

# Viroid

**Viroids** are the smallest infectious pathogens known. They are composed solely of a short strand of circular, single-stranded **RNA** that has no protein coating. All known viroids are inhabitants of **higher plants**, and most cause diseases, whose respective economic importance on humans vary widely.

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 by **Dmitri Iosifovich Ivanovsky** (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>[1]</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>[2][3]</sup> This viroid is now called Potato spindle tuber viroid, abbreviated PSTVd.

Although viroids are composed of nucleic acid, they do not code for any **protein**.<sup>[4][5]</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. Some viroids are **ribozymes**, having **catalytic** properties that allow self-cleavage and ligation of unit-size genomes from larger replication intermediates.<sup>[6]</sup>

With Diener's 1989 hypothesis<sup>[7]</sup> that viroids may represent "living relics" from the widely assumed, ancient, and non-cellular **RNA world**—extant before the evolution of DNA or proteins—viroids have assumed significance beyond plant pathology to evolutionary science, by representing the most plausible RNAs capable of performing crucial steps in **abiogenesis**, the evolution of life from inanimate matter.

The human pathogen **hepatitis D virus** is a subviral agent similar to a viroid.<sup>[8]</sup>

<b>Viroid</b>	
<span></span>	
<b>Virus classification</b> <span><span></span></span>	
(unranked):	<b>Viroid</b>
<b>Families</b>	
<i>Pospiviroidae</i>	
<i>Avsunviroidae</i>	

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## Taxonomy

- Family **Pospiviroidae**
  - Genus *Pospiviroid*; type species: *Potato spindle tuber viroid*; 356–361 nucleotides(nt)<sup>[9]</sup>
  - Genus *Pospiviroid*; another species: *Citrus exocortis viroid*; 368–467 nt<sup>[9]</sup>
  - Genus *Hostuviroid*; type species: *Hop stunt viroid*; 294–303 nt<sup>[9]</sup>
  - Genus *Cocadviroid*; type species: *Coconut cadang-cadang viroid*; 246–247 nt<sup>[9]</sup>
  - Genus *Apscaviroid*; type species: *Apple scar skin viroid*; 329–334 nt<sup>[9]</sup>
  - Genus *Coleviroid*; type species: *Coleus blumei viroid 1*; 248–251 nt<sup>[9]</sup>



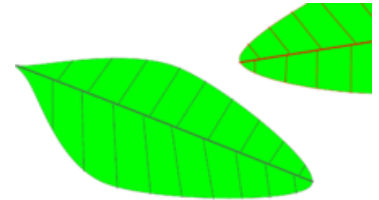
Putative secondary structure of the PSTVd viroid. The highlighted nucleotides are found in most other viroids.

- Family *Avsunviroidae*

- Genus *Avsunviroid*; type species: *Avocado sunblotch viroid*; 246–251 nt<sup>[9]</sup>
- Genus *Pelamoviroid*; type species: *Peach latent mosaic viroid*; 335–351 nt<sup>[9]</sup>
- Genus *Elaviroid*; type species: *Eggplant latent viroid*; 332–335 nt<sup>[9]</sup>

## Transmission

Viroid infections can be transmitted 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>[9][10]</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.

## Replication

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>[11][12]</sup>

## RNA silencing

There has long been uncertainty over how viroids induce symptoms in plants without encoding any protein products within their sequences. Evidence suggests that RNA silencing is involved in the process. First, changes to the viroid genome can dramatically alter its virulence.<sup>[13]</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>[14]</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>[15]</sup>

## RNA world hypothesis

Diener's 1989 hypothesis<sup>[16]</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>[17]</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.

## History

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>[18]</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>[3]</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>[2]</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 nucleobases) of single-stranded RNA and, unlike viruses, did not have a protein coat. Compared with other infectious plant pathogens, viroids are extremely small in size, ranging from 246 to 467 nucleobases; 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 nucleobases long.<sup>[19]</sup>

In 1976, Sanger et al.<sup>[20]</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 together. Sanger et al. also provided evidence for the true circularity of viroids by finding that the RNA could not be phosphorylated at the 5' terminus. Then, 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.

The single-strandedness and circularity of viroids was confirmed by electron microscopy,<sup>[21]</sup> and Gross et al. determined the complete nucleotide sequence of potato spindle tuber viroid in 1978.<sup>[22]</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>[19][23]</sup>

In 2014, *New York Times* science writer Carl Zimmer published a popularized piece that mistakenly credited Flores et al. with the hypothesis' original conception.<sup>[24]</sup>

## See also

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

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## External links

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- [Viroids/ATSU \(http://www.atsu.edu/faculty/chamberlain/Website/Lects/Prions.htm\)](http://www.atsu.edu/faculty/chamberlain/Website/Lects/Prions.htm)
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