvd*<sup>[49]</sup>)
  - *Apscaviroid betadiospyri* (former name *Apscaviroid pvd-2*<sup>[50]</sup>)
  - *Apscaviroid nanocitri* (former name *Citrus dwarfing viroid*<sup>[51]</sup>)
  - *Apscaviroid epsiloncitri* (former name *Citrus viroid V*<sup>[52]</sup>)
  - *Apscaviroid zetacitri* (former name *Citrus viroid VI*<sup>[53]</sup>)
  - *Apscaviroid japanvitis*<sup>[54]</sup>

- Genus *Coleviroid*; type species: *Coleviroid alphacolei* (former name *Coleus blumei viroid 1*<sup>[55]</sup>); (CbVd-1); 248–251 nt<sup>[20]</sup>
  - *Coleviroid betacolei* (former name *Coleus blumei viroid 2*<sup>[56]</sup>); (CbVd-2); accession X95365, genome length 301nt
  - *Coleviroid gammacolei* (former name *Coleus blumei viroid 3*<sup>[57]</sup>); (CbVd-3); accession X95364, genome length 361nt
  - *Coleviroid epsiloncolei* (former name *Coleviroid cbvd-5*<sup>[58]</sup>)
  - *Coleviroid zetacolei* (former name *Coleviroid cbvd-6*<sup>[59]</sup>)
- Family *Avsunviroidae*: autocatalytic cleavage<sup>[5]</sup>
  - Genus *Avsunviroid*; type species: *Avsunviroid albamaculaperseae* (former name *Avocado sunblotch viroid*<sup>[60]</sup>); 246–251 nt<sup>[20]</sup>
  - Genus *Pelamoviroid*; type species: *Pelamoviroid latenspruni* (former name *Peach latent mosaic viroid*<sup>[61]</sup>); 335–351 nt<sup>[20]</sup>
    - *Pelamoviroid maculachrysanthemi* (former name *Chrysanthemum chlorotic mottle viroid*<sup>[62]</sup>)
    - *Pelamoviroid malleusmali* (former name *Apple hammerhead viroid*<sup>[63]</sup>)
  - Genus *Elaviroid*; type species: *Elaviroid latensmelongenae* (former name *Eggplant latent viroid*<sup>[64]</sup>); 332–335 nt<sup>[20]</sup>

## Transmission and replication

Viroids are only known to infect plants, and infectious viroids can be transmitted to new plant hosts by aphids, by cross contamination following mechanical damage to plants as a result of horticultural or agricultural practices, or from plant to plant by leaf contact.<sup>[20][65]</sup> Upon infection, viroids replicate in the nucleus (*Pospiviroidae*) or chloroplasts (*Avsunviroidae*) of plant cells in three steps through an RNA-based mechanism. They require RNA polymerase II, a host cell enzyme normally associated with synthesis of messenger RNA from DNA, which instead catalyzes "rolling circle" synthesis of new RNA using the viroid as template.<sup>[66]</sup>

Unlike plant viruses which produce movement proteins, viroids are entirely passive, relying entirely on the host. This is useful in the study of RNA kinetics in plants.<sup>[9]</sup>



The reproduction mechanism of a typical viroid. Leaf contact transmits the viroid. The viroid enters the cell via its plasmodesmata. RNA polymerase II catalyzes rolling-circle synthesis of new viroids.

## RNA silencing

There has long been uncertainty over how viroids induce symptoms in plants without encoding any protein products within their sequences.<sup>[67]</sup> Evidence suggests that RNA silencing is involved in the process. First, changes to the viroid genome can dramatically alter its virulence.<sup>[68]</sup> This reflects the fact that any siRNAs produced would have less complementary base pairing with target messenger RNA. Secondly, siRNAs corresponding to sequences from viroid genomes have been isolated from infected plants. Finally, transgenic expression of the noninfectious hpRNA of potato spindle tuber viroid develops all the corresponding viroid-like symptoms.<sup>[69]</sup> This indicates that when viroids replicate via a double stranded intermediate RNA, they are targeted by a dicer enzyme and cleaved into siRNAs that are then loaded onto the RNA-induced silencing complex. The viroid siRNAs contain sequences capable of complementary base pairing with the plant's own messenger RNAs, and induction of degradation or inhibition of translation causes the classic viroid symptoms.<sup>[70]</sup>

## Viroid-like elements

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Viroid-like elements are pieces of covalently closed circular (ccc) RNA molecules that do not share the viroid's lifecycle. The category encompasses satellite RNAs (including small plant satRNAs "virusoids", fungal "ambivirus", and the much larger HDV-like *Ribozyviria*) and "retroviroids". Most of them also carry some type of a ribozyme.<sup>[5]</sup>

### Viroid-like satellite RNAs

Viroid-like satellite RNAs are infectious circular RNA molecules that depend on a carrier virus to reproduce, being carried in their capsids. Like Avsunviroidae, however, they are capable of self-cleavage.<sup>[71]</sup>

### Ambiviruses

In the 2020s, mobile genetic elements called ambiviruses were discovered in fungi. Their RNA genomes are circular, circa 5 kb in length. One of at least two open reading frames encodes a viral RNA-directed RNA polymerase, that firmly places "ambiviruses" into ribovirian kingdom *Orthornavirae*; a separate phylum *Ambiviricota* has been established since the 2023 ICTV Virus Taxonomy Release because of the unique features of encoding RNA-directed RNA polymerases but also having divergent ribozymes in various combinations in both sense and antisense orientation – the detection of circular forms in both sense orientations suggest that "ambiviruses" use rolling circle replication for propagation.<sup>[72][73][74]</sup>

### Retroviroids

"Retroviroids", more formally "retroviroid-like elements", are viroid-like circular RNA sequences that are also found with homologous copies in the DNA genome of the host.<sup>[75]</sup> The only types found are closely related to the original "carnation small viroid-like RNA" (CarSV).<sup>[76][77]</sup> These elements may act as a homologous substrate upon which recombination may occur and are linked to double-stranded break repair.<sup>[77][78]</sup>

These elements are dubbed retroviroids as the homologous DNA is generated by reverse transcriptase that is encoded by retroviruses.<sup>[79][80]</sup> They are neither true viroids nor viroid-like satellite RNAs: there is no extracellular form of these elements; instead, they are spread only through pollen or egg-cells.<sup>[71]</sup> They appear to co-occur with a pararetrovirus.<sup>[81]</sup>

### Obelisks

After applying metatranscriptomics – the computer-aided search for RNA sequences and their analysis – biologists reported in January 2024 the discovery of "obelisks", a new class of viroid-like elements, and "oblins", their related group of proteins, in the human microbiome. Given that the RNA sequences recovered do not have homologies in any other known life form, the researchers suggest that the obelisks are distinct from viruses, viroids and viroid-like entities, and thus form an entirely new class of organisms.<sup>[82][83]</sup>

## RNA world hypothesis

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Diener's 1989 hypothesis<sup>[84]</sup> had proposed that the unique properties of viroids make them more plausible macromolecules than introns, or other RNAs considered in the past as possible "living relics" of a hypothetical, pre-cellular RNA world. If so, viroids have assumed significance beyond plant virology for evolutionary theory, because their properties make them more plausible candidates than other RNAs to perform crucial steps in the evolution of life from inanimate matter (abiogenesis). Diener's hypothesis was mostly forgotten until 2014, when it was resurrected in a review article by Flores et al.,<sup>[79]</sup> in which the authors summarized Diener's evidence supporting his hypothesis as:

1. Viroids' small size, imposed by error-prone replication.
2. Their high guanine and cytosine content, which increases stability and replication fidelity.

3. Their circular structure, which assures complete replication without genomic tags.
4. Existence of structural periodicity, which permits modular assembly into enlarged genomes.
5. Their lack of protein-coding ability, consistent with a ribosome-free habitat.
6. Replication mediated in some by ribozymes—the fingerprint of the RNA world.

The presence, in extant cells, of RNAs with molecular properties predicted for RNAs of the RNA world constitutes another powerful argument supporting the RNA world hypothesis. However, the origins of viroids themselves from this RNA world has been cast into doubt by several factors, including the discovery of retrozymes (a family of retrotransposon likely representing their ancestors) and their complete absence from organisms outside of the plants (especially their complete absence from prokaryotes including bacteria and archaea).<sup>[15][16][17]</sup> However, recent studies suggest that the diversity of viroids and others viroid-like elements is broader than previously thought and that it would not be limited to plants, encompassing even the prokaryotes. Matches between viroid cccRNAs and CRISPR spacers suggest that some of them might replicate in prokaryotes.<sup>[5]</sup>

## Control

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The development of tests based on ELISA, PCR, and nucleic acid hybridization has allowed for rapid and inexpensive detection of known viroids in biosecurity inspections, phytosanitary inspections, and quarantine.<sup>[85]</sup>

## History

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In the 1920s, symptoms of a previously unknown potato disease were noticed in New York and New Jersey fields. Because tubers on affected plants become elongated and misshapen, they named it the potato spindle tuber disease.<sup>[86]</sup>

The symptoms appeared on plants onto which pieces from affected plants had been budded—indicating that the disease was caused by a transmissible pathogenic agent. A fungus or bacterium could not be found consistently associated with symptom-bearing plants, however, and therefore, it was assumed the disease was caused by a virus. Despite numerous attempts over the years to isolate and purify the assumed virus, using increasingly sophisticated methods, these were unsuccessful when applied to extracts from potato spindle tuber disease-afflicted plants.<sup>[8]</sup>

In 1971, Theodor O. Diener showed that the agent was not a virus, but a totally unexpected novel type of pathogen, 1/80th the size of typical viruses, for which he proposed the term "viroid".<sup>[7]</sup> Parallel to agriculture-directed studies, more basic scientific research elucidated many of viroids' physical, chemical, and macromolecular properties. Viroids were shown to consist of short stretches (a few hundred nucleotides) of single-stranded RNA and, unlike viruses, did not have a protein coat. Viroids are extremely small, from 246 to 467 nucleotides, smaller than other infectious plant pathogens; they thus consist of fewer than 10,000 atoms. In comparison, the genomes of the smallest known viruses capable of causing an infection by themselves are around 2,000 nucleotides long.<sup>[87]</sup>

In 1976, Sanger et al.<sup>[88]</sup> presented evidence that potato spindle tuber viroid is a "single-stranded, covalently closed, circular RNA molecule, existing as a highly base-paired rod-like structure"—believed to be the first such molecule described. Circular RNA, unlike linear RNA, forms a covalently closed continuous loop, in which the 3' and 5' ends present in linear RNA molecules have been joined. Sanger et al. also provided evidence for the true circularity of viroids by finding that the RNA could not be phosphorylated at the 5' terminus. In other tests, they failed to find even one free 3' end, which ruled out the possibility of the molecule having two 3' ends. Viroids thus are true circular RNAs.<sup>[89]</sup>

The single-strandedness and circularity of viroids was confirmed by electron microscopy,<sup>[90]</sup> The complete nucleotide sequence of potato spindle tuber viroid was determined in 1978.<sup>[91]</sup> PSTVd was the first pathogen of a eukaryotic organism for which the complete molecular structure has been established. Over thirty plant diseases have since been identified as viroid-, not virus-caused, as had been assumed.<sup>[87][92]</sup>



Four additional viroids or viroid-like RNA particles were discovered between 2009 and 2015.<sup>[85]</sup>

In 2014, *New York Times* science writer Carl Zimmer published a popularized piece that mistakenly credited Flores et al. with the viroid - RNA world hypothesis' original conception.<sup>[93]</sup>

In January 2024, biologists reported the discovery of "obelisks", a new class of viroid-like elements, and "oblins", their related group of proteins, in the human microbiome.<sup>[82][83]</sup>

## See also



[Biology portal](#)



[Medicine portal](#)



[Viruses portal](#)

- [Circular RNA](#)
- [Microparasite](#)
- [Non-cellular life](#)
- [Obelisk](#)
- [Plant pathology](#)
- [Plasmid](#)
- [Prion](#)
- [RNA world hypothesis](#)
- [Satellite](#)
- [Virus](#)
- [Virus classification](#)
- [Virusoid](#)

## References

- Navarro B, Flores R, Di Serio F (29 September 2021). "Advances in Viroid-Host Interactions" (<https://doi.org/10.1146%2Fannurev-virology-091919-092331>). *Annual Review of Virology*. **8** (1): 305–325. doi:10.1146/annurev-virology-091919-092331 (<https://doi.org/10.1146%2Fannurev-virology-091919-092331>). ISSN 2327-056X (<https://search.worldcat.org/issn/2327-056X>). PMID 34255541 (<https://pubmed.ncbi.nlm.nih.gov/34255541>).
- Di Serio F, Owens RA, Li SF, Matoušek J, Pallás V, Randles JW, Sano T, Verhoeven JT, Vidalakis G, Flores R (November 2020). Zerbini FM, Sabanadzovic S (eds.). "Viroids" ([https://web.archive.org/web/20201202061614/https://talk.ictvonline.org/ictv-reports/ictv\\_online\\_report/subviral-agents/w/viroids](https://web.archive.org/web/20201202061614/https://talk.ictvonline.org/ictv-reports/ictv_online_report/subviral-agents/w/viroids)). Archived from the original ([https://talk.ictvonline.org/ictv-reports/ictv\\_online\\_report/subviral-agents/w/viroids](https://talk.ictvonline.org/ictv-reports/ictv_online_report/subviral-agents/w/viroids)) on December 2, 2020. Retrieved February 3, 2021.
- Hadidi A (January 2019). "Next-Generation Sequencing and CRISPR/Cas13 Editing in Viroid Research and Molecular Diagnostics" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6409718>). *Viruses*. **11** (2): 120. doi:10.3390/v11020120 (<https://doi.org/10.3390%2Fv11020120>). PMC 6409718 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6409718>). PMID 30699972 (<https://pubmed.ncbi.nlm.nih.gov/30699972>).
- Adkar-Purushothama CR, Perreault JP (August 2020). "Impact of Nucleic Acid Sequencing on Viroid Biology" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7432327>). *International Journal of Molecular Sciences*. **21** (15): 5532. doi:10.3390/ijms21155532 (<https://doi.org/10.3390%2Fijms21155532>). PMC 7432327 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7432327>). PMID 32752288 (<https://pubmed.ncbi.nlm.nih.gov/32752288>).
- Lee BD, Neri U, Roux S, Wolf YI, Camargo AP, Krupovic M, et al. (RNA Virus Discovery Consortium; Simmonds P, Kyrpides N, Gophna U, Dolja VV, Koonin EV) (2 Feb 2023). "Mining metatranscriptomes reveals a vast world of viroid-like circular RNAs" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC9911046>). *Cell*. **186** (3): 646–661. bioRxiv 10.1101/2022.07.19.500677 (<https://doi.org/10.1101%2F2022.07.19.500677>). doi:10.1016/j.cell.2022.12.039 (<https://doi.org/10.1016%2Fj.cell.2022.12.039>). PMC 9911046 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC9911046>). PMID 36696902 (<https://pubmed.ncbi.nlm.nih.gov/36696902>).
- King AM, Adams MJ, Carstens EB, Lefkowitz EJ, et al. (2012). *Virus Taxonomy. Ninth Report of the International Committee for Virus Taxonomy*. Burlington, Massachusetts, US: Elsevier Academic Press. pp. 1221–1259. ISBN 978-0-12-384685-3.
- Diener TO (August 1971). "Potato spindle tuber "virus". IV. A replicating, low molecular weight RNA". *Virology*. **45** (2): 411–28. doi:10.1016/0042-6822(71)90342-4 (<https://doi.org/10.1016%2F0042-6822%2871%2990342-4>). PMID 5095900 (<https://pubmed.ncbi.nlm.nih.gov/5095900>).
- "ARS Research Timeline – Tracking the Elusive Viroid" (<https://www.ars.usda.gov/oc/timeline/viroid/>). 2006-03-02. Retrieved 2007-07-18.

9. Flores R, Hernández C, Martínez de Alba AE, Daròs JA, Di Serio F (2005). "Viroids and viroid-host interactions". *Annual Review of Phytopathology*. **43**: 117–39. doi:10.1146/annurev.phyto.43.040204.140243 (https://doi.org/10.1146/annurev.phyto.43.040204.140243). PMID 16078879 (https://pubmed.ncbi.nlm.nih.gov/16078879).
10. Tsagris EM, Martínez de Alba AE, Gozmanova M, Kalantidis K (November 2008). "Viroids" (https://doi.org/10.1111%2Fj.1462-5822.2008.01231.x). *Cellular Microbiology*. **10** (11): 2168–79. doi:10.1111/j.1462-5822.2008.01231.x (https://doi.org/10.1111%2Fj.1462-5822.2008.01231.x). hdl:10662/23889 (https://hdl.handle.net/10662%2F23889). PMID 18764915 (https://pubmed.ncbi.nlm.nih.gov/18764915). S2CID 221581424 (https://api.semanticscholar.org/CorpusID:221581424).
11. Flores R, Di Serio F, Hernández C (February 1997). "Viroids: The Noncoding Genomes". *Seminars in Virology*. **8** (1): 65–73. doi:10.1006/smvy.1997.0107 (https://doi.org/10.1006%2Fsmvy.1997.0107).
12. Moelling K, Broecker F (March 2021). "Viroids and the Origin of Life" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8036462). *International Journal of Molecular Sciences*. **22** (7): 3476. doi:10.3390/ijms22073476 (https://doi.org/10.3390%2Fijms22073476). PMC 8036462 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8036462). PMID 33800543 (https://pubmed.ncbi.nlm.nih.gov/33800543).
13. Diener TO (December 1989). "Circular RNAs: relics of precellular evolution?" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC298497). *Proceedings of the National Academy of Sciences of the United States of America*. **86** (23): 9370–4. Bibcode:1989PNAS...86.9370D (https://ui.adsabs.harvard.edu/abs/1989PNAS...86.9370D). doi:10.1073/pnas.86.23.9370 (https://doi.org/10.1073%2Fpnas.86.23.9370). PMC 298497 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC298497). PMID 2480600 (https://pubmed.ncbi.nlm.nih.gov/2480600).
14. Moelling K, Broecker F (2021-03-28). "Viroids and the Origin of Life" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8036462). *International Journal of Molecular Sciences*. **22** (7): 3476. doi:10.3390/ijms22073476 (https://doi.org/10.3390%2Fijms22073476). ISSN 1422-0067 (https://search.worldcat.org/issn/1422-0067). PMC 8036462 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8036462). PMID 33800543 (https://pubmed.ncbi.nlm.nih.gov/33800543).
15. Cervera A, Urbina D, de la Peña M (2016-06-23). "Retrozymes are a unique family of non-autonomous retrotransposons with hammerhead ribozymes that propagate in plants through circular RNAs" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4918200). *Genome Biology*. **17** (1): 135. doi:10.1186/s13059-016-1002-4 (https://doi.org/10.1186%2Fs13059-016-1002-4). ISSN 1474-760X (https://search.worldcat.org/issn/1474-760X). PMC 4918200 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4918200). PMID 27339130 (https://pubmed.ncbi.nlm.nih.gov/27339130).
16. de la Peña M, Cervera A (2017-08-03). "Circular RNAs with hammerhead ribozymes encoded in eukaryotic genomes: The enemy at home" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5680766). *RNA Biology*. **14** (8): 985–991. doi:10.1080/15476286.2017.1321730 (https://doi.org/10.1080%2F15476286.2017.1321730). ISSN 1547-6286 (https://search.worldcat.org/issn/1547-6286). PMC 5680766 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5680766). PMID 28448743 (https://pubmed.ncbi.nlm.nih.gov/28448743).
17. Lee BD, Koonin EV (2022-01-12). "Viroids and Viroid-like Circular RNAs: Do They Descend from Primordial Replicators?" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8781251). *Life*. **12** (1): 103. Bibcode:2022Life...12..103L (https://ui.adsabs.harvard.edu/abs/2022Life...12..103L). doi:10.3390/life12010103 (https://doi.org/10.3390%2Flife12010103). ISSN 2075-1729 (https://search.worldcat.org/issn/2075-1729). PMC 8781251 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8781251). PMID 35054497 (https://pubmed.ncbi.nlm.nih.gov/35054497).
18. ICTV (30 October 2024). "Virus Taxonomy: 2023 Release (release v4)" (https://ictv.global/taxonomy). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
19. ICTV. "Pospiviroid fusicuberis: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304527&taxon\_name=Pospiviroid%20fusicuberis). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
20. Brian W. J. Mahy, Marc H. V. Van Regenmortel, ed. (2009-10-29). *Desk Encyclopedia of Plant and Fungal Virology*. Academic Press. pp. 71–81. ISBN 978-0123751485.
21. ICTV. "Pospiviroid chloronani: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304529&taxon\_name=Pospiviroid%20chloronani). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
22. ICTV. "Pospiviroid machoplantae: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304530&taxon\_name=Pospiviroid%20machoplantae). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
23. ICTV. "Pospiviroid exocortiscitri: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304523&taxon\_name=Pospiviroid%20exocortiscitri). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
24. ICTV. "Pospiviroid impedichrysanthemi: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304522&taxon\_name=Pospiviroid%20impedichrysanthemi). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
25. ICTV. "Pospiviroid apicimpeditum: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304528&taxon\_name=Pospiviroid%20apicimpeditum). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
26. ICTV. "Pospiviroid alphasinis: Taxon Details" (https://ictv.global/taxonomy/taxondetails?taxnode\_id=202304525&taxon\_name=Pospiviroid%20alphasinis). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.

27. ICTV. "Pospiviroid latenscolumneae: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=2304524&taxon\\_name=Pospiviroid%20latenscolumneae](https://ictv.global/taxonomy/taxondetails?taxnode_id=2304524&taxon_name=Pospiviroid%20latenscolumneae)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
28. ICTV. "Pospiviroid latensportulacae: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=2313877&taxon\\_name=Pospiviroid%20latensportulacae](https://ictv.global/taxonomy/taxondetails?taxnode_id=2313877&taxon_name=Pospiviroid%20latensportulacae)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
29. ICTV. "Pospiviroid parvicapsici: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304526&taxon\\_name=Pospiviroid%20parvicapsici](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304526&taxon_name=Pospiviroid%20parvicapsici)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
30. ICTV. "Hostuviroid impedi humuli: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304520&taxon\\_name=Hostuviroid%20impedi humuli](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304520&taxon_name=Hostuviroid%20impedi humuli)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
31. ICTV. "Hostuviroid latensdahliae: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304519&taxon\\_name=Hostuviroid%20latensdahliae](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304519&taxon_name=Hostuviroid%20latensdahliae)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
32. ICTV. "Cocadviroid cadangi: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304511&taxon\\_name=Cocadviroid%20cadangi](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304511&taxon_name=Cocadviroid%20cadangi)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
33. ICTV. "Cocadviroid tinangajae: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304512&taxon\\_name=Cocadviroid%20tinangajae](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304512&taxon_name=Cocadviroid%20tinangajae)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
34. ICTV. "Cocadviroid latenshumuli: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304513&taxon\\_name=Cocadviroid%20latenshumuli](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304513&taxon_name=Cocadviroid%20latenshumuli)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
35. ICTV. "Cocadviroid rimocitri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304510&taxon\\_name=Cocadviroid%20rimocitri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304510&taxon_name=Cocadviroid%20rimocitri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
36. ICTV. "Apscaviroid cicatricimali: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304500&taxon\\_name=Apscaviroid%20cicatricimali](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304500&taxon_name=Apscaviroid%20cicatricimali)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
37. ICTV. "Apscaviroid fossulamali: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304499&taxon\\_name=Apscaviroid%20fossulamali](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304499&taxon_name=Apscaviroid%20fossulamali)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
38. ICTV. "Apscaviroid alphaflavivitis: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304506&taxon\\_name=Apscaviroid%20alphaflavivitis](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304506&taxon_name=Apscaviroid%20alphaflavivitis)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
39. ICTV. "Apscaviroid betaflavivitis: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304507&taxon\\_name=Apscaviroid%20betaflavivitis](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304507&taxon_name=Apscaviroid%20betaflavivitis)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
40. ICTV. "Apscaviroid curvifoliumcitri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304502&taxon\\_name=Apscaviroid%20curvifoliumcitri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304502&taxon_name=Apscaviroid%20curvifoliumcitri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
41. ICTV. "Apscaviroid pustulapyri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304508&taxon\\_name=Apscaviroid%20pustulapyri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304508&taxon_name=Apscaviroid%20pustulapyri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
42. ICTV. "Apscaviroid austravitis: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304501&taxon\\_name=Apscaviroid%20austravitis](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304501&taxon_name=Apscaviroid%20austravitis)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
43. ICTV. "Apscaviroid maculamali: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313867&taxon\\_name=Apscaviroid%20maculamali](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313867&taxon_name=Apscaviroid%20maculamali)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
44. ICTV. "Apscaviroid etacitri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313868&taxon\\_name=Apscaviroid%20etacitri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313868&taxon_name=Apscaviroid%20etacitri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
45. ICTV. "Apscaviroid dendrobii: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313869&taxon\\_name=Apscaviroid%20dendrobii](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313869&taxon_name=Apscaviroid%20dendrobii)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
46. ICTV. "Apscaviroid latensvitis: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313870&taxon\\_name=Apscaviroid%20latensvitis](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313870&taxon_name=Apscaviroid%20latensvitis)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
47. ICTV. "Apscaviroid litchis: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313871&taxon\\_name=Apscaviroid%20litchis](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313871&taxon_name=Apscaviroid%20litchis)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
48. ICTV. "Apscaviroid latenspruni: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313874&taxon\\_name=Apscaviroid%20latenspruni](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313874&taxon_name=Apscaviroid%20latenspruni)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
49. ICTV. "Apscaviroid diospyri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313872&taxon\\_name=Apscaviroid%20diospyri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313872&taxon_name=Apscaviroid%20diospyri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
50. ICTV. "Apscaviroid betadiospyri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313873&taxon\\_name=Apscaviroid%20betadiospyri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313873&taxon_name=Apscaviroid%20betadiospyri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
51. ICTV. "Apscaviroid nanocitri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304503&taxon\\_name=Apscaviroid%20nanocitri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304503&taxon_name=Apscaviroid%20nanocitri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
52. ICTV. "Apscaviroid epsiloncitri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304504&taxon\\_name=Apscaviroid%20epsiloncitri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304504&taxon_name=Apscaviroid%20epsiloncitri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
53. ICTV. "Apscaviroid zetacitri: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304505&taxon\\_name=Apscaviroid%20zetacitri](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304505&taxon_name=Apscaviroid%20zetacitri)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
54. ICTV. "Apscaviroid japanvitis: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202319071&taxon\\_name=Apscaviroid%20japanvitis](https://ictv.global/taxonomy/taxondetails?taxnode_id=202319071&taxon_name=Apscaviroid%20japanvitis)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.



55. ICTV. "Coleviroid alphacolei: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304515&taxon\\_name=Coleviroid%20alphacolei](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304515&taxon_name=Coleviroid%20alphacolei)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
56. ICTV. "Coleviroid betacolei: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304516&taxon\\_name=Coleviroid%20betacolei](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304516&taxon_name=Coleviroid%20betacolei)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
57. ICTV. "Coleviroid gammacolei: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202304517&taxon\\_name=Coleviroid%20gammacolei](https://ictv.global/taxonomy/taxondetails?taxnode_id=202304517&taxon_name=Coleviroid%20gammacolei)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
58. ICTV. "Coleviroid epsiloncolei: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313875&taxon\\_name=Coleviroid%20epsiloncolei](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313875&taxon_name=Coleviroid%20epsiloncolei)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
59. ICTV. "Coleviroid zetacolei: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202313876&taxon\\_name=Coleviroid%20zetacolei](https://ictv.global/taxonomy/taxondetails?taxnode_id=202313876&taxon_name=Coleviroid%20zetacolei)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
60. ICTV. "Avsunviroid albamaculaperseae: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202302648&taxon\\_name=Avsunviroid%20albamaculaperseae](https://ictv.global/taxonomy/taxondetails?taxnode_id=202302648&taxon_name=Avsunviroid%20albamaculaperseae)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
61. ICTV. "Pelamoviroid latenspruni: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202302653&taxon\\_name=Pelamoviroid%20latenspruni](https://ictv.global/taxonomy/taxondetails?taxnode_id=202302653&taxon_name=Pelamoviroid%20latenspruni)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
62. ICTV. "Pelamoviroid maculachrysanthemi: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202302652&taxon\\_name=Pelamoviroid%20maculachrysanthemi](https://ictv.global/taxonomy/taxondetails?taxnode_id=202302652&taxon_name=Pelamoviroid%20maculachrysanthemi)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
63. ICTV. "Pelamoviroid malleusmali: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202307651&taxon\\_name=Pelamoviroid%20malleusmali](https://ictv.global/taxonomy/taxondetails?taxnode_id=202307651&taxon_name=Pelamoviroid%20malleusmali)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
64. ICTV. "Elaviroid latensmelongenae: Taxon Details" ([https://ictv.global/taxonomy/taxondetails?taxnode\\_id=202302650&taxon\\_name=Elaviroid%20latensmelongenae](https://ictv.global/taxonomy/taxondetails?taxnode_id=202302650&taxon_name=Elaviroid%20latensmelongenae)). *ICTV Taxonomy Browser*. Retrieved 9 December 2024.
65. De Bokx JA, Piron PG (1981). "Transmission of potato spindle tuber viroid by aphids". *Netherlands Journal of Plant Pathology*. **87** (2): 31–34. Bibcode:1981EJPP...87...31D (<https://ui.adsabs.harvard.edu/abs/1981EJPP...87...31D>). doi:10.1007/bf01976653 (<https://doi.org/10.1007%2Fbf01976653>). S2CID 44660564 (<https://api.semanticscholar.org/CorpusID:44660564>).
66. Flores R, Serra P, Minoia S, Di Serio F, Navarro B (2012). "Viroids: from genotype to phenotype just relying on RNA sequence and structural motifs" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3376415>). *Frontiers in Microbiology*. **3**: 217. doi:10.3389/fmicb.2012.00217 (<https://doi.org/10.3389%2Ffmicb.2012.00217>). PMC 3376415 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3376415>). PMID 22719735 (<https://pubmed.ncbi.nlm.nih.gov/22719735>).
67. Flores R, Navarro B, Kovalskaya N, Hammond RW, Di Serio F (October 2017). "Engineering resistance against viroids". *Current Opinion in Virology*. **26**: 1–7. doi:10.1016/j.coviro.2017.07.003 (<https://doi.org/10.1016%2Fj.coviro.2017.07.003>). hdl:10251/107457 (<https://hdl.handle.net/10251%2F107457>). PMID 28738223 (<https://pubmed.ncbi.nlm.nih.gov/28738223>).
68. Hammond RW (April 1992). "Analysis of the virulence modulating region of potato spindle tuber viroid (PSTVd) by site-directed mutagenesis" (<https://zenodo.org/record/1258280>). *Virology*. **187** (2): 654–662. doi:10.1016/0042-6822(92)90468-5 (<https://doi.org/10.1016%2F0042-6822%2892%2990468-5>). PMID 1546460 (<https://pubmed.ncbi.nlm.nih.gov/1546460>).
69. Wang MB, Bian XY, Wu LM, Liu LX, Smith NA, Isenegger D, et al. (March 2004). "On the role of RNA silencing in the pathogenicity and evolution of viroids and viral satellites" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC365780>). *Proceedings of the National Academy of Sciences of the United States of America*. **101** (9): 3275–3280. Bibcode:2004PNAS..101.3275W (<https://ui.adsabs.harvard.edu/abs/2004PNAS..101.3275W>). doi:10.1073/pnas.0400104101 (<https://doi.org/10.1073%2Fpnas.0400104101>). PMC 365780 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC365780>). PMID 14978267 (<https://pubmed.ncbi.nlm.nih.gov/14978267>).
70. Pallas V, Martinez G, Gomez G (2012). "The Interaction Between Plant Viroid-Induced Symptoms and RNA Silencing". *Antiviral Resistance in Plants*. Methods in Molecular Biology. Vol. 894. pp. 323–343. doi:10.1007/978-1-61779-882-5\_22 ([https://doi.org/10.1007%2F978-1-61779-882-5\\_22](https://doi.org/10.1007%2F978-1-61779-882-5_22)). hdl:10261/74632 (<https://hdl.handle.net/10261%2F74632>). ISBN 978-1-61779-881-8. PMID 22678590 (<https://pubmed.ncbi.nlm.nih.gov/22678590>).
71. Balázs E, Hegedűs K, Divéki Z (15 April 2022). "The unique carnation stunt-associated pararetroviroid". *Virus Research*. **312** 198709. doi:10.1016/j.virusres.2022.198709 (<https://doi.org/10.1016%2Fj.virusres.2022.198709>). PMID 35183574 (<https://pubmed.ncbi.nlm.nih.gov/35183574>). S2CID 246987005 (<https://api.semanticscholar.org/CorpusID:246987005>).
72. Sutela S, Forgia M, Vainio EJ, Chiapello M, Daghino S, Vallino M, Martino E, Girlanda M, Perotto S, Turina M (1 July 2020). "The virome from a collection of endomycorrhizal fungi reveals new viral taxa with unprecedented genome organization" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7724248>). *Virus Evolution*. **6** (2) veaa076. doi:10.1093/ve/veaa076 (<https://doi.org/10.1093%2Fve%2Fveaa076>). PMC 7724248 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7724248>). PMID 33324490 (<https://pubmed.ncbi.nlm.nih.gov/33324490>).

73. Chong LC, Lauber C (12 May 2023). "Viroid-like RNA-dependent RNA polymerase-encoding ambiviruses are abundant in complex fungi" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10237039>). *Frontiers in Microbiology*. **14**. doi:10.3389/fmicb.2023.1144003 (<https://doi.org/10.3389%2Fmicb.2023.1144003>). PMC 10237039 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10237039>). PMID 37275138 (<https://pubmed.ncbi.nlm.nih.gov/37275138>).
74. "ICTV Virus Taxonomy: 2023 Release" (<https://ictv.global/taxonomy>). ICTV. Retrieved 2 May 2024.
75. Daròs JA, Flores R (1995). "Identification of a retroviroid-like element from plants" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC41428>). *Proceedings of the National Academy of Sciences of the United States of America*. **92** (15): 6856–6860. Bibcode:1995PNAS...92.6856D (<https://ui.adsabs.harvard.edu/abs/1995PNA...92.6856D>). doi:10.1073/pnas.92.15.6856 (<https://doi.org/10.1073%2Fpnas.92.15.6856>). PMC 41428 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC41428>). PMID 7542779 (<https://pubmed.ncbi.nlm.nih.gov/7542779>).
76. Hegedűs K, Palkovics L, Tóth EK, Dallmann G, Balázs E (March 2001). "The DNA form of a retroviroid-like element characterized in cultivated carnation species" (<https://doi.org/10.1099%2F0022-1317-82-3-687>). *The Journal of General Virology*. **82** (Pt 3): 687–691. doi:10.1099/0022-1317-82-3-687 (<https://doi.org/10.1099%2F0022-1317-82-3-687>). PMID 11172112 (<https://pubmed.ncbi.nlm.nih.gov/11172112>).
77. Hegedűs K, Dallmann G, Balázs E (2004). "The DNA form of a retroviroid-like element is involved in recombination events with itself and with the plant genome" (<https://doi.org/10.1016%2Fj.virol.2004.04.035>). *Virology*. **325** (2): 277–286. doi:10.1016/j.virol.2004.04.035 (<https://doi.org/10.1016%2Fj.virol.2004.04.035>). PMID 15246267 (<https://pubmed.ncbi.nlm.nih.gov/15246267>).
78. Truong LN, Li Y, Shi LZ, Hwang PY, He J, Wang H, et al. (May 2013). "Microhomology-mediated End Joining and Homologous Recombination share the initial end resection step to repair DNA double-strand breaks in mammalian cells" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3651503>). *Proceedings of the National Academy of Sciences of the United States of America*. **110** (19): 7720–25. Bibcode:2013PNAS..110.7720T (<https://ui.adsabs.harvard.edu/abs/2013PNAS..110.7720T>). doi:10.1073/pnas.1213431110 (<https://doi.org/10.1073%2Fpnas.1213431110>). PMC 3651503 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3651503>). PMID 23610439 (<https://pubmed.ncbi.nlm.nih.gov/23610439>).
79. Flores R, Gago-Zachert S, Serra P, Sanjuán R, Elena SF (June 18, 2014). "Viroids: survivors from the RNA world?" (<https://digital.csic.es/bitstream/10261/107724/1/Annu.%20Rev.%20Microbiol.%20Flores%20et%20a%202014.pdf>) (PDF). *Annual Review of Microbiology*. **68**: 395–414. doi:10.1146/annurev-micro-091313-103416 (<https://doi.org/10.1146%2Fannurev-micro-091313-103416>). hdl:10261/107724 (<https://hdl.handle.net/10261%2F107724>). PMID 25002087 (<https://pubmed.ncbi.nlm.nih.gov/25002087>).
80. Hull R (October 2013). "Chapter 5: Agents Resembling or Altering Virus Diseases" (<https://books.google.com/books?id=PYrZAAAAQBAJ&pg=PA199>). *Plant virology* (Fifth ed.). London, UK: Academic Press. ISBN 978-0-12-384872-7.
81. Breit TM, de Leeuw WC, van Olst M, Ensink WA, van Leeuwen S, Dekker RJ (16 March 2023). "Genome Sequence of a New Carnation Small Viroid-Like RNA, CarSV-1" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10019309>). *Microbiology Resource Announcements*. **12** (3) e0121922. doi:10.1128/mra.01219-22 (<https://doi.org/10.1128%2Fmra.01219-22>). PMC 10019309 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10019309>). PMID 36840552 (<https://pubmed.ncbi.nlm.nih.gov/36840552>).
82. Koumoundouros T (29 January 2024). "'Obelisks': Entirely New Class of Life Has Been Found in The Human Digestive System" (<https://www.sciencealert.com/obelisks-entirely-new-class-of-life-has-been-found-in-the-human-digestive-system>). *ScienceAlert*. Archived (<https://archive.today/20240129133614/https://www.sciencealert.com/obelisks-entirely-new-class-of-life-has-been-found-in-the-human-digestive-system>) from the original on 29 January 2024. Retrieved 29 January 2024.
83. Zheludev IN, Edgar RC, Lopez-Galiano MJ, de la Peña M, Artem B, Bhatt AS, Fire AZ (21 January 2024). "Viroid-like colonists of human microbiomes" (<https://www.biorxiv.org/content/10.1101/2024.01.20.576352v1.full>). *bioRxiv*. bioRxiv 10.1101/2024.01.20.576352 (<https://doi.org/10.1101%2F2024.01.20.576352>). doi:10.1101/2024.01.20.576352 (<https://doi.org/10.1101%2F2024.01.20.576352>). PMC 10827157 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10827157>). PMID 38293115 (<https://pubmed.ncbi.nlm.nih.gov/38293115>). Wikidata Q124389714. Archived (<https://web.archive.org/web/20240129125227/https://www.biorxiv.org/content/10.1101/2024.01.20.576352v1.full>) from the original on 29 January 2024. Retrieved 29 January 2024.
84. Diener, T O. "Circular RNAs: relics of precellular evolution?." *Proc.Natl.Acad.Sci.USA*, 1989;86(23):9370-9374
85. Wu Q, Ding SW, Zhang Y, Zhu S (2015). "Identification of viruses and viroids by next-generation sequencing and homology-dependent and homology-independent algorithms" (<https://doi.org/10.1146%2Fannurev-phyto-080614-120030>). *Annual Review of Phytopathology*. **53**: 425–44. doi:10.1146/annurev-phyto-080614-120030 (<https://doi.org/10.1146%2Fannurev-phyto-080614-120030>). PMID 26047558 (<https://pubmed.ncbi.nlm.nih.gov/26047558>).
86. Owens RA, Verhoeven JT (2009). "Potato Spindle Tuber". *Plant Health Instructor*. doi:10.1094/PHI-I-2009-0804-01 (<https://doi.org/10.1094%2FPHI-I-2009-0804-01>).

87. Pommerville JC (2014). *Fundamentals of Microbiology*. Burlington, MA: Jones and Bartlett Learning. p. 482. ISBN 978-1-284-03968-9.
88. Sanger HL, Klotz G, Riesner D, Gross HJ, Kleinschmidt AK (November 1976). "Viroids are single-stranded covalently closed circular RNA molecules existing as highly base-paired rod-like structures" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC431239>). *Proceedings of the National Academy of Sciences of the United States of America*. **73** (11): 3852–6. Bibcode:1976PNAS...73.3852S (<https://ui.adsabs.harvard.edu/abs/1976PNAS...73.3852S>). doi:10.1073/pnas.73.11.3852 (<https://doi.org/10.1073/pnas.73.11.3852>). PMC 431239 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC431239>). PMID 1069269 (<https://pubmed.ncbi.nlm.nih.gov/1069269>).
89. Wang Y (April 2021). "Current view and perspectives in viroid replication" (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8068583>). *Current Opinion in Virology*. **47**: 32–37. doi:10.1016/j.coviro.2020.12.004 (<https://doi.org/10.1016/j.coviro.2020.12.004>). PMC 8068583 (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8068583>). PMID 33460914 (<https://pubmed.ncbi.nlm.nih.gov/33460914>).
90. Sogo JM, Koller T, Diener TO (September 1973). "Potato spindle tuber viroid. X. Visualization and size determination by electron microscopy". *Virology*. **55** (1): 70–80. doi:10.1016/s0042-6822(73)81009-8 ([https://doi.org/10.1016/s0042-6822\(73\)81009-8](https://doi.org/10.1016/s0042-6822(73)81009-8)). PMID 4728831 (<https://pubmed.ncbi.nlm.nih.gov/4728831>).
91. Gross HJ, Domdey H, Lossow C, Jank P, Raba M, Alberty H, Sanger HL (May 1978). "Nucleotide sequence and secondary structure of potato spindle tuber viroid". *Nature*. **273** (5659): 203–8. Bibcode:1978Natur.273..203G (<https://ui.adsabs.harvard.edu/abs/1978Natur.273..203G>). doi:10.1038/273203a0 (<https://doi.org/10.1038/273203a0>). PMID 643081 (<https://pubmed.ncbi.nlm.nih.gov/643081>). S2CID 19398777 (<https://api.semanticscholar.org/CorpusID:19398777>).
92. Hammond RW, Owens RA (2006). "Viroids: New and Continuing Risks for Horticultural and Agricultural Crops". *APSnet Feature Articles*. doi:10.1094/APSnetFeature-2006-1106 (<https://doi.org/10.1094/APSnetFeature-2006-1106>).
93. Zimmer C (September 25, 2014). "A Tiny Emissary From the Ancient Past" (<https://www.nytimes.com/2014/09/25/science/a-tiny-emissary-from-the-ancient-past.html>). *New York Times*. Retrieved November 22, 2014.

## External links

- [Viroids/ATSU](http://www.atsu.edu/faculty/chamberlain/Website/Lects/Prions.htm) (<http://www.atsu.edu/faculty/chamberlain/Website/Lects/Prions.htm>)
- [ViroidDB](https://viroids.org/) (<https://viroids.org/>), a database of viroids and viroid-like circular RNAs

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