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Brevipalpus-transmitted viruses: parallelism beyond a common vector or convergent evolution of distantly related pathogens?

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Although diseases caused by *Brevipalpus*-transmitted viruses (BTV) became relevant for agriculture a century ago, their causal agents have been only recently characterized and classified in two new genera of plant-infecting viruses: *Cilevirus* and *Dichorhavirus*. In this review, we highlight both similarities and differences between these viruses emphasizing their current taxonomy and historical classification, phylogeny, genomic organization, gene expression, and the latest research developments on BTVs. Additionally, we stress particular features of interactions with their mite vectors and plant hosts that support, from an evolutionary perspective, the potential convergence of both viral groups.

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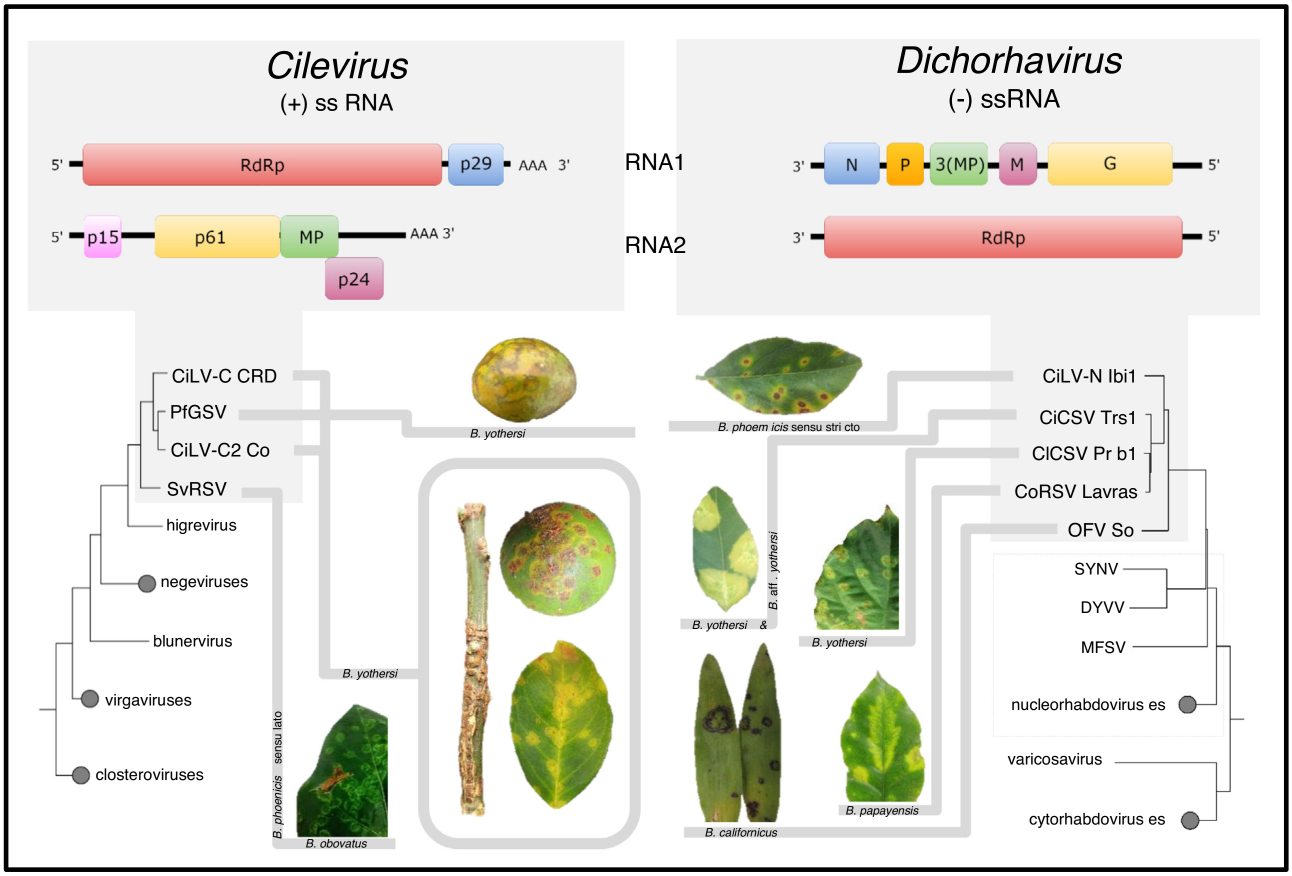
From citrus leprosis to a broad concept of diseases caused by *Brevipalpus*-transmitted viruses

The first described and most studied disease caused by a BTV is citrus leprosis. Reported first in Florida, USA, around 1860 and shown to be associated with tenuipalpid mites in the 1940s [1], the disease is now absent from that region, but still occurs in several countries on the American continent (reviewed by [2]). In the first half of the 20th century, two other diseases associated with *Brevipalpus* mites were reported in Brazil and Argentina, respectively, affecting *Coffea* sp. and *Ligustrum* sp. plants [3,4]. The only features they seemed to share, at that time, were the typical localized spots — sometimes ringspots — observed in the aerial parts of infected plants, and the association with *Brevipalpus* mites [5,6]. In 1968, Knorr [7] confirmed citrus leprosis transmission by *Brevipalpus* sp., and over the following decades, new diseases with similar features were reported in orchids [8], passion fruit [9], and, more recently, in at least 40 different plant species [10] (Figure 1).

BTVs do not invade plants systemically and their infections remain restricted to the localized lesions under natural field conditions. Transmission electron microscopy analyses of these lesions revealed that BTVs cause one of two distinct cytopathological patterns in infected tissues [11]. In the cytoplasmic type (-C), short (~50 nm × 110–120 nm), membrane-bounded particles appear with elements of the endoplasmic reticulum and are associated with the presence of electron dense, vacuolated inclusions (viroplasms). In the nuclear type (-N), short (~40 nm × 100–110 nm) rodlike particles are present in the nucleus and cytoplasm, associated with electron lucent viroplasms in the nucleus. Rodlike particles may form large aggregates within the nucleus, and commonly appear associated perpendicularly with inner or outer membranes of the nuclear envelope and endoplasmic reticulum (ER) in the cytoplasm. Often particles are arranged radially in tubular arrangement of the ER, producing structures referred to as spoke wheels [12,13] (Figure 2). Both BTV-C and BTV-N accumulate mainly in the parenchyma and in the epidermal cells, and are rarely seen in vascular parenchyma cells, which may explain the conspicuous symptoms they cause [14,15].

The year 2006 was a turning point for the study of BTVs. While available data suggested BTV-C and BTV-N as putative cyto- and nucleorhabdoviruses, respectively [14], a clearer picture began to arise as genome sequences of BTVs became available. The complete genome sequences from two Brazilian isolates of citrus leprosis virus C (CiLV-C, a BTV-C) [16,17], and an isolate of orchid fleck virus (OFV, a BTV-N) from Japan [18] were obtained. Supporting the differences in

Figure 1



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Brevipalpus-transmitted viruses (BTV): genome organization, phylogenetic relationships and symptoms. Viruses in the genera *Cilevirus* and *Dichorhavirus* have bisegmented genomes of different polarities. *Brevipalpus* mites vector both types of viruses plant to plant, where their infections remain restricted to local lesions. Cileviruses show evolutionary relationships with the plant-infecting higreviruses and blunerviruses and to a lesser degree with the arthropod-infecting negeviruses. Dichorhaviruses likely share a common ancestry with nucleorhadoviruses (inside a dashed line box), especially with sonchus yellow net virus (SYNV), datura yellow vein virus (DYVV), and maize fine streak virus (MFSV). Viral symptoms are shown on hosts where they were firstly detected: citrus leprosis virus C (CiLV-C) and citrus leprosis virus C2 (CiLV-C2) in sweet orange (*Citrus sinensis*), passionfruit green spot virus (PfGSV) in *Passiflora* sp., *Solanum violaefolium* ringspot virus (SvRSV) in *Solanum violaefolium*, citrus leprosis virus N (CiLV-N) and citrus chlorotic spot virus (CiCSV) in sweet orange, *Clerodendrum* chlorotic spot virus (ClCSV) in *Clerodendrum* sp., coffee ringspot virus (CoRSV) in *Coffea* sp. and orchid fleck virus (OFV) in *Oncidium* sp. RdRp: RNA-dependent RNA polymerase; p29, p61 and p24: putative structural proteins, p15: unknown function, MP: putative movement protein, N: nucleocapsid protein, P: phosphoprotein, M: matrix protein, and G: glycoprotein.

intracellular characteristics, despite the resemblance in particle morphology, symptoms, and vector, BTV-C and BTV-N had completely different genome sequences and organization. Aside from being bisegmented, OFV has a negative-sense (−) single strand (ss) RNA genome of ~6–7 kb per segment, whereas CiLV-C has a positive-sense (+) ssRNA genome of ~9 and ~5 kb for RNA1 and RNA2, respectively [16–18], which lead to distinct replication strategies of these viruses. In 2009 and 2017, respectively, CiLV-C and OFV became the type members of two new genera accepted by the International Committee on Taxonomy of Viruses: *Cilevirus*, a free-floating genus, and *Dichorhavirus* (family *Rhabdoviridae*, order *Mononegavirales*) [19–21].

In addition to viruses classified in these two genera, the trisegmented hibiscus green spot virus 2, the single member of the genus *Higrevirus*, also causes BTV-like lesions in citrus and hibiscus plants in the USA (Hawaii) [22]. However, although this virus shares some features with cileviruses (nucleotide sequence similarity, non-systemic infections in the plant hosts), data supporting transmission by *Brevipalpus* mites are lacking; hence, higreviruses will not be further addressed in this review.