Review

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An update on cactus viruses (2025)

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ABSTRACT: The Cactaceae family is known for its adaptation to dry habitats and peculiar morphology of different forms and sizes, composed of perennial succulent stem-bearing spine plants, lacking broad green leaves. Cactaceous plants have been cultivated for food production, medicinal and cosmetic products, animal fodder, construction, and ornamental applications. Among them, the widely cultivated dragon fruit (genus *Hylocereus* and *Selenicereus*) is gaining prominence. Physiologically, they have reduced their photorespiration and achieved higher water-use efficiency rates than the other metabolic types. For this reason, cacti have the potential to become a stable food source in the future scenario of global climate change. Many pests and diseases have been described affecting cactaceous plants, including viruses. Viral infection of cacti is mostly asymptomatic though examples of mottling, chlorotic, or necrotic ringspots have been described, and their economic impact is unknown as yet. The cytopathic effect, such as spindle-shaped inclusions in epidermal and parenchymal cells, was first observed in the late 19th century. Subsequently, it was discovered that they were indeed aggregate particles of potexvirus. Until the turn of the 21st century, few viruses among cacti were known (genera *Potexvirus, Tobamovirus, Carlavirus,* and *Alphacarmovirus*); however, since the advent of advances in molecular tools, several new cactus viruses (families *Tospoviridae, Solemoviridae, Caulimoviridae, Geminiviridae* and *Genomoviridae*) have been described. Currently, 31 distinct virus species, belonging to 13 genera of nine families, as well as three viroids of two genera, have been documented to naturally infect cacti. This review updates the number of known cactus viruses, providing a brief description of each of them.

Keywords: *Hylocereus*, *Selenicereus*, *Opuntia*, Cactaceae, virome

Introduction

The Cactaceae family is recognized for its distinctive morphology, diverse forms, and varied sizes, as well as its adaptation to dry environments (Nobel, 2002). Generally, a cactus lacks typical broad green leaves. Instead, the leaves have become the signature spines produced on highly specialized axillary buds, known as areoles. Cacti belong to the Caryophyllales order, with five subfamilies: Pereskeoideae, Leuenbergioideae, Maihuenioideae, Opuntioideae, and Cactoideae (Stevens, 2017; Kamikawachi, 2019; Singh, 2019; Anderson, 2001; Nobel, 2002). These subfamilies are subdivided based on structural criteria, such as the presence or absence of leaves, aspects of the seeds, and the presence or absence of glochidia (Nobel, 2002). The family Cactaceae consists of 177 genera, from which 2,360 different species are grouped (Lodé, 2015).

These perennial succulent stem plants are native to the New World, ranging from Canada to the Southern tip of South America (Anderson, 2001). It has a wide ecological and climatic range, comprising deserts with limited rain such as western Atacama, Chile, at one extreme to the tropical rainforest at the other (Taylor, 1997); their endemism and center of diversity are located in Mexico, the southern United States, the central region of the Andes Mountains, and eastern Brazil (Taylor and Zappi, 2004). Due to their Crassulacean Acid Metabolism (CAM) pathway, Cactaceae plants can reduce their photorespiration and achieve higher water use efficiency rates than other metabolism types. Thus, cacti demonstrate a remarkable ability to thrive in water-constrained environments, emerging as innovative food and water resources, playing a crucial role in the future scenario of minimum demand for irrigation and water-stress tolerance (Mizrahi et al., 2002).

Archaeological records indicate the presence of cacti plants around 12,000 and 9,000 years ago associated with human activities. One such record was found in a cave at Serra da Capivara, in the state of Piauí, Brazil, where the painting depicted what appeared to be *Tacinga inamoena* (K. Schum.) N. P. Taylor & Stuppy. The production of fishhooks from the spines of *Neoraimondia arequipensis* (Meyen) Backeb. is another example from the pre-Ceramic period. Numerous other data support cacti becoming a significant element in human subsistence following the human migration from North and South America, nearly 40,000 years ago (Anderson, 2001).

Cacti plants have had significance as cultural, religious, and food sources. *Lophophora williamsii* (Lem. ex J. F. Cels) J. M. Coult. (peyote) and *Echinopsis pachanoi* (Britton & Rose) H. Friedrich & G. D. Rowley (San Pedro cactus), which contains the mind-affecting alkaloid mescaline, were used in the religious-medicinal practices of Native Americans. Saguaro (*Carnegiea gigantea* Britton & Rose) and Indian fig cactus [*Opuntia ficus-indica* (L.)

Mill.] have had a significant role in ancient cultures such as provision of wine and food, respectively (Anderson, 2001). Plants of the genus *Opuntia*, commonly known as prickly pears and nopales, are used to cultivate female cochineal insects (*Dactylopius coccus* Costa), which produce the dye carminic acid. This dye remains widely in use in the food, textile, cosmetic, and pharmaceutical industries (Greenfield, 2009; Galappaththi and Patabendige, 2021; Renita et al., 2023).

In the modern context, cacti have a diverse range of uses: human and animal food, medicine, ornamental, living fence, ceremonial and religious cults, sources of dye, horticulture, and other common usages, especially by indigenous and rural populations, in areas where cacti are abundant (Anderson, 2001; Lucena et al., 2013). New applications have emerged, such as employing 'leather' made from *O. ficus-indica* by craftsmen for the production of shoes and bags, registered as Desserto® (Desserto, 2023). In cosmetics, extracts from *Cereus jamacaru* Hort. Vindob. ex Salm-Dyck, known as Mandacaru, are also utilized (L'occitane au Brésil, 2016). Another tendency is the inclusion of some cacti, such as *Cereus hildmannianus* Schumann, *Opuntia cochenillifera* (L.) Mill., *O. ficus-indica*, *Pereskia aculeata* (L.) Karsten among "Non-Conventional Food Plants" (Kinupp and Lorenzi, 2014; Sartori et al., 2020).

Within this family, dragon fruit (species of *Hylocereus* and *Selenicereus*- see below) has gained significant economic relevance internationally. Originally from Central and South America, its production is distributed among most of these countries, and the fruit has now been introduced in the Bahamas, Bermuda, the United States, Australia, Israel, and the Asian continent. Recently, dragon fruit has become a significant crop in Southeast Asia, having been the world's largest producer since its introduction in the 16th century. The high aggregated value of the fruit, combined with its growing demand, makes the cultivation of this fruit tree especially attractive (Ortiz-Hernández and Carrillo-Salazar, 2012; Faleiro, 2022).

Authors have cited dragon fruit as belonging to the genera *Hylocereus* and *Selenicereus,* with a preference for *Hylocereus.* Although Korotkova et al. (2017) used various comparisons to conclude that both genera are similar and suggested merging them under the name *Selenicereus*, a preference favors *Hylocereus*. Among the 14 species of this genus, four are the most cultivated worldwide: *Hylocereus undatus* (Haw.) Britton & Rose; *H. monacanthus* (Lem.) Britton & Rose (Syn. *H. polyrhizus*); *H. costaricensis* Britton & Rose; and *H. megalanthus* (K. Schum. ex Vaupel) Ralf Bauer (Syn. *Selenicereus megalanthus*). However, it has been challenging to identify dragon fruit species and cultivars due to intense intra- and interspecific hybridization (Abirami et al., 2021).

The global dragon fruit market is estimated to be worth almost US$ 14 billion in 2024, and is expected to reach US$ 18 billion by 2029 (Mordorintelligence, 2024). Vietnam is one of the world's largest dragon fruit producers, with a planted area of more than 55,000 ha and an average productivity of 22-35 ton ha^{-1}. Together with Indonesia and China, they represent over 90 % of the world's dragon fruit production (Dragonfruit.net, 2024). The leading dragon fruit importers are the United States, Germany, France, the Netherlands, Russia, the United Kingdom and Canada (Faleiro, 2022; Dragonfruit.net, 2024).

Several pests and diseases have been reported affecting Cactaceae, including viruses (Zimmermann and Granata, 2002). Initial studies identified mainly potexviruses, tobamoviruses, and carlaviruses (Chessin, 2002). Until 2019, the comprehensive list of plant viruses compiled by Sastry et al. (2019) included a several species from the genera *Orthotospovirus* and *Polerovirus*. Because of the rapidly expanding culture of dragon fruit worldwide, more attention has been focused on viral diseases. Moreover, the intensive use of genome sequencing techniques allowed for the detection and identification of numerous new viruses infecting cacti, mostly in asymptomatic plants. In this review, we update and provide brief comment on viruses identified as naturally infecting species of the Cactaceae family.

Viruses in Cactaceae

Observation of spindle-shaped inclusion in epidermal cells of *Epiphyllum* sp. by Molisch (1885), now known to be the aggregate of the potexvirus cactus virus X (CVX) particles (Amelunxen, 1958; Brandes and Wetter, 1959), is the oldest report of cactus viruses. This initial description of CVX in cacti was followed by the finding of the tobamovirus Sammon's Opuntia virus (SOV) (Sammons and Chessin, 1961) and the alphacarmovirus saguaro cactus virus (SgCV) (Milbrath, 1971; Milbrath et al., 1973). After these pioneering works, new potexvirus and tobamovirus species as well as viruses of the genera *Carlavirus, Orthotospovirus* and *Polerovirus* infecting cacti have been described (Brunt et al., 1990; Chessin, 2002; Sastry et al., 2019).

In the last decade, use of genome sequencing has revealed new viruses, with DNA genome (families *Caulimoviridae* and *Geminiviridae*), in the genera *Badnavirus, Cavemovirus, Becurtovirus, Opunvirus, Gemykolovirus, Gemyduguivirus, Gemygorvirus, Gemykroznavirus, Gemycircularvirus*, and *Gemykibivirus,* mostly in asymptomatic cacti (Lan et al., 2019; Zheng et al., 2020; Fontenele et al., 2020a, b; 2021a). Furthermore, three viroids were detected by High-Throughput Sequencing (HTS) in *O. ficus-indica* in Mexico (Ortega-Acosta et al., 2023; 2024).

Presently, 31 distinct virus species, belonging to 13 genera and nine families, and three viroids, from two genera, were found to be naturally infecting Cactaceae plants (Table 1). Table 2 presents a list of species of Cactaceae found naturally infected by one or more viruses, as well as the three viroids identified in Mexico. Most of them seem to be specific to cacti (genera *Potexvirus*,

Table 1 – List of viruses and viroids described infecting Cactaceae plants.

Family; genus	Virus and viroid species	Host plant where description was made	References#	Geographical distribution
Geminiviridae; *Opunvirus*	*Opunvirus opuntiae* (OpV1)	*Opuntia* spp.	Fontenele et al. (2020b, 2021a)	USA
Geminiviridae; *Becurtovirus*	*Becurtovirus spinaciae* (SCTAV)	*Opuntia* spp.	Fontenele et al. (2021a)	USA
Geminiviridae; putative *Becurtovirus*	"*Opuntia virus 2*" (OpV2)*	*Opuntia* spp.	Fontenele et al. (2021a)	USA
Geminiviridae; unclassified	Utkilio virus	*Opuntia discolor*	Fontenele et al. (2021b)	Bolivia
Genomoviridae; *Gemycircularvirus*	*Gemycircularvirus opunt1* (PaGmV25)	*Opuntia* sp.	Fontenele et al. (2020a)	France
Genomoviridae; *Gemygorvirus*	*Gemygorvirus opunt1* (PaGmV26)	*Opuntia* sp.	Fontenele et al. (2020a)	USA
Genomoviridae; *Gemykibivirus*	PaGmV 27**	*Cylindropuntia ramosissima*	Fontenele et al. (2020a)	USA
	PaGmV 28**	*Carnegiea gigantea*	Fontenele et al. (2020a)	USA
	Gemykibivirus planta2 (PaGmV 29)	*C. gigantea*	Fontenele et al. (2020a)	USA
Virgaviridae; *Tobamovirus*	*Tobamovirus cacti* (CMMoV)	*Gymnocalycium mihanovichii*	Min et al. (2006a, 2006b)	South Korea
Virgaviridae; *Tobamovirus*	"*Opuntia virus 2*" (OpV2)*	*Opuntia* spp.	Salgado-Ortíz et al. (2020)	Mexico
Virgaviridae; *Tobamovirus*	*Tobamovirus muricaudae* (RCNaV)	*Aporocactus flagelliformis*	Kim et al. (2012b)	South Korea
Virgaviridae; *Tobamovirus*	*T. muricaudae* (RCNaV)	*Opuntia macrocentra*	Murcia-Bermudez et al. (2024)	USA
Virgaviridae; *Tobamovirus*	*T. muricaudae* (RCNaV)	*Notocactus leninghausii* f. *cristatus*	Park et al. (2018)	South Korea
Virgaviridae; *Tobamovirus*	*T. muricaudae* (RCNaV)	*Opuntia albicarpa*	De La Torre-Almaráz et al. (2016a)	Mexico
Virgaviridae; *Tobamovirus*	*T. muricaudae* (RCNaV)	*Opuntia leucotricha*	Guimarães et al. (2025)	Brazil
Virgaviridae; *Tobamovirus*	*Tobamovirus opuntiae* (SOV)	*Opuntia* spp.	Morris (1977)	Germany, UK
Virgaviridae; *Tobamovirus*	*Tobamovirus tabaci* (TMV)	*Opuntia basilaris*	Giri and Chessin (1975b)	USA
Alphaflexiviridae; *Potexvirus*	*Potexvirus alternanthera* (AltMV)	*Epiphyllum* spp.	Wu et al. (2019)	USA
Alphaflexiviridae; *Potexvirus*	*P. alternanthera* (AltMV)	*Pereskia aculeata*	Eiras et al. (2025)	Brazil
Alphaflexiviridae; *Potexvirus*	*Potexvirus ecscacti* (CVX)	*Opuntia monachanta*	Amelunxen (1958)	Germany
Alphaflexiviridae; *Potexvirus*	*P. ecscacti* (CVX)	*O. monachanta*	Brandes and Wetter (1959)	Germany, Austria
Alphaflexiviridae; *Potexvirus*	*P. ecscacti* (CVX)	*O. monachanta*	Brandes and Wetter (1959)	Yugoslavia, Russia, the Netherlands, Scotland, England, Sweden, Portugal, Ukraine, Japan, China, Taiwan, South Korea, Malaysia, India, USA, Brazil
Alphaflexiviridae; *Potexvirus*	*Potexvirus ecsopuntiae* (OpVX)	*Opuntia* sp.	Koenig et al. (2004)	Germany, Brazil
Alphaflexiviridae; *Potexvirus*	*Potexvirus ecspitayae* (PiVX)	*Selenicereus* sp.	Mao (2008); Li (2010)	Taiwan, Brazil
Alphaflexiviridae; *Potexvirus*	*Potexvirus ecschlumbergerae* (SchVX)	*Schlumbergera bridgesii*	Koenig et al. (2004)	Germany, Brazil, Mexico, Taiwan, South Korea, China, Spain, Ecuador
Alphaflexiviridae; *Potexvirus*	*P. ecschlumbergerae* (SchVX)	*Opuntia* spp.	Koenig et al. (2004)	Brazil, Mexico, Taiwan, China, Spain
Alphaflexiviridae; *Potexvirus*	*Potexvirus ecszygocacti* (ZyVX)	*Zygocactus* spp.	Giri and Chesin (1972; 1975a)	USA, Germany, Mexico, Taiwan, Brazil, South Korea, India

Continue...

Table 1 – Continuation.

Alphaflexiviridae; *Potexvirus*	(OpV-A)	*Opuntia ficus-indica*	Ortega-Acosta et al. (2023)	Mexico
Betaflexiviridae; *Carlavirus*	*Carlavirus cacti* (CV2)	*Opuntia* spp.	Brandes and Wetter (1959)	Germany, Austria, the Netherlands, UK, Spain, Portugal, Georgia, USA, Brazil
	Carlavirus unicacti (CCV-1)	*Epiphyllum* spp.	Peng et al. (2019)	USA
	Carlavirus duocacti (CCV-2)	*Epiphyllum* spp.	Peng et al. (2019)	USA
Tombusviridae; *Alphacarmovirus*	*Alphacarmovirus cacti* (SgCV)	*Carnegiae gigantea*	Milbrath and Nelson (1972)	USA
Tospoviridae; *Orthotospovirus*	*Orthotospovirus impatiensnecromaculae* (INSV)	*Opuntia microdasys*	Blockley and Mumford, (2001)	UK
	Orthotospovirus tomatoflavi (TCSV)	*Schlumbergera truncata*	Baker and Adkins (2015)	USA
	Orthotospovirus tomatomaculae (TSWV)	*Opuntia* sp., *S. truncata*	Tehrani et al. (1990)	USA, Canada
Solemoviridae; *Polerovirus*	*Polerovirus BWYV* (BWYV)	*Epiphyllum* spp.	Eicholtz et al. (2018)	USA
Caulimoviridae; *Badnavirus*	*Badnavirus maculaepiphylli* (EpMoaV)	*Epiphyllum* sp.	Lan et al. (2019)	USA
Caulimoviridae; *Cavemovirus*	*Cavemovirus deltaepiphylli* (EpV-4)	*Epiphyllum* sp.	Zheng et al. (2020)	USA
Pospiviroidae, Apscaviroid	OVd-1	*O. ficus-indica*	Ortega-Acosta et al. (2023)	Mexico
	OVd-2	*O. ficus-indica*	Ortega-Acosta et al. (2024)	Mexico
Pospiviroidae, Pospiviroid	MOVd	*O. ficus-indica*	Ortega-Acosta et al. (2024)	Mexico

#First description. *The name OpV2 was given to two distinct cactus viruses, almost simultaneously, a tobamovirus and a possible becurtovirus, respectively. None are included in the most recent ICTV species list (ICTV_Master_Species_List_2023_MSL39.v2.xlsx). **not included in the list of *Genomoviridae* of Varsani and Krupovic (2021). OpV1 = Opuntia virus 1; SCTAV = spinach curly top Arizona virus; OpV2 = "*Opuntia virus 2*"; PaGmV 25 = plant associated genomovirus 25; PaGmV 26 = plant associated genomovirus 26; PaGmV 27 = plant associated genomovirus 27; PaGmV 28 = plant associated genomovirus 28; PaGmV 29 = plant associated genomovirus 29; CMMoV = cactus mild mottle virus; RCNaV = rattail cactus necrosis-associated virus; SOV = Sammon's Opuntia virus; TMV = tobacco mosaic virus; AltMV = Alternanthera mosaic virus; CVX = cactus virus X; OpVX = Opuntia virus X; PiVX = pitaya virus X; SchVX = Schlumbergera virus X; ZyVX = Zygocactus virus X; OpV-A = Opuntia potexvirus A; CV2 = cactus virus 2; CCV-1 = carlavirus cactus carlavirus 1; CCV-2 = carlavirus cactus carlavirus 2; SgCV = saguaro cactus virus; INSV = impatiens necrotic spot virus; TCSV = tomato chlorotic spot virus; TSWW = tomato spotted wilt virus; BWYV = beet western yellows virus; EpMoaV = Epiphyllum mottle-associated virus; EpV-4 = Epiphyllum virus 4; OVd-1 = Opuntia viroid 1; OVd-2 = Opuntia viroid 2; MOVd = mexican Opuntia viroid.

Tobamovirus, *Carlavirus*, *Alphacarmovirus*, families *Caulimoviridae*, and *Geminiviridae*). However, just a few of them (genera *Orthotospovirus* and *Polerovirus*) must have been transmitted from non-cacti plants. Although virus-infected cacti have a large geographic distribution, cacti-specific viruses likely originate from the Americas, the center of the origin of most cacti species, where they were spread by human activities such as cloning, grafting, and plant manipulation, especially among commercially exploitable species.

The lines below provide a brief description of these virus along with comments, presented in chronological order. Nomenclature and classification of the viruses follow the most recent ICTV Master Species List "ICTV_Master_Species_List_2023_MSL39.v2.xlsx", of the International Committee for Virus Taxonomy (ICTV, 2024). Additionally, comments are also made on both internal and external symptoms caused by cacti viruses in infected plants, and there have been several previous brief reviews on cacti viruses (Uschdraweit, 1965; Chessin and Lesemann, 1972; Chessin, 2002), with an emphasis on dragon fruits (Li et al., 2015; Mao et al., 2018; Balendres and Bengoa, 2019; Evallo et al., 2021).

Realm *Riboviria*, Kingdom *Orthornavirae*, Phylum *Kitrinoviricota*, Class *Alsuviricetes*, Order *Tymovirales*, Family *Alphaflexiviridae*

Genus *Potexvirus* (7 species)

Cactus virus X (CVX) - *Potexvirus ecscacti*

The presence of spindle-shaped inclusions in epidermal cells of several cacti species such as *Epiphyllum* sp., *Schlumbergera* sp., and *Zygocactus* sp. (Molisch, 1885) was one of the first reports of the cytopathic effect of viral infection in plants. Mikosch (1908) and Rosenzopf (1951) demonstrated that such cytopathology was graft-transmissible. Detailed research by Amelunxen (1958) in Germany revealed that such spindle-shaped inclusions from *Opuntia monacantha* (Wild.) Haw represented aggregates of elongated (ca. 500 nm long) particles, which were included in the potato virus X (PVX) group and named CVX (Brandes and Wetter, 1959).

Several authors also described cell inclusions in cactus species as *Rhipsalis cereuscula* Haw. ex Phil.,

Table 2 – Cactus species found naturally infected by viruses and viroids, descriptor, geographic localization, virus and viroids acronyms.

Cactus species	Descriptor	Geographic localization	Virus and viroids acronyms[#]
Aporocactus flagelliformis Lem.	Kim et al. (2012b)	South Korea	RCNaV
Cactus bahiensis Rose & Russell	Aragão et al. (1993)	Brazil	CVX
Carnegiae gigantea Britton & Rose	Milbrath and Nelson (1972)	USA	SgCV
	Fontenele et al. (2020a)	USA	PaGmV 28; PaGmV 29
Cereus hexagonus (L.) Miller	Aragão et al. (1993)	Brazil	CVX
Cereus hildmannianus Schumann	Aragão et al. (1993)	Brazil	CVX
Cereus triangularis Haw.	Aragão et al. (1993)	Brazil	CVX
Cereus sp.	Goldin and Fedontina (1956)	Russia	CVX
Chamaecereus silvestrii Britton & Rose '*aureus*'	Samyn and Welvaert (1978)	Belgium	SgCV
Cylindropuntia arbuscula (Engelm.) F. M. Knuth	Fontenele et al. (2020b; 2021)	USA	OpV1
Cylindropuntia echinocarpa (Engelm. & J. M. Bigelow)	Fontenele et al. (2020b; 2021)	USA	OpV1
Cylindropuntia fulgida (Engelm.) F. M. Knuth	Fontenele et al. (2020b; 2021)	USA	OpV1
C *Cylindropuntia ramosissima* (Engelm.) F. M. Knuth	Fontenele et al. (2020a)	USA	PaGmV 27
Cylindropuntia spinosior (Engelm.) F. M. Knuth	Fontenele et al. (2020b; 2021a)	USA	OpV1
Echinocereus sp.	Goldin and Fedontina (1956)	Russia	CVX
Echinocereus sp.	Aragão et al. (1993)	Brazil	CVX
Echinocereus sp.	Marliarenko and Mudrak (2013)	Ukraine	CVX
Echinopus sp.	Goldin and Fedontina (1956)	Russia	CVX
Echinopus sp.	Marliarenko and Mudrak (2013)	Ukraine	CVX
Echinopus sp.	Peng et al. (2019)	USA	CCV-1; CCV-2
Epiphyllum hybrid	Zheng et al. (2020)	USA	CVX; ZyVX; EpV-4; EpMoaV
Echinopus sp.	Wu et al. (2019)	USA	AltMV
Echinopus sp.	Eicholtz et al. (2018)	USA	BWYV
Echinopus sp.	Lan et al. (2019)	USA	EpMoaV
Epiphyllum sp.	Goldin and Fedontina (1956)	Russia	CVX
Epiphyllum sp.	Amelunxen (1958)	Germany	CVX
Epiphyllum truncatum Haw.	Amelunxen (1958)	Germany	CVX
Ferocactus acanthodes (Lem.) Britton & Rose	Attathom et al. (1978)	USA	CVX
Gymnocalycium mihanovichii (Frič & Gürke) Britton & Rose	Lim et al. (2022)	South Korea	SgCV
G. mihanovichii (Frič & Gürke) Britton & Rose	Min et al. (2006a, 2006b)	South Korea	CMMoV
Hylocereus monacanthus (Lem.) Britton & Rose (=*Selenicereus monacanthus*)	Evallo et al. (2022)	Philippines	CVX
Hylocereus undatus (Haw.) Britton & Rose	Fudl-Allah et al. (1983)	USA	CVX
H. undatus (Haw.) Britton & Rose	Hung et al. (1999); Liou et al. (2001, 2004); Liao et al. (2003)	Taiwan	CVX
H. undatus (Haw.) Britton & Rose	Natsuaki and Shinkai (2001)	Japan	CVX
H. undatus (Haw.) Britton & Rose	Kim et al. (2023)	South Korea	PiVX
H. undatus (Haw.) Britton & Rose	Duarte et al. (2008)	Brazil	SchVX; ZyVX
H. undatus (Haw.) Britton & Rose	Bae and Park. (2022)	South Korea	ZyVX
Hylocereus sp.	Masanto et al. (2018); De Soto et al. (2014); Gazis et al. (2018)	USA	CVX
Hylocereus sp.	Peng et al. (2016)	China	CVX
Hylocereus sp.	Kim et al. (2016); Bae and Park (2022)	South Korea	CVX
Hylocereus sp.	Parameswari et al. (2022)	India	CVX
Hylocereus sp.	Silveira et al. (2024)	Brazil	CVX; PiVX; SchVX; ZyVX;
Hylocereus sp.	Mao et al. (2018)	Taiwan	PiVX; SchVX; ZyVX
Hylocereus sp.	Kim et al. (2023)	South Korea	PiVX
Hylocereus sp.	Zeng et al. (2017)	China	SchVX; ZyVX
Hylocereus sp.	Janssen et al. (2022)	Spain	CVX; SchVX
Hylocereus sp.	Parameswari et al. (2023)	India	ZyVX
Hylocereus sp.	Espinoza-Lozano et al. (2024)	Ecuador	SchVX
Hylocereus (=*Selenicereus*) spp.	Silveira et al. (2024)	Brazil	CVX; PiVX; SchVX; ZyVX

Continue...

Table 2 – Continuation.

Laphocereus schotii (Engelm.) Britton & Rose	Fontenele et al. (2020b; 2021a)	USA	OpV1
Lobivia sp.	Aragão et al. (1993)	Brazil	CVX
Mammillaria sp.	Aragão et al. (1993)	Brazil	CVX
Mammillaria sp.	Marliarenko and Mudrak (2013)	Ukraine	CVX
Notocactus leninghausii f. cristatus P. V. Heath.	Park et al. (2018)	South Korea	CVX; PiVX; SchVX; ZyVX; CMMoV; RCNaV
Opuntia albicarpa Scheinvar	De La Torre-Almaráz et al. (2016a)	Mexico	RCNaV
O. albicarpa Scheinvar	Salgado-Ortíz et al. (2020)	Mexico	OpV2*
Opuntia arbuscula Engelm.	Fontenele et al. (2020b; 2021a)	USA	OpV1
O. aureispina (S. Brack & K. D.Heil) Pinkava & B. D. Parfitt	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia basilaris Engelm. & J. M. Bigelow	Giri and Chessin (1975b)	USA	TMV
O. basilaris Engelm. & J. M. Bigelow	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia cespitosa Raf.	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia cochellinifera (L.) Mill. [=*Nopallea cochenillifera* (L.) Salm	Aragão et al. (1993)	Brazil	CVX
O. cochellinifera (L.) Mill. [=*Nopallea cochenillifera* (L.) Salm	Izaguirre-Mayoral and Marys (1996)	Venezuela	CVX
O. cochellinifera (L.) Mill. [=*Nopallea cochenillifera* (L.) Salm	Lamas et al. (2014)	Brazil	SchVX; ZyVX
Opuntia curassavica Mill.	Amelunxen (1958)	Germany	CVX
Opuntia discolor Britton & Rose	Fontenele et al. (2021b)	Bolivia	Utkilio virus
Opuntia echios T. Howeell	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia engelmannii Salm-Dick	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia ficus-indica (L.) Mill.	Chen and Tzeng (1996)	Taiwan	CVX
O. ficus-indica (L.) Mill.	De La Torre - Almaraz et al. (2016b)	Mexico	SchVX
O. ficus-indica (L.) Mill.	Salgado-Ortíz et al. (2020)	Mexico	OpV2*
O. ficus-indica (L.) Mill.	Ortega-Acosta et al. (2023; 2024)	Mexico	OVd-1; OVd-2; MOVd
Opuntia herrfeldtii Kupper	Amelunxen (1958)	Germany	CVX
Opuntia lemaireana Cons.	Amelunxen (1958)	Germany	CVX
Opuntia leucotricha DC	Aragão et al. (1993)	Brazil	CVX
O. leucotricha DC	Guimarães et al. (2025)	Brazil	RCNaV
Opuntia lindheimeri Engelm.	Amelunxen (1958)	Germany	CVX
O. lindheimeri Engelm.	Sammons and Chessin (1961)	USA	SOV
Opuntia mackensenii Rose	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia macrocentra Engelmann	Bermudez et al. (2024)	USA	RCNaV
Opuntia martiniana (L. D. Benson) B. D. Parfitt	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia microdasys (Lehm.) Pfeiff. var. *albata*	Blockley and Mumford (2001)	UK	INSV
Opuntia monachanta (Wild.) Haw.	Amelunxen (1958)	Germany	CVX; SOV
O. monachanta (Wild.) Haw.	Sammons and Chessin (1961)	USA	CVX; SOV
Opuntia phaeacantha Engelm.	Fontenele et al. (2020b; 2021a	USA	OpV1
Opuntia polyacantha Haw.	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia robusta H. L. Wend. ex Pfeiff.	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia rooneyi M. P. Griff	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia rufida Englem.	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia santa-rita (Griffiths & Hare) Rose	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia spinosibacca M. S. Anthony	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia stenopetala Engelm.	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia tapona Engelm.	Fontenele et al. (2020b; 2021a)	USA	OpV1
Opuntia tuna Mill.	Duarte et al. (2008)	Brazil	ZyVX
Opuntia vulgaris Mill.	Aragão et al. (1993)	Brazil	CVX
Opuntia sp.	Sammons and Chessin (1961)	USA	CVX
Opuntia sp.	Asatani and Inoue (1969)	Japan	CVX
Opuntia sp.	Morris (1977)	Germany, the Netherlands, UK, Scotland, Austria, Sweden, Portugal, Russia, USA and Brazil	CVX
Opuntia sp.	Morris (1977)	Germany and UK	SOV

Continue...

Table 2 – Continuation.

Opuntia sp.	Morris (1977)	Germany, the Netherlands, Austria, Georgia, Portugal, Spain UK, USA and Brazil	CV2
Opuntia sp.	Koenig et al. (2004)	Germany	OpVX
Opuntia sp.	Brandes and Wetter (1959); Richert-Pöggeler et al. (2015)	Germany	CV2
Opuntia sp.	Mudrak et al. (2008)	Ukraine	CV2
Opuntia sp.	Casper et al. (1970)	Germany	SgCV
Opuntia sp.	Hausbeck and Gildow (1991); Hausbeck et al. (1992)	USA	TSWV
Opuntia sp.	Fontenele et al. (2021a)	USA	SCTAV; OpV2**
Opuntia sp.	Fontenele et al. (2020a)	France	PaGmV25; PaGmV 26
Peniocereus maculatus (Weing.) Cutak	Richert-Pöggeler et al. (2015)	Germany	CV2
Pereskia aculeata (L.) Karsten	Aragão et al. (1993)	Brazil	CVX
P. aculeata (L.) Karsten	Eiras et al. (2025)	Brazil	AltMV
Pereskia bleo (HBK) De Candole	Aragão et al. (1993)	Brazil	CVX
Platypuntia sp.	Milbrath et al. (1973)	USA	CVX
Schlumbergera bridgesii (Lem.) Loefgr.	Tehrani et al. (1990)	Canada	TSWV
Schlumbergera sp.	Koenig et al. (2004)	Germany	SchVX
Schlumbergera truncata (Haw.) Moran	Duarte et al. (2008)	Brazil	OpVX; ZyVX
S. truncata (Haw.) Moran	De La Torre-Almaráz et al. (2016b)	Mexico	SchVX
S. truncata (Haw.) Moran	Baker and Adkins (2015)	USA	TCSV
Selenicereus sp.	Medeiros et al. (2023)	Brazil	CVX
Zygocactus sp.	Giri and Chesin (1972; 1975a)	USA	ZyVX
	Koenig et al. (2004)	Germany	ZyVX

[#]Key for abbreviation of virus names: AltMV = Alternanthera mosaic virus (*Potexvirus alternantherae*); BWYV = beet western yellows virus (*Polerovirus BWYV*); CV2 = cactus virus 2 (*Carlavirus cacti*); CCV-1 = cactus carlavirus 1 (*Carlavirus unicacti*); CCV-2 = cactus carlavirus 2 (*Carlavirus duocacti*); CMMoV = Cactus mild mottle virus (*Tobamovirus cacti*); CVX = cactus virus X (*Potexvirus ecscacti*); EpMoaV = Epiphyllum mottle-associated virus (*Badnavirus maculaepiphylii*); EpV-4 = Epiphyllum virus 4 (*Cavemovirus deltaepiphyllii*); INSV = impatiens necrotic spot virus (*Orthotospovirus impatiensnecromaculae*); MOVd = mexican Opuntia viroid; OpV1 = Opuntia virus 1 (*Opunvirus opuntiae*); OpV2* = "Opuntia virus 2"/tobamovirus; OpV2** = "Opuntia virus 2"/putative becurtovirus; OVd-1 = Opuntia viroid 1; OVd-2 = Opuntia viroid 2; OpVX = Opuntia virus X (*Potexvirus ecsopuntiae*); PaGmV 25 = plant associated genomoviridae 25 (*Gemycirularvirus opunt1*); PaGmV 26 = plant associated genomoviridae 26 (*Gemygorvirus opunt1*); PaGmV 27 = plant associated genomoviridae 27/ *Gemykibivirus*; PaGmV 28 = Plant associated genomoviridae 28/ *Gemykibivirus*; PaGmV 29 = plant associated genomoviridae 29 (*Gemykibivirus planta 2*); PiVX = pitaya virus X (*Potexvirus ecspitayae*); RCNaV = rattail cactus necrosis-associated virus (*Tobamovirus muricaudae*); SchVX = Schlumbergera virus X (*Potexvirus ecschlumbergerae*); SgCV = saguaro cactus virus (*Alphacarmovirus cacti*); SOV = Sammon's Opuntia virus (*Tobamovirus opuntiae*); SCTAV = spinach curly top Arizona virus (*Becurtovirus spinaciae);* TCSV = tomato chlorotic spot virus (*Orthotospovirus tomatoflavi*); TMV = tobacco mosaic virus (*Tobamovirus tabaci*); TSWV = tomato spotted wilt virus (*Orthotospovirus tomatomaculae*); ZyVX = Zygocactus virus X (*Potexvirus ecszygocacti*). *,**The tobamovirus OpV2 has not been included yet in the ICTV Master species list. The same name was given to a virus close to the genus *Becurtovirus* (fam. *Geminivirus*), which is also absent in the ICTV list.

Epiphyllum truncatum Haw., *Opuntia subulata* Engelm in Austria (Weber and Kenda, 1952a, b), in *Opuntia brasiliensis* Haw., in Yugoslavia (Miličić, 1954; Miličić and Plavšić, 1956), in *Epiphyllum* sp., *Cereus* sp., *Echinocereus* sp., and *Echinopsis* sp. in Russia [Goldin and Fedotina, 1956, quoted in the review by Miličić (1959/1960)], which may have been associated with CVX. In the USA, Sammons and Chessin (1961) detected tobamovirus (Sammon's Opuntia virus- SOV) and potexvirus-like (possibly CVX) particles in samples of *O. monacantha* and *Opuntia* sp., from Montana and California, associated with the presence of spindle-shaped inclusions in the hypodermal cells.

Surveys made in southern Arizona by Milbrath et al. (1973) detected CVX in *Platypuntia* sp. CVX was also found infecting barrel cactus [*Ferocactus acanthodes* (Lem.) Britton & Rose] showing mottling, necrosis and distorted areoles, collected in the Clark Mountains (southeast California, USA) (Attathom et al., 1978). Fudl-Allah et al. (1983) described CVX infecting the ornamental *H. undatus* exhibiting stunting and deformation in a nursery in California, USA. In Japan, Nakamura and Mukoo (1973) sampled a large number (112) of cacti species, varieties, and hybrids, mostly symptomatic, in which they detected spindle-shaped inclusions, potex- and tobamovirus-like particles, but did not identify these possible viruses. These authors had previously (Mukoo et al., 1967) similarly sampled 40 symptomatic cacti species, detecting cell inclusions and potexvirus-like particles, and suggested cases of infection with CVX.

Morris (1977) analyzed the presence of cacti viruses in 137 *Opuntia* spp. samples from several countries [Europe (Germany, the Netherlands, Austria, Scotland, UK, Sweden, Russia, Portugal) and the Americas (USA and Brazil)], and, based on the morphology of particles present in extracts, observed by electron microscopy, suggested that these plants were infected by CVX. An extensive survey made on several cacti species in Brazil resulted in the detection of CVX in *Cactus bahiensis* Rose & Russel, *Cereus triangularis* Haw., *C. hildmannianus*, *C. hexagonus* (L.) Miller, *Echinocereus* sp., *Lobivia* sp., *Mamillaria* sp., *Myrtilocactus* sp., *Nopallea cochenillifera* (L.) Salm-Dick, *Opuntia vulgaris* Mill., *O. leucotricha* DC., *P. aculeata*, *Pereskia bleo* (HBK) De Candolle (Aragão et al., 1993).

In Taiwan, CVX was found to induce stunting and chlorosis in *O. ficus-indica* (Chen and Tzeng, 1996), as well as in in dragon fruit (*H. undatus*) with systemic mottling (Hung et al., 1999; Liou et al., 2001; 2004; Liao et al., 2003). CVX was also detected in dragon fruit with mosaic symptoms in Japan (Natsuaki and Shinkai, 2001). In Ukraine, Marliarenko and Mudrak (2013) reported infection of *Echinocereus, Echinopsis,* and *Mammilaria* by CVX. A case of simultaneous infection of *Notocactus leninghausii f. cristatus* P. V. Heath. by six different viruses: the potexviruses CVX, Schlumbergera virus X (SchVX), pitaya virus X (PiVX) and Zygocactus virus X (ZyVX), the tobamoviruses cactus mild mottle virus (CMMoV) and rattail cactus necrosis-associated virus (RCNaV) was reported by Park et al. (2018) in South Korea.

Lee (2020), in Taiwan, studied the transcriptome of healthy and CVX- and PiVX-infected dragon fruit plants and observed differences in the expression of several proteins. In Venezuela, Izaguirre-Mayoral and Marys (1996) evaluated the effect of radiation levels on CAM and infection by CVX in *N. cochenillifera* and *Acanthocereus tetragonus* (L.) Hummelinck. They concluded that there was a 1.3-fold increase in virus concentration under lower illumination, but there was no effect on CAM. In South Korea, transgenic *Hylocereus trigonus* Saff., used as rootstock, expressed CVX capsid protein up to the 5th generation. Such a transgenic plant was immune to CVX upon experimental inoculation (Kim et al. 2011; 2012a).

Dragon fruit (*Hylocereus* spp., *Selenicereus* spp.) crop is in a period of rapid expansion around the world. Following the initial description of potexvirus infection in Taiwan, Japan, and Brazil, several cases of infection of dragon fruit with CVX have been reported worldwide: Malaysia (Masanto et al., 2018), USA (De Soto et al., 2014; Gazis et al., 2018), China (Peng et al., 2016; Zeng et al., 2017), Philippines (Evallo et al., 2022), India (Parameswari et al., 2022), and South Korea (Kim et al., 2016). Santos et al. (2022) and Medeiros et al. (2023) mentioned the infection of dragon fruit (*Selenicereus* sp.) by CVX in Brazil. A recent and extensive virus survey in Brazilian dragon fruit orchards, covering the northern, midwestern, southeastern, and southern regions was conducted using RT-PCR. The survey detected not only CVX but also PiVX, SchVX, and ZyVX, either alone or in combination, associated with external symptoms (Silveira et al., 2024).

Opuntia virus X (OpVX) - *Potexvirus ecsopuntiae,* Schlumbergera virus X (SchVX) - *Potexvirus ecschlumbergerae,* and Zygocactus virus X (ZyVX) - *Potexvirus ecszygocacti*

Further works with cacti potexviruses revealed that what was considered CVX was indeed a complex of distinct potexvirus species. Brandes and Bercks (1963) described a potex-like virus in *Zygocactus* sp. and regarded it as possibly distinct from CVX. The virus had a distant serological relationship with other potexviruses, and had distinct symptomatology in assay plants. Later, Casper and Brandes (1969) described a potexvirus infecting an asymptomatic hybrid of *Zygocactus* × *Schlumbergera* and considered it distinct from CVX due to signifícent serological differences, tentatively naming this virus Zygocactus virus. Miličić et al. (1966) and Pleše and Miličić (1966) had also noticed differences between CVX isolates. Giri and Chessin (1972; 1975a) described in the USA, a *Zygocactus*-infecting potexvirus, with host range and serological relationship distinct from CVX and Zygocactus virus, and named it Zygocactus virus X (ZyVX).

This diversity of potexviruses infecting cacti was suggested by Miličić et al. (1966) when they noticed remarkable serological differences among isolates of CVX. Such diversity was confirmed by Koenig et al. (2004) when comparing genome sequences of several isolates of cacti potexviruses obtained from *Opuntia* sp., *Schlumbergera* sp., and *Zygocactus* sp. They concluded that what had been referred to as CVX was indeed several different potexviruses, named SchVX, ZyVX, and Opuntia virus X (OpVX).

Schlumbergera virus X and another potexvirus (CVX or ZyVX) were detected infecting *Opuntia cochellinifera* (L.) Mill. [=*N. cochenillifera* (L.) Saim.] in the state of Pernambuco, Brazil (Lamas et al., 2014); the genome of this SchVX isolate was entirely sequenced (Sanches et al., 2015). In Mexico, Alonso-Barrera et al. (2015) cited an unidentified potexvirus inducing chlorotic spots in *O. ficus-indica*, possibly the same situation in which De La Torre-Almaráz et al. (2016b) detected SchVX in this host plant. SchVX as well as ZyVX and PiVX were identified infecting dragon fruit (*Hylocereus* spp.) in Taiwan [Mao (2008), quoted in Mao et al., 2018]. In Brazil, studies of samples of certain cacti species [(*Opuntia tuna* Mill., *Schlumbergera truncata* (Haw.) Moran, *H. undatus*] collected in the state of São Paulo, demonstrated infection of *O. tuna* by ZyVX, mixed infection by SchVX and ZyVX in *H. undatus*, and triple infection of *S. truncata* by OpVX, SchVX, and ZyVX, by RT-PCR assays (Duarte et al., 2008).

Zygocactus virus X was detected infecting dragon fruit (*Hylocereus* spp.) in India (Parameswari et al., 2023). Bae and Park (2022) reported ZyVX co-infecting dragon fruit with PiVX in South Korea. SchVX was detected on dragon fruit in China (Zeng et al., 2017), Spain (Janssen et al., 2022), and Ecuador (Espinoza-Lozano et al., 2024). SchVX and ZyVX, together with CVX and PiVX were found in samples of dragon fruit collected in several parts of Brazil (Silveira et al., 2024). Koenig et al. (2006) generated a ZyVX-based expression vector for capsid proteins of soil-borne cereal mosaic virus and beet necrotic yellow vein virus. Up till now OpVX has not been reported in dragon fruit.

Pitaya virus X (PiVX) - *Potexvirus ecspitayae*

Pitaya virus X was first described and characterized in Taiwan, infecting dragon fruit (*Hylocereus* sp.) (Mao, 2008; Li, 2010), and in South Korea (Kim et al., 2023; Bae and Park, 2022), being the fourth potexvirus described in this fruit cacti, as well as CVX, SchVX, and ZyVX. RT-PCR assays are the most commonly used for the detection and identification of viruses infecting dragon fruit. However, methods such as loop-mediated isothermal amplification have been proposed to detect CVX (Zhang et al., 2016) and PiVX (Zhao et al., 2023). Furthermore, a multiplex assay, which simultaneously detects the five potexvirus that cause cacti infections, was developed by Park et al. (2021). Zhao et al. (2023) suggested that PiVX capsid protein suppresses the RNA silencing mechanism. PiVX was part of the complex of potexviruses found in field dragon fruit plants from different regions in Brazil (Silveira et al., 2024).

Opuntia potexvirus A (OpV-A)

HTS analysis was carried out on samples of *O. ficus-indica*, collected from fruits and "nopalitos" (edible pads) in the state of Mexico, Mexico, showing chlorotic spots and rings. The complete genome sequence of a new potexvirus, designated Opuntia potexvirus A (OpV-A) was found, together with genomes of the tobamovirus Opuntia virus 2 (OV-2), the carlavirus cactus carlavirus 1 (CCV-1), as well as of the apscaviroid Opuntia viroid 1 (OVd-1), Opuntia viroid 2 (OVd-2), and the pospiviroid mexican Opuntia viroid (MOVd) (Ortega-Acosta et al., 2023; 2024).

Alternanthera mosaic virus (AltMV) - *Potexvirus alternantherae*

Alternanthera mosaic virus (AltMV), initially described in Australia infecting *Alternanthera pungens* Kunth, was detected in a hybrid of *Epiphyllum* ('Dragon heart') showing irregular chlorotic patches, in the USA. The sequence of AltMV was obtained by metagenomics, and the virus was demonstrated to be graft-transmissible to the same cacti species. Further surveys by RT-PCR detected AltMV also in an asymptomatic *Epiphylllum* hybrid (Wu et al., 2019). AltMV was found naturally infecting *Pereskia aculeata* in Brazil, inducing mosaic and ringspot symptoms (Eiras et al., 2025).

Realm *Riboviria*, Kingdom *Orthornavirae*, Phylum *Kitrinovicola*, Class *Alsuviricetes*, Order *Martellivirales*, Family *Virgaviridae*

Genus *Tobamovirus* (5 species)

Sammon's Opuntia Virus (SOV) - *Tobamovirus opuntiae*

A tobamovirus was the second virus recorded among cacti plants, following CVX. In 1961, during the initial works on cacti viruses in the USA, the presence of spindle-shaped inclusions in the cells of *O. monacantha* (Wild.) Haw. f. *variegata* and *Opuntia lindheimeri* Engelm was observed by Sammons and Chesin (1961). This condition was mechanically transmitted by sap injection, and transmission electron microscopy (TEM) revealed the presence of tobamovirus and potexvirus-like particles in the extracts. Potexvirus was not identified; however, the tobamovirus was later considered distinct from other known species and was named SOV (Brandes and Chessin, 1965). Serological assays confirmed that SOV was distinct from other tobamoviruses (Wetter and Paul, 1967). A survey made on *Opuntia* spp. by Morris (1977) detected SOV in samples from Germany and the UK.

Tobacco mosaic virus (TMV) - *Tobamovirus tabaci*

Giri and Chessin (1975b) reported the infection of *Opuntia basilaris* Engelm. & J. M. Bigelow, collected in Kingman, AZ, USA by a tobamovirus, identified as an isolate of tobacco mosaic virus (TMV) based on mechanical transmission assays, virion morphology, and immunoassays.

Cactus mild mottle virus (CMMoV) - *Tobamovirus cacti*

A tobamovirus was detected in *Gymnocalycium mihanovichii* (Frič & Gürke) Britton & Rose, grafted onto the top of *H. trigonus*, in Suwon, South Korea, associated with ringspot mottling symptoms. Immunoassays demonstrated that this tobamovirus was unrelated to SOV, and subsequent sequence analysis of the 3'- terminal of the viral genome revealed that it was a distinct species, and was named CMMoV (Min et al., 2006a, b). The complete genome sequence of CMMoV was reported by Min et al. (2009). Park et al. (2018) described a case of mixed infection of the tobamoviruses CMMoV and RCNaV, with four other potexviruses (CVX, PiVX, SchVX, and ZyVX) in the cactus *N. leninghausii* f. *cristatus*, collected in the province of Gyeonggi, South Korea.

Rattail cactus necrosis-associated virus (RCNaV) - *Tobamovirus muricaudae*

Infection of the Cactaceae *Aporocactus flagelliformis* Lem., characterized by necrotic lesions, with a tobamovirus was observed in a sample obtained from the National

Institute of Horticultural & Herbal Science Institute, Suwon, South Korea. This tobamovirus was identified as a new species and named RCNaV and its genome entirely sequenced (Kim et al., 2012b). *Opuntia albicarpa* Scheinvar plants were found on the Central High Plateau of Mexico exhibiting small yellow ringspots. Tobamovirus-like particles were detected in these plants and mechanical transmission assays resulted in the infection of several test plants. Molecular assays identified the causal virus as RCNaV (De La Torre-Almaráz et al., 2016a).

Rattail cactus necrosis-associated virus was found infecting native black-spined prickly pear (*Opuntia macrocentra* Engelmann) in Phoenix, AZ, USA, showing concentric ringspots and chlorotic spots. Molecular assays made the detection and identification of the virus. This virus was graft-transmitted to *Opuntia* sp. and mechanically to *Phaseolus vulgaris* L. and *Medicago sativa* L. (Murcia-Bermudez et al., 2024).

Park et al. (2018) described a case of co-infection of *N. leninghausii* f. *cristatus* with several potexviruses (CVX, PiVX, SchVX, and ZyVX) and the tobamoviruses CMMoV and RCNaV, by molecular assays, during a survey of cactus viruses in samplings carried out in Gyeonggi province, South Korea. RCNaV was detected in Brazil in a case of symptomless infection of *O. leucotricha* from a cactus collection in the Instituto Plantarum. Identification was made based on electron microscopy, mechanical transmission, and molecular assays (Guimarães et al., 2025).

Opuntia virus 2 (OpV2)*

HTS of samples from prickly pears (*O. albicarpa, O. ficus-indica*) with chlorotic annular spots, collected in Otumba, Mexico, detected a new species of tobamovirus, tentatively named Opuntia virus 2 (OpV2)* (Salgado-Ortíz et al., 2020).

*Obs.: The tobamovirus OpV2 has not been included in the ICTV species list yet.

Realm *Riboviria,* Kingdom *Orthornaviae,* Phylum *Kitrinoviricota,* Class *Alsuviricetes,* Order *Tymovirales,* Family *Betaflexiviridae,* Subfamily *Quinviridae*

Genus *Carlavirus* (3 species)

Cactus virus 2 (CV2) - *Carlavirus cacti*

Brandes and Wetter (1959) were responsible for the first attempt to classify elongated plant viruses based on their true intrinsic characteristics (particle morphology and immuno-properties), and not by symptoms of the diseases they caused. Two cacti viruses were part of their classification- CVX among potexviruses (flexible particles ca. 500 nm long), and another from *Opuntia* sp., collected in Germany, in the group which today is referred to as the *Carlavirus* genus (semi-rigid particles, ca. 600 nm long), and was designated as Cactus virus 2 (CV2).

Based on particle morphology, Morris (1977) described the presence of CV2 in *Opuntia* spp. samples from several European countries (Germany, the Netherlands, Austria, Georgia, Portugal, Spain, UK) as well as from the Americas (USA and Brazil). Mudrak et al. (2008) identified CV2 infecting *Opuntia* spp., based on serological assays, after screening cactus viruses in a collection from the botanical garden of the Kyiv at Krakov National University in Ukraine. Richert-Pöggeler et al. (2015) also found CV2 infecting *Opuntia* sp. and *Peniocereus maculatus* (Weing.) Cutak, by biological, morphological, and molecular assays, in Germany, during a survey of ornamental viruses.

Cactus carlavirus 1 (CCV-1) and cactus carlavirus 2 (CCV-2)

Molecular analysis by HTS carried out in the USA, on samples of *Epiphyllum* sp., with mottling and ringspot symptoms, detected two new carlavirus species, designated respectively cactus carlavirus 1 (CCV-1) and cactus carlavirus 2 (CCV-2). These viruses could not be mechanically transmitted to certain test plants, but were graft-transmitted onto the *Epiphyllum* hybrid 'prof. Ebert' (Peng et al., 2019).

Realm *Riboviria,* Kindgom *Orthornavira,* Phylum *Kitrinoviricota,* Class *Tolucaviricetes,* Order *Tolivirales,* Family *Tombusviridae,* Subfamily *Procedovirinae*

Genus *Alphacarmovirus* (1 species)

Saguaro cactus virus (SgCV) - *Alphacarmovirus cacti*

An isometric virus was found infecting the saguaro cactus (*Carnegiae gigantea*) asymptomatically in Saguaro National Monument, near Tucson, AZ, USA. The virus was purified, demonstrating a content of 20 % RNA. Mechanically inoculated *Chenopodium quinoa* Willd. reacted with chlorotic local lesions, while *C. capitatum* (L.) Asch became systemically infected. This virus was named SgCV (Milbrath, 1971; Milbrath and Nelson, 1972). Specific additional physicochemical properties of SgCV were determined, as well as the absence of a serological relationship with several other isometric viruses (Nelson and Tremaine, 1975).

Saguaro cactus virus was found infecting asymptomatic *Chamacereus sylvestrii* Britton & Rose '*aureus*', grown in Ghent, Belgium (Samyn and Welvaert, 1978), and more recently in Gyeonggi Province, South Korea, infecting asymptomatically *G. mihanovichii* (Lim et al., 2022). The complete genome sequence of SgCV was obtained, comprising 3,879 nucleotides and covering five open reading frames, and was confirmed as as a distinct species of the genus *Alphacarmovirus* genus (Weng and Xiong, 1997). An isometric virus, co-infecting *Opuntia* sp. with a phytoplasma, found in Europe, was considered a possible isolate of SgCV (Casper et al., 1970).

Realm *Riboviria,* Kingdom *Orthornavirae,* Phlum *Pisuviricota,* Class *Pisoviricetes,* Order *Sobolivirales,* Family *Solemoviridae*

Genus *Polerovirus* (1 species)

Beet western yellows virus (BWYV) - *Polerovirus BWYV*

Eicholtz et al. (2018) found hybrids of *Epiphyllum* with mottling and chlorotic ringspots at a nursery in New York, USA. Molecular tools detected several previously described cacti viruses, and in one asymptomatic hybrid ('prof. Ebert'), the HTS assay detected an isolate of beet western yellows virus (BWYV). This virus could be graft-transmitted to virus-free *Epiphyllum* plants.

Realm *Riboviria.* Kingdom *Orthornavirae,* Phylum *Negarnaviricola,* subphylum *Polyploviricotina,* Class *Elioviricetes,* Order *Bunyavirales,* Family *Tospoviridae*

Genus *Orthotospovirus* (3 species)

Impatiens necrotic spot virus (INSV) – *Orthotospovirus impatiensnecromaculae*

Impatiens necrotic spot virus (INSV) was detected infecting *Opuntia microdasys* (Lehm.) Pfeiff. var. '*albata*', in the UK, causing necrotic ringspots. Identification was made by serological and molecular assays (Blockley and Mumford, 2001).

Tomato chlorotic spot virus (TCSV) - *Orthotospovirus tomatoflavi*

Schlumbebergera truncata plants showing chlorotic blotches and stripes were found at a nursery in Lake County, FL, USA. RT-PCR assays detected tomato chlorotic spot virus (TCSV) in these plants (Baker and Adkins, 2015).

Tomato spotted wilt virus (TSWV) - *Orthotospovirus tomatomaculae*

Incidence of tomato spotted wilt virus (TSWV) in *Schlumbergera bridgesii* (Lem.) Loefgr., in Canada, was quoted by Tehrani et al. (1990). During a survey of tospoviruses in ornamentals in commercial nurseries in the state of Pennsylvania, USA, an isolate of TSWV/Impatiens was detected in potted *Opuntia* sp. exhibiting mosaic and necrosis (Hausbeck and Gildow, 1991; Hausbeck et al., 1992).

Realm *Riboviria* Kingdom *Pararnavirae* Phylum *Artverviricota* Class *Revtraviricetes* Order *Ortervirales* Family *Caulimoviridae*

Genus *Badnavirus* (1 species)

Epiphyllum mottle-associated virus (EpMoaV) - *Badnavirus maculaepiphylli*

A hybrid of *Epiphyllum,* exhibiting mottling, necrotic and chlorotic spots, was discovered in a garden in California, USA. Molecular assays to detect viruses reported in Cactaceae were negative. Semi-purified preparations revealed the presence of badnavirus-like particles, and molecular assays directed to this virus group allowed the detection and the obtention of the complete sequence of a new badnavirus, named Epiphyllum mottle-associated virus (EpMoaV). This virus was demonstrated to be graft-transmissible (Lan et al., 2019). EpMoaV could have been the uncharacterized badnavirus described in *Epiphyllum* sp., which exhibits ringspot symptoms in Japan (Yamashita et al., 1991).

Genus *Cavemovirus* (1 species)

Epiphyllum virus 4 (EpV-4) - *Cavemovirus deltaepiphyllii*

A plant of the *Epiphyllum* hybrid, 'Prof.Ebert', with stripes in flowers, from a commercial nursery in the USA, was found to have a mixed infection with CVX, ZyVX, and EpMoaV. Additional molecular assays permitted the detection of a new cavemovirus, whose genome was entirely sequenced, and the virus was named Epiphyllum virus 4 (EpV-4) (Zheng et al., 2020).

Realm *Monodnaviria,* Kingdom *Shotokuvirae*, Phylum *Cressdnaviricola*, Class *Repensivircetes*, Order *Geplafuvirales*

Family *Geminiviridae*

Genus *Opunvirus*

Opuntia virus 1 (OpV1) - *Opunvirus opuntiae*

An extensive survey was conducted by HTS on 527 samples of cactaceae (Cactoideae and Opuntioideae clades), collected worldwide (Americas, Africa, Asia, Europe). A single divergent virus species of the family *Geminiviridae* was identified and named Opuntia virus 1 (OpV1) (Fontenele et al., 2020b; 2021a). A new genus, *Opunvirus,* was subsequently created for this species (Roumagnac et al., 2022).

This virus was detected only in samples collected in Arizona, USA, and Baja California, Mexico, mostly belonging to the *Opuntia* species [*O. arbuscula* Engelm., *O. aureispina* (S. Brack & K .D. Heil) Pinkava & B. D. Parfitt, *O. basilaris, O. cespitosa* Raf., *O. echios* T. Howell, *O. engelmannii* Salm-Dick, *O. mackensenii* Rose, *O. martiniana,* (L. D. Benson) B. D. Parfitt, *O. phaeacantha* Engelm., *O. polyacantha* Haw., *O. robusta* H. L. Wend. ex Pfeiff., *O. rooneyi* M. P. Griff., *O. rufida* Engelm., *O. santa-rita* (Griffiths & Hare) Rose, *O. spinosibacca* M. S.

Anthony, *O. stenopetala* Engelm., *O. tapona* Engelm., and also in *Laphocereus schotii* (Engelm.) Britton & Rose, *Cylindropuntia arbuscula* (Engelm.) F. M. Knuth., *Cylindropuntia echinocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth., *Cylindropuntia fulgida* (Engelm.) F. M. Knuth., *Cylindropuntia spinosior* (Engelm.) F. M. Knuth. OpV1 was also detected in the cochineal insect *Dactylopius* sp. *Nicotiana benthamiana* Domin., and *O. microdasys* plants were successfully infected by an infectious clone but remained symptomless (Fontenele, 2020b; 2021a).

Genus *Becurtovirus*

Spinach curly top Arizona virus (SCTAV) - *Becurtovirus spinaciae*

In continuing the survey of cactus geminiviruses by HTS to evaluate their diversity, genomes of an *Opuntia*-infecting becurtovirus were identified and considered as a strain of the spinach curly top Arizona virus (SCTAV). This virus was detected only in samples obtained in the USA, mainly from Arizona, and one from Utah, in several *Opuntia* species and cochineal insects (Fontenele et al., 2021a).

Opuntia virus 2 (OpV2) (Putative Genus *Becurtovirus)*

In the same study, these authors identified another geminivirus, considered closely related to becurtovirus, which was designated OpV2*. It was also present only in *Opuntia* samples from the USA (Arizona and Utah). These viruses occurred mostly in mixed infection, together with the Opuntia virus OpV1 (Fontenele et al., 2021a).

Note: The name OpV2 was also given to a recently described cactus tobamovirus from Mexico (Salgado-Ortíz et al., 2020). Since none of these viruses are mentioned in the last ICTV Master virus species list (2024), the question is likely under discussion in the pertinent committee.

Unclassified putative *Geminiviridae*

Utkilio virus

A bipartite, circular single-stranded DNA virus, made up of two 1.8 kb circular DNA components, possibly of bipartite nature, was found in wild prickly pear *Opuntia discolor* Britton & Rose from the Chaco ecoregion (Bolivia) of South America, and was named the utkilio virus (Fontenele et al., 2021b).

Family *Genomoviridae*

In an extensive study, screening 88 plant species from 19 families collected in various parts of the world, Fontenele et al. (2020a) detected 98 genomoviruses, circular single-stranded DNA viruses, representing genus *Gemykolovirus, Gemyduguivirus, Gemygorvirus, Gemykroznavirus, Gemycircularvirus,* and *Gemykibivirus*, using molecular means. The authors suggest that these *Genomoviridae* viruses were likely present in fungi associated with the cacti; however, they do not rule out the possibility that these viruses could also be infecting the cactus plants. Five *Genomoviridae* viruses were detected in Cactaceae plants as follows.

Genus *Gemycircularvirus*

Plant-associated genomoviridae 25 (PaGmV 25) *Gemycircularvirus opunt1*

Opuntia sp. (France).

Genus *Gemygorvirus*

Plant-associated genomoviridae 26 (PaGmV 26) *Gemygorvirus opunt1*

Opuntia sp. (France).

Genus *Gemykibivirus*

Plant-associated genomoviridae 27 (PaGmV 27)*

Cylindropuntia ramosissima (Engelm.) F. M. Knuth (USA).

Plant-associated genomoviridae 28 (PaGmV 28)* and plant-associated genomoviridae 29 (PaGmV 29) - *Gemikibivirus planta2*

Carnegiea gigantea (USA).

(*) not included in the list of *Genomoviridae* of Varsani and Krupovic (2021) and the last ICTV Master species list (2024).

Viroids

Family *Pospiviroidae*

Genus *Apscaviroid*

Opuntia viroid 1 (OVd-1)

Opuntia viroid 2 (OVd-2)

Genus *Pospiviroid*

Mexican Opuntia viroid (MOVd)

A survey using HTS was conducted to detect viruses in *O. ficus-indica*, which exhibited chlorotic spots and rings in the pads from commercially producing areas in the state of Mexico, Mexico. In addition to viruses such as the tobamovirus OpV2, CCV-1, potexviruses OpV-A, sequences of three viroids, respectively from the genus *Apscaviroid*, Opuntia viroid 1 and 2 (OVd-1 and OVd-2), and genus *Pospiviroid*, MOVd were also described (Ortega-Acosta et al., 2023; 2024).

Viruses found in Cactaceae plants pending identification

Chessin and Lesemann (1972) reported the presence of tobamovirus and potexvirus in cacti samples collected in the southeastern USA, but did not identify them. Studies conducted on *O. ficus-indica* cladodes exhibiting mosaic, chlorosis, fruit deformation, and thickening symptoms, collected in Nopaltepec, Mexico, detected dsRNA and particles 950-1,700 nm long. This presumptive virus was mechanically transmitted to several test plants. RT-PCR assays were negative for tobamovirus, potexvirus or potyviruses (Suaste-Dzul et al., 2012).

Symptoms of viral infection in cacti

External symptoms

External symptoms caused by cacti viruses have been described as mottling or mosaic, chlorotic or necrotic streaks and ringspots, depression, reddening, distortion of the cladode, spine malformation, which are mainly caused by potexviruses (Chessin, 2002) (Figure 1). However, many of them cause asymptomatic infection, and these viruses have been detected by cytology (detection of inclusions), electron microscopy (detection of particles in extracts), serology, and, more recently, by molecular assays.

Weingart (1920) seems to have been the first to associate the presence of cellular inclusions in cacti with external symptoms. He detected inclusions in *C. triangularis, Cereus pictus* DC and *Opuntia monachanta* f. *variegata* Anon. with white/yellowish spots. Soon after, Blattny and Vukolov (1932) observed sap-transmitted mosaic symptoms in *E. truncatum.* Mosaic/mottling in several cacti species was described by Pape (1932), though no association with cytological changes was mentioned.

Studies by the Austrian group of Weber at the Universität Ganz (Kenda, 1954; Weber, 1953a, b, c; Weber, 1954; Weber and Kenda, 1952a, b; Weber and Kenda, 1953; Weber et al., 1952a, b; Weber et al., 1953), and the Yugoslavian group of Miličić, at the University of Zagreb (Miličić, 1954; Miličić, 1956; Miličić, 1959/1960; Miličić and Plavšić, 1956) reported cases of cell inclusions in different cacti species, some of which were associated with symptoms (mostly mottling and chlorotic flecking), and others, with asymptomatic plants.

These examples were related to CVX-infection. Potexviruses (CVX, OpVX, PiVX, SchVX, ZyVX, AltMV) - infection of cacti has been mostly associated with symptom expression (Asatani and Inoue, 1969; Chessin and Lesemann, 1972; Milbrath et al., 1973; Nakamura and Mukoo, 1973; Giri and Chessin, 1972; Giri and Chessin, 1975a; Attathom et al. 1978; Liou et al., 2001; Natsuaki and Shinkai, 2001; Liao et al., 2003; De Soto et al., 2014; Duarte et al., 2008; Park et al., 2018; Alonso-Barrera et al., 2015; De La Torre-Almaráz et al., 2016a; Peng et al., 2016; Gazis et al., 2018; Masanto et al., 2018; Parameswari et al., 2022; Parameswari et al., 2023; Bae and Park, 2022; Janssen et al., 2022; Kim et al., 2023). However, there are reports of symptomless infection with cacti potexviruses (Lamas et al., 2014; Sanches et al., 2015; Kim et al., 2016). Figure 1 A-C illustrates cases of external symptoms associated with infection in some cacti, associated with infection by potexviruses. Recently, *P. aculeata* plants were found to be infected with AltMV, exhibiting conspicuous rings and mosaic symptoms on their leaves (Eiras et al., 2025) (Figure 1D).

The tobamovirus SOV causes diagnostic chlorotic rings and arcs in the cladodes (Chessin et al., 1963; Milbrath et al., 1973). The description of TMV infecting *O. basilaris* (Giri and Chessin, 1975b) was based on an asymptomatic plant. CMMoV (Min et al., 2006b), RCNaV (Kim et al., 2012; De La Torre-Almaráz et al., 2016a), and OpV2 (Salgado-Ortíz et al., 2020) were found in symptomatic (mottling, chlorotic and/or necrotic spots) cacti species.

The CV2, like most carlaviruses, causes asymptomatic infection and was initially identified in co-infection with CVX (Brandes and Wetter, 1959). CV2, CCV-1 and 2 were detected in co-infection with CVX and SOV (Richert-Pogler et al., 2015) but probably cause asymptomatic infection as in the case of *Epiphyllum* (Peng et al., 2019).

Alphacarmovirus SgCV was originally found in an asymptomatic saguaro cactus in the USA (Milbrath, 1971; Milbrath and Nelson, 1972), and was described

Figure 1 – Examples of symptoms associated with viral infection in Cactaceae plants. A) *Cereus jamacaru* infected by an unidentified potexvirus, showing yellow blotches in cladodes; B and C) symptoms associated with Zygocactus virus X infection (B = mottling; C = chlorotic rings) in dragon fruit (*Hylocereus* sp.); D) Symptoms of rings and mosaic on a leaf of *Pereskia aculeata* infected with Alternanthera mosaic virus (Eiras et al., 2025).

later in Belgium, infecting asymptomatically *C. sylvestrii* imported from Brazil (Samyn and Welvaert, 1978), and *G. mihanovichii* in South Korea (Lim et al., 2022).

Eicholtz et al. (2018) detected BWYV in the USA, in co-infection with several other previously described cacti viruses by HTS in *Epiphyllum* hybrids with mottling and chlorotic spots; however, it remains unclear whether BWYV infection alone causes symptoms.

Orthotospoviruses TCSV and TSWV were found in symptomatic (chlorotic/necrotic spots, sunken lesions, distortion of cladodes) in *Opuntia* and *Epiphyllum* in nurseries, in the USA and UK (Hausbeck and Gildow, 1991; Hausbeck et al., 1992; Blockley and Mumford, 2001; Baker and Adkins, 2015).

The EpMoaV, a badnavirius, was found in an *Epiphyllum* hybrid with mottling and chlorotic/necrotic ringspots in the USA. RT-PCR assays for known cactus viruses were negative (Lan et al., 2019). Yamashita et al. (1991) described an uncharacterized badnavirus in *Epiphyllum*, which showed ringspots, co-infected with CVX and SOV.

The cavemovirus, Epiphyllum virus 4, was detected in an *Epiphyllum* hybrid with flower stripes and co-infected with CVX, ZyVX and EpMoaV (Zheng et al., 2020).

Species of genera *Opunvirus, Becurtovirus* (family *Geminiviridae*), *Gemycircularvirus, Gemygorvirus,* and *Gemykibivirus* (family *Genomoviridae*) were found by metagenomics in a large number of asymptomatic cacti, collected randomly from several parts of the world (Fontenele et al., 2020a, b; Fontenele et al., 2021a, b).

Subcellular

As already mentioned, the first evidence of viral infection in cacti was subcellular, through the detection of spindle-shaped inclusions ("proteinkörper") in *Epiphyllum* by Molisch (1885). These inclusions were initially considered reservoir substances (Molisch, 1885), or products of a secretion process (Chmielewsky, 1887). There were subsequently several similar descriptions involving numerous cacti species (Mikosch, 1890; Mikosch, 1908; Gicklhorn, 1913; Küster, 1934). Demonstration that these inclusions were graft or sap-transmissible (Weingart, 1920; Blattny and Vukolov, 1932; Rosenzopf, 1951; Weber and Kenda, 1952b; Miličić and Plavšić, 1956) led to the suggestion of their viral nature (Rosenzopf, 1951; Weber et al., 1952b; Weber and Kenda, 1952a, b).

The viral nature of the inclusions was unequivocally demonstrated by Amelunxen (1958), who combined physicochemical techniques with electron microscopy. The virus, with filamentous particles ca. 500 nm long, was named CVX and placed in the group of PVX (Brandes and Wetter, 1959). These spindle-shaped inclusions have been observed in a large number of cacti species (Table 3), in symptomatic or asymptomatic plants. Later Štefanac et al. (1967) confirmed by immunofluorescence that the spindle-shaped inclusions in *E. bridgesii* are formed by CVX particles. Spindle-shaped inclusions were also detected in assay plants experimentally infected by CVX (Miličić, 1962a, b; Miličić and Udjbinac, 1961; Pleše and Miličić, 1966).

Before morphological, immunological, or molecular techniques for virus detection were available, these inclusions were the sole diagnostic evidence for possible viral infection in cacti. Stomatal abnormalities, such as deformation and fusion of guard cells with accessory cells, were also associated with viral infection (Weber and Kenda, 1953). After these pioneer works on viral inclusions of cacti made by European researchers, similar works were carried out in the USA (Sammons and Chessin, 1961; Chessin et al., 1963; Milbrath et al., 1973; Giri and Chessin, 1975b; Attathom et al., 1978; Fudl-Allah et al., 1983), in Japan (Mukoo et al., 1967; Asatani and Inoue, 1969; Nakamura and Mukoo, 1973), and in Brazil (Aragão et al., 1993) as part of investigations to detect and characterize cacti viruses, mostly potexviruses. Descriptions of cell inclusions, however, have been mostly neglected after the introduction of molecular assays for their detection. An example of a spindle-shaped inclusion in dragon fruit cortical cells, infected by the potexvirus ZyVX, as seen under a light microscope is presented in Figure 2.

Ultrastructural

There are not too many i*n situ* observations of cactus viruses. Virions of cactus viruses have been detected by TEM in extracts from potexviruses CVX-, ZyVX-, CV2-, SOV-, SgCV-infected plants (Amelunxen, 1958; Brandes and Wetter, 1959; Sammons and Chessin, 1961; Mukoo et al., 1967; Casper and Brandes, 1969; Casper et al., 1970; Milbrath and Nelson, 1972; Chessin and Lesemann, 1972; Nakamura and Mukoo, 1973; Milbrath et al., 1973; Giri and Chessin, 1975a, b), and in most of the recent works with cacti potexvirus, tobamovirus, carlavirus, alphacarmovirus, and badnavirus. On the contrary, images of polerovirus, orthotospovirus, cavemovirus, as well as of geminivirus and genomoviridae particles from cacti are not available.

A witches' broom type of symptoms in *O. tuna*, previously considered to be of viral etiology (Uschdraweit, 1965), was demonstrated to be of phytoplasma etiology, after the detection of pleomorphic, wall-less bodies in the lumen of sieve tubes (Casper et al., 1970). In this study, the authors also detected particles of CVX and isometric particles ca. 30 nm in extracts and tissue sections. The latter was not identified but may have represented the alphacarmovirus SgCV. Maramorosch et al. (1972) confirmed the phytoplasma etiology of this witches' broom type of symptoms in *O. tuna* Mill. "*monstruosa*", demonstrating the disappearance of pleomorphic bodies from the sieve tube, after tetracycline treatment. These authors also found the aggregate of unidentified

Table 3 – List of cactus species in which spindle-shaped inclusions were described*

Species	References
Astrophytum asterias Leu.	Nakamura and Mukoo (1973)**
Cephalocereus senilis Pfeiff. F. *crist.*	Nakamura and Mukoo (1973)
Cephalocereus leucephala (P) B. & R.	Nakamura and Mukoo (1973)
Cereus peruvianus (L.) Mill.	Goldin and Fedontina (1956); Nakamura and Mukoo (1973)
Cereus triangularis (L.) Haw.	Weingart (1920)**; Aragão et al. (1993)
Cereus triangularis var. *pictus* DC	Weingart (1920)**
Cereus bonplandii J. Parm. ex Pfeiff.	Goldin and Fedontina (1956)
Coryphantha andreae J.A. Purp. & Bob.	Nakamura and Mukoo (1973)
Coryphantha elephantidens Lem.	Nakamura and Mukoo (1973)
Echinocereus procumbens (Engelm.) Lem.	Goldin and Fedontina (1956)
Echinopis nigerrima Schelle	Goldin and Fedontina (1956)
Echinopi eyriesii Zucc.	Nakamura and Mukoo (1973)**
Echinopi tubiflora Zucc.	Nakamura and Mukoo (1973)**
Epiphyllum altensteinii Pfeiff.	Molisch (1885)
Epiphyllum bridgesii Lem.	Molisch (1885); Rosenzopf (1951)
Epiphyllum hookeri Haw.	Molisch (1885)
Epiphyllum oxypetalum (DC.) Haw	Goldin and Fedontina (1956)
Epiphyllum russelianum Hook.	Molisch (1885)
Epiphyllum truncatum Haw.	Molisch (1885); Chmielewsky (1887); Mikosch (1908); Blattny and Vukolov (1932)**; Küster (1934); Rosenzopf (1951); Weber and Kenda (1952a)**; Suhov and Nikiforova (1955); Weber (1953c)**; Reiter (1956); Amelunxen (1958)
Epiphyllum hybrid	Molisch (1885)
Eriocereus jusbertii (Reb.) Ricc.	Nakamura and Mukoo (1973)**
Ferocactus acanthodes (Lemaire) Britton & Rose	Attathom et al. (1978)
Gymnocalycium ventrianum Backbg.	Nakamura and Mukoo (1973)**
Gymnocalycium mihanovichii (Frič & Gürke) Britton & Rose	Nakamura and Mukoo (1973)**
Hylocereus trigonus Saff.	Nakamura and Mukoo (1973)**
Hylocereus undatus (Haw.) Britton & Rose	Fudl-Allah et al. (1983)**
Lobivia sp.	Nakamura and Mukoo (1973)**
Lophophora williamsii (Lem. ex J.F.Cels) J. M. Coult.	Nakamura and Mukoo (1973)
Marginatocereus marginatus (DC) Bachbc.	Nakamura and Mukoo (1973)
Myrtillocactus geometrizans Cons.	Nakamura and Mukoo (1973)
Opuntia brasiliensis Haw.	Miličić (1954)**; Chessin et al. (1963)
Opuntia curassavica Mill.	Amelunxen (1958)
Opuntia engelmannii Salm-Dyck	Gicklhorn (1913); Milbrath et al. (1973); Chessin (1969)
Opuntia glomerata Haw.	Nakamura and Mukoo (1973)**
Opuntia grandis Hort.Angl. ex Pfeiff.	Gicklhorn (1913)
Opuntia haematocarpa A. Berger	Gicklhorn (1913)
Opuntia herrfeldtii Kupper	Amelunxen (1958)
Opuntia inermis DC (= *O. stricta* Haw)	Miličić (1956b); Miličić (1959/1960)
Opuntia kleiniae DC.	Weber (1954)
Opuntia lemaireana Console ex Bois	Amelunxen (1958)
Opuntia leucotricha DC	Amelunxen (1958)
Opuntia lindheimeri Engelm.	Amelunxen (1958)
Opuntia macrocentra Engelmann	Chessin (1965)
Opuntia maxima Salm-Dyck ex DC	Gicklhorn (1913)
Opuntia microdasys (Lehm.) Pfeiff.	Gicklhorn (1913); Nakamura and Mukoo (1973)**
Opuntia monacantha (Wild.) Haw.	Gicklhorn (1913); Amelunxen (1955;1958); Miličić (1959/1960)**; Chessin et al. (1963)
O. monacantha (Wild.) Haw. f. *variegata*	Weingart (1920); Kenda (1954); Miličić (1959/1960); Sammons and Chessin (1961)
Opuntia nana DC.	Miličić (1956)
Opuntia phaeacantha Engelm.	Chessin (1965)
Opuntia robusta H.L. Wendl. ex Pfeiff.	Gicklhorn (1913)
Opuntia spirocentra Engelm. & J. M. Begelow ex Haage	Gicklhorn (1913)
Opuntia stricta Haw.	Miličić (1956;1959/1960)
Opuntia subulata Engelm.	Weber et al. (1952a); Weber and Kenda (1952b); Weber (1954)
Opuntia tomentosa Salm-Dyck	Miličić (1959/1960)
Opuntia vulgaris Mill.	Gicklhorn (1913); Nakamura and Mukoo (1973)**
Opuntia spp.	Asatani and Inoue (1969)
Pereskia aculeata (L.) Karsten	Mikosch (1908); Weber (1953a); Nakamura and Mukoo (1973)
Pereskiopsis pititache Britton & Rose	Weber (1953b); Weber et al. (1953)
Pereskiopsis spathulata Britton & Rose	Mole-Bajer (1953)
Rebutia krainziana Kess.	Nakamura and Mukoo (1973)**
Rhipsalis boliviana Lauterb.	Nakamura and Mukoo (1973)**
Rhipsalis cereuscula Haw. ex Phil.	Weber and Kenda (1952a); Weber et al. (1952a)
Rhipsalis eliptica Lindbg.	Nakamura and Mukoo (1973)**
Rhipsalis ramulosa (SD) Pfeiff.	Nakamura and Mukoo (1973)**

*Modified from Milbrath (1971). **Presence of inclusions associated with external symptoms.

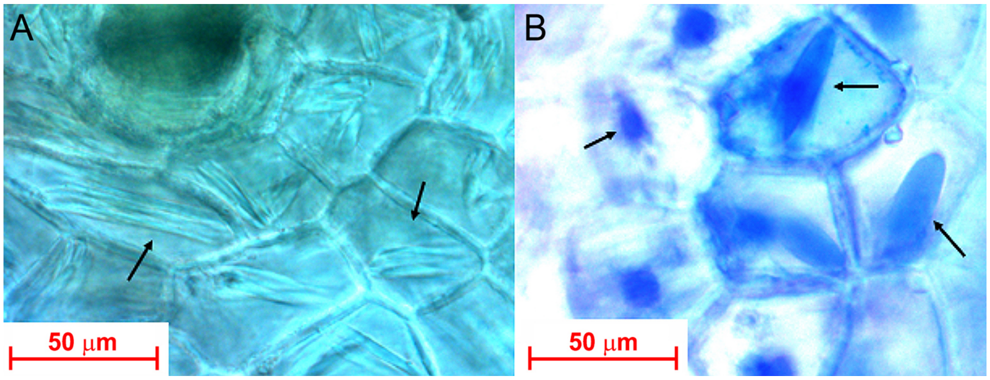

Figure 2 – Light micrographs of spindle-shaped fibrous inclusions (arrows) in cortical cell of cladode from an asymptomatic moonlight cactus [*Selenicereus inermis* (Otto) Britton & Rose] infected by Zygocactus virus X. A) Image of a fresh unstained, handmade section showing spindle-shaped inclusions in most cortical cells; B) Same sample, after being stained with Azure A. Inclusions were deeply stained in blue (Del Corona, unpublished data).

tobamovirus-like particles in the cytoplasm. Attathom et al. (1978) reported masses of elongated particles in the cytoplasm of *C. quinoa* and *Amaranthus caudatus* L. after experimental inoculation withan isolate of CVX from barrel cactus (*F. acanthodes*). Similar observations were made with Brazilian isolates of CVX in naturally infected *O. vulgaris* and *C. triangularis*, as well as in experimentally infected *C. quinoa* and *Gomphrena globosa* L. (Aragão et al., 1993). Duarte et al. (2008) described aggregates of filamentous particles of potexvirus in the cytoplasm of parenchymal cells in *Hylocereus undata* Haw.) Britton & Rose co-infected withy ZyVX and SchVX, *S. truncata* co-infected with ZyX, SchVX, OpVX, and *O. tuna* infected with ZyVX. Kim et al. (2016) in South Korea, detected CVX in symptomless *Hylocereus* sp., and fibrous inclusion bodies in the cells. Cytoplasmic inclusions formed by aggregation of different potexvirus and tobamoviruses do not present peculiarities; thus, the detection of such inclusions does not have diagnostic value at the species level.

Detection and identification of cactus viruses

Although external symptoms, as mentioned above, may indicate a possible viral infection, virus infections of cacti are usuallyasymptomatic. Indeed, early detection of a cactus virus was a consequence of a cytological study that detected spindle-shaped inclusions (Molisch, 1885), later demonstrated to be formed by CVX particles (Amelunxen, 1958). Although not widely exploited in recent research on cactus viruses, searching for cell inclusions remains a powerful tool for detecting viral infections in cacti (Figure 2). In economically important crops, such as dragon fruit (*Selenicereus* spp.) and prickly pear (*O. ficus-indica*), potexviruses and tobamoviruses have been associated with external symptoms as well as in asymptomatic plants. However, there are no reports of economically significant outbreaks of diseases being caused by these viruses.

Identification of viruses in Cactaceae may pose several difficulties due to the frequent occurrence of mixed infection with two or more viruses. Additionally, handling extracts of these plants poses difficulty due to their sticky nature, which is caused by excess mucilage. This problem can be minimized by adding calcium chloride (0.3-0.5 M), which fluidizes the solution (Aragão et al., 1993). Metagenomics of bulk extracts from the sample cactus under study appears to be the best and the most effective method for detecting both known and novel viruses. However, though these methods are still costly and should be used selectively. Most recently described cacti viruses have been identified by metagenomics (Peng et al., 2019; Wu et al., 2019; Salgado-Ortíz et al., 2020; Zheng et al., 2020; Fontenele et al., 2020a, b; Fontenele et al., 2021a, b; Bae and Park, 2022; Ortega-Acosta et al., 2023; Ortega-Acosta et al., 2024; Guimarães et al., 2025).

For routine surveys, examination of negatively stained tissue extracts (Figure 3) and tissue sections (Figure 4) by transmission electron microscopy may provide initial hints of viral infection through the detection of presumptive viral particles, especially those occurring in high concentrations as tobamoviruses, potexviruses, carlaviruses, and alphacarmoviruses. Moreover, trials to detect cell inclusion bodies in fresh sections of cacti tissues (Figure 2) may provide clues for viral infection. Mechanical and graft transmission assays may provide additional evidence for viral detection. Definitive identification can be achieved by serology, if specific antibodies are available, or by molecular RT-PCR or RT-qPCR assays, using specific primers and nucleotide sequencing of the amplicons, or by the metagenomic approach. It is always desirable, after their detection, to add some of the biological properties of the detected viruses.

Dissemination of cactus viruses

Cacti tobamoviruses and potexviruses have been described in a large number of cultivated cacti

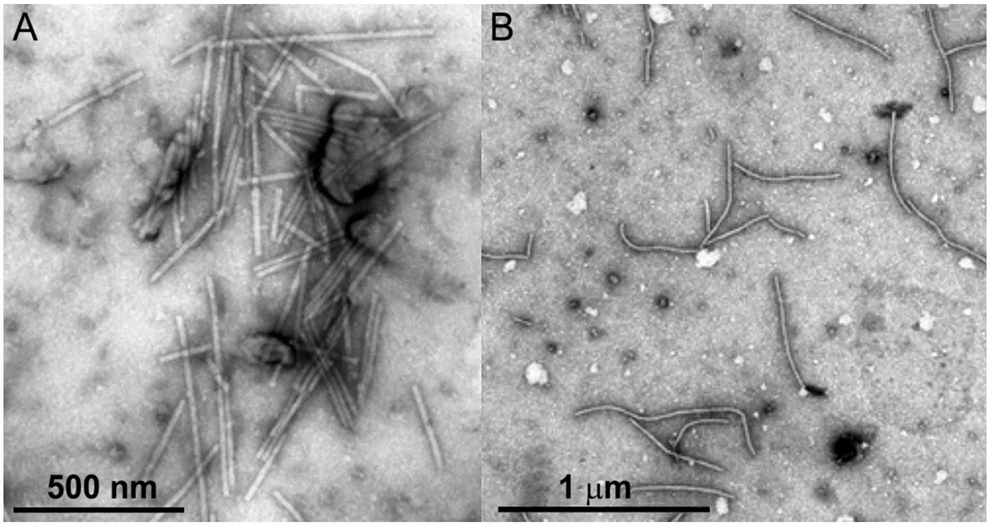

Figure 3 – Transmission electron micrographs of virions present in extract from cladode, negatively stained with uranyl acetate. A) Rod-shaped particles of rattail cactus necrosis-associated virus, a tobamovirus, in cladode extract from asymptomatic *Opuntia leucotricha*, sampled at Instituto Plantarum, Nova Odessa, SP, Brazil; B) Elongated, flexible particles of the potexvirus Zygocactus virus X present in cladode extract of an asymptomatic dragon fruit (*Selenicereus* sp.) collected in an experimental field at Piracicaba, SP, Brazil.

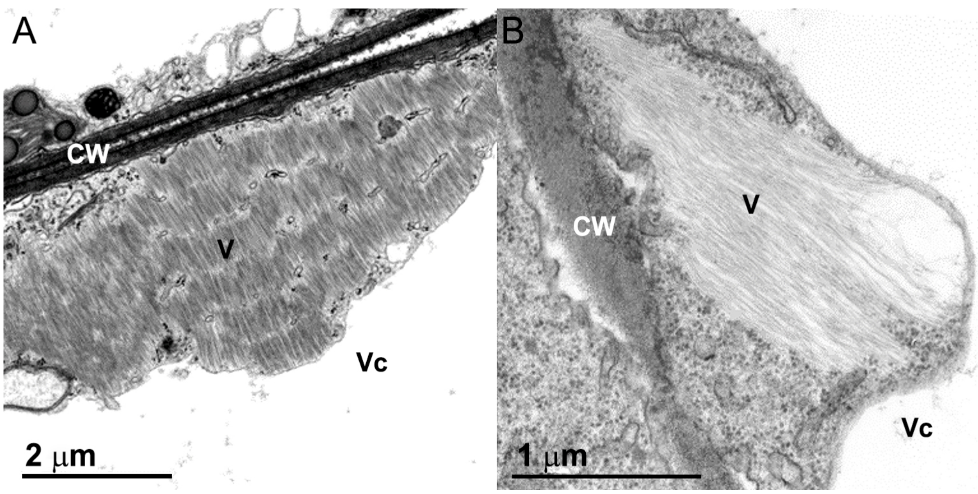

Figure 4 – Transmission electron micrographs of tissue sections exhibiting aggregates of virions. A) A stacked mass of rod-like particles (V) of the tobamovirus rattail cactus necrosis associated virus in a cortical cell of a cladode from an asymptomatic *Opuntia leucotricha*; B) Fibrous bundle of elongated particles of the potexvirus Zygocactus virus in a cortical cell of an asymptomatic dragon fruit (*Selenicereus* sp.) plant. CW = cell wall; Vc = vacuole.

(ornamentals, forage, fruit-producing) species. In most of these cases, the transmission must have occurred using infected rootstocks (such as *H. trigonus, H. undatus, Cereus peruvianus* (L.) Mill.*, Trichocereus pachanoi* Britton & Rose, etc.) for grafting or by handling of plants during cultivation (such as pruning and harvesting).

The situation worsens since frequent virus infections in cacti are often symptomless, leading to the use of infected mother plants for vegetative propagation through cloning, for example, in dragon fruit cultivation. This fact may explain the widespreaddistribution of potexviruses infecting this crop globally. In the wild, one possibility means of dissemination for viruses, although likely with low efficiency, could involve flower-visiting organisms (insects, birds, bats), potentially through contaminated pollen, as suggested for SgCV (Milbrath et al., 1973); however, this has yet to be demonstrated. Therefore, the widespread distribution of some cactus viruses is the result of human activities, including the large-scale relocation of cactus species from their center of origin and the transmission of viruses through mechanical handling and grafting.

In the case of cacti infection by poleroviruses and orthotospoviruses, this was certainly mediated by infected aphids and thrips, originating from a non-cactus source. No information is available about the dissemination of newly described and widely spread *Geminiviridae* and *Genomoviridae* species detected by mass sequencing.

Final Remarks

To date, 31 distinct viruses, belonging to 13 genera and nine families, and three viroids of two genera, have been described as naturally infecting approximately 70 Cactaceae species, mostly belonging to the genus *Opuntia,* worldwide. Until recently, all of them belonged to the *Riboviria realm*, *Orthornavirae* kingdom (genera *Potexvirus, Tobamovirus, Carlavirus, Alphacarmovirus, Polerovirus* and *Orthotospovirus*), but in the last two decades, after the use of genome deep sequencing, several novel species belonging to the *Pararnavirae kingdom,* (family *Caulimoviridae,* genera *Badnavirus* and *Cavemovirus*) and *Monodnaviria realm, Shotokuvirae kingdom, Geminiviridae family,* (genera *Opunvirus, Becurtovirus*) and *Genomoviridae family,* (genera *Gemykolovirus, Gemyduguivirus, Gemygorvirus, Gemykroznavirus, Gemycircularvirus* and *Gemykibivirus*), as well as viroids, were found.

In general, these cacti viruses cause asymptomatic infections; however, cases of ringspots, necrosis, mottling, and deformations of cladodes have been reported, especially in dragon fruit and prickly pear. A number of these viruses infect economically important cacti such as dragon fruit and prickly pear, but there is no information available on possible losses due to the infection. Certain viruses found infecting cacti, such as AltMV, TMV, BWYV, and orthotospoviruses probably originate from non-Cactaceae plants, representing cases of accidental infections. However, cactus-specific potexviruses (CVX, OpVX, PiVX, SchVX, ZyVX), tobamoviruses (SOV, CMMoV, RCNaV, OpV2), carlaviruses (CV2, CCV-1 and 2), alphacarmovirus (SgCV), and the viruses discovered by metagenomics (*Badnavirus, Cavemovirus* and *Geminiviridae*, and *Genomoviridae*) are probably cacti viruses, present in the wild growing cacti species.

Several of them have been found in cultivated ornamental or economically exploited cacti, likely originating from wild plants and disseminated via nurseries through handling and grafting procedures. Interestingly, although these viruses can experimentally infect non-cactus plants, no naturally infecting plants outside the Cactaceae family have been identified yet; thus, their host range seems limited to cacti. More viruses in cactus plants, both wild and cultivated, will likely be found, especially with the increasing use of metagenomics.

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Conflict of interest

The authors declare that there is no conflict of interest.

Data availability statement

All information used in this review is available upon request to the corresponding author.

Declaration of use of AI Technologies

AI technologies or supported applications and programs were not used in the creation of the text, figures and tables.

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