



Review Article

Plant Virome

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Abstract | The viromes of land plants are enormous and diverse, and they are dominated by RNA viruses. However, reverse-transcription and single-stranded (ss) DNA viruses also make significant contributions to the viromes of land plants. In this article, we present a thorough taxonomy of viruses that was recently adopted and is based on phylogenomic investigations. This taxonomy is then applied to the plant virome. We continue our investigation by tracing the evolutionary origins of various plant virus lineages all the way back to the first genetic mobile components. We investigate the role of horizontal viral transfer from invertebrates to plants during terrestrialization, which was enabled by strong ecological linkages. The intimate evolution of invertebrates and plants permitted these relationships. We hope that plant biologists and virologists will be interested in the evolving big picture of the plant virome's origins and global architecture, which will encourage further research into virus-plant coevolution.

Keywords: Plant virus, Virome, Phylogeny, Virus evolution, Virus taxonomy

Received | November 04, 2024; **Accepted** | January 21, 2024; **Published** | January 24, 2024

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Citation | El-DougDoug, K. A. , W. S. El-Araby, E. M. Halawa and R. A. Dawoud. 2024. Plant virome. Journal of Virological Sciences, 12(1): 26-45.

DOI | <https://dx.doi.org/10.17582/journal.jvs/2023/12.1.26.45>

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Introduction

The term “virome” is referring to the group of viruses that are frequently studied and described by means of metagenomic sequencing of viral nucleic acids when they are discovered to be related with a specific ecosystem, organism, or holobiont. The ambient viral shotgun metagenomes are usually referred to by this term. Insights on food cycling, immunity development, as well as a substantial source of genes through lysogenic conversion

have all been gleaned from studies of the virome, which includes viruses and bacteriophages (1, 2, 3).

Both eukaryotic as well as prokaryotic viruses can be discovered in plants, and together they form the plant virome (4) (Fig. 1). The effect of eukaryotic viruses on plant health is wide ranging, from self-limiting, acute infections to lethal ones. The microbiome of a plant can be impacted by the presence of prokaryotic viruses by altering the composition and activity of the bacterial communities that make up the microbiome (5).

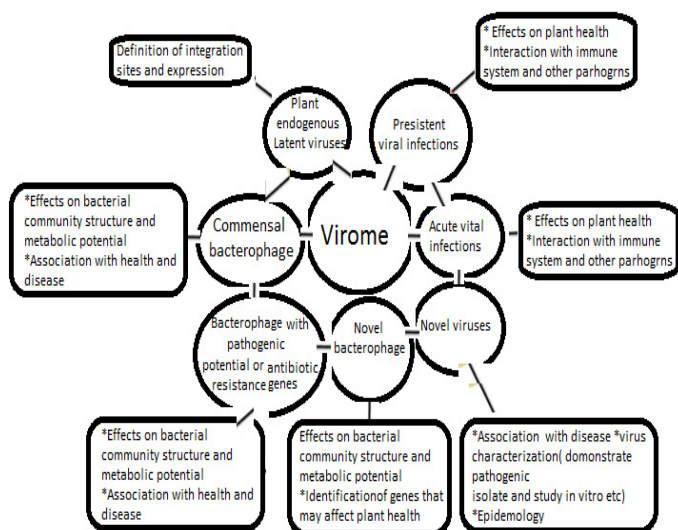


Figure 1: *The plant's viral components. Virome components that can be defined by metagenomic sequencing are depicted as circles. These groups are not exclusive of one another. When viruses are discovered, we may then examine how they influence plant wellness as well as the microbiome. Each component of the virome is accompanied by a set of questions and implications. Based on work by Wylie et al. (2012), with some changes.*

To refer to the viral component of the plant microbiome, we use the term “plant virome (6).” Viruses producing persistent, acute, or latent infection, as well as viruses united with the plant genome, like Latent viruses, are all part of the plant virome (sometimes called the “viral metagenome”), which is the assembly of all viruses discovered in or on plants (7). Both eukaryotic viruses and prokaryotic viruses (bacteriophages) make up the plant virome (8). There is no doubt that eukaryotic viruses significantly impact plant wellbeing. Viruses are capable of causing a diverse array of symptoms in plant life, from mild infections that clear up on their own to fulminant, uncontrolled infections that can cause severe illness in humans. In addition, viruses are often suspected as the root cause of numerous diseases with an etiological mystery (9). Over 8% of the human genome is made up of dormant viruses found only in plants. They are continuously being transcribed in healthy tissues (10). Some diseases, for instance multiple sclerosis, amyotrophic lateral sclerosis, as well as rheumatoid arthritis, have been linked to them in the past, although no proof of causation has been provided. Because of their potential to modify bacterial population structure or pathogenicity, bacteriophages may also have an impact on human health. Insight into virome stability, diversity, gene function, and phenotype correlation has become available with the advent

of high-throughput, deep sequencing technology. The complexity of microbial communities and the function viruses play within them can be better comprehended with this knowledge (11).

Each plant has its own unique virome, which is full with viruses like bacteriophages that haven't been studied much but could be used to fight against disease (12). The Plant Microbiome study looked at the dsDNA viruses present in 102 different people, finding an average of 5.5 different viral genera per person. Herpes viruses, polyomaviruses, papillomaviruses, anelloviruses, adenoviruses, parvoviruses, as well as circoviruses were all among these viruses. The vast majority of these pathogens did not evolve over time. However, because of their rapid evolution, horizontal gene transfers, as well as tight interactions with host nucleic acids, the viral communities in plants are still mostly a mystery (13). A portion equal to 8 percent of the genome of humans is considered to be comprised of endogenous retroviral DNA, and this integration is associated with the promotion of certain diseases like cancer as well as autoimmune disorders. These sequences are also maternally inherited, thus their effects are passed on to future generations (14). Bacteriophages, which are prokaryotic viruses, are another component of the virome (15). There is a lack of knowledge on plant dsDNA viruses as well, despite the fact that many of them switch between the two among infectious virions in circulation as well as incorporated endogenous viral elements (EVEs) (16, 17). When plants are under stress, certain endogenous viral elements can become active, causing systemic infection of the host (18). Other endogenous viral elements are ‘molecular fossils’ in domesticated plants (19). Host plants can use from dormant plant viruses via inducing transcriptional or post-transcriptional silencing of homologous regions, hence aiding in plant virus resistance (20, 21). The genomes of potato (*Solanum tuberosum*), tomato (*Lycopersicon sp.*), rice (*Oryza sativa*), tobacco (*Nicotiana sp.*), bitter orange (*Poncirus trifoliata*), petunia (*Petunia sp.*) and banana (*Musa spp.*) have been exposed to harbor for example integrates. A run of bananas because new hybrids get infected by the integration of viruses from the wild *M. balbisiana*, international banana (*Musa spp.*) breeding operations have been seriously hampered by Obino l'Ewai virus (22, 23). If a badnavirus promoter is implanted next to an indigenous plant gene, it has the potential to affect the quantities of transcription produced by the gene as well as the

tissue specificity of its expression, which will impede banana breeding initiatives (24).

Banana a model group of natural endophytic viromes

In most cases, viruses are responsible for disease, however some viruses may actually be beneficial to their hosts by acting as resident regulators of host microbiomes (25). Viruses that are connected with plants can assist plants in surviving by boosting their resistance to stress or by managing the populations of endophytes (26). The purpose of this research was to distinguish endophytic virus populations in banana along with plantain (*Musa* spp.) genotypes, encompassing both cultivated as well as wild species, in order to evaluate virome repertoires as well as recognize novel viruses (27). The phylogenetic composition of the improved banana microbiome as well as the DNA viral community that was discovered there Initial taxonomic classification of the enriched microbiome layers, utilizing DIAMOND blastx as well as correcting for average genome sizes indicated that these microbiomes comprised extremely little plant or fungal genomes in comparison to bacterial and viral genomes. The percentages were 0.11 and 0.28%, respectively (27). Bananas and plantains, both members of the genus *Musa*, are examples of a model group for which the natural endophytic viromes have not been thoroughly defined (27). Over 130 countries regard the banana as an essential food staple and an important economic product (28). The natural viral community variance is unknown, however banana bunchy top virus (BBTV), common pathogenic viruses including banana streak virus (BSV) as well as banana bract mosaic virus (BBRMV) have been extensively researched (29). Although plant tissue and cultivars are responsible for shaping microbiomes, the influence of the host on plant viromes is not as well understood (30). In addition to this, there is evidence that domestication reduces bacterial and fungal microbiomes, however, the effects of this on banana viromes are not known (27). As a vital 1st step in determining how these viromes may influence microbiomes, we equated the endophytic virus-like sequences that were obtained from sympatric banana plants. These plants included both native diploid as well as domesticated triploid forms of banana. In spite of the fact that these plants grow in similar conditions, the results revealed a large number of novel or highly divergently predicted phages as well as dsDNA viruses or endogenous viral elements with generally non-overlapping community structures. This finding suggests that hosts

are the primary factor in determining the makeup of DNA virus communities. In the endophytic microbiome of *Musa* species, there are variants that are unique to *Musa*, as well as there is a possibility that these hosts have undergone phylo diversification. The viruses that infect DNA in plants, which include the banana streak viruses, almost always take the form of endogenous, replicating forms that are universally incorporated into the genomes of *Musa* plants (27). Our analysis indicates great coverage as well as abundance of them, confirming their huge copy number in host DNA despite low quantities. Even with little host DNA. We also identified genotype variants. We found that triploids had a more limited range of DNA plant virus populations than diploids did, and that there were many viruses that did not exist across the two genotypes. This was a surprising finding. The fact that these viruses comprised a significant number of viruses that were not streak or *Musa* viruses provides evidence that the samples in question had a combination of resident and transitory DNA viruses. These findings are significant since commercial banana cultivars (triploid *M. acuminata*) are vulnerable to infection by many different badnaviruses (31), causing problems for breeding operations when viral DNA becomes incorporated into the nuclear genome of *M. balbisiana* (BB genotype) and spreads causing the plants to become infected throughout their systems when they are under stress (32). The closeness of a badnavirus promoter to an endogenous plant gene can impact transcription levels, change expression tissue specificity, as well as lead to infection. However, it is believed that the majority of EVEs are “viral molecular fossils” in wild plants and that certain dormant plant viruses may provide a benefit to wild host plants in the future (27). Based on our findings, which display that EVEs and other relatively abundant non-streak disease-causing dsDNA viruses (for instance Fig badnavirus 1, Grapevine Roditis leaf discoloration-associated virus, Taro bacilliform CH virus, Yacon necrotic mottle virus, in addition Dioscorea bacilliform RT virus) are amenable to economic assay, we recommend future concentrated efforts on improving enhancement protocols, which includes target capture (27, 33).

Overview of virus origins, host ranges and megataxonomy

As the cost of nucleotide sequencing has decreased and metagenomics, metatranscriptomics, as well as metaviromics have risen rapidly in popularity over

the past decade, our knowledge of the world's viruses has exploded. There has been a historical bias in global virome research toward diseases with significant medical or economic consequences (34). At the time, the virus world appeared relatively disjointed, despite widespread recognition of the tremendous variety of virus genome replication and expression cycles. The exponential rise in the discovery of novel viruses has resulting in the identification of many previously unknown relationships across viral families, the formulation of new unifying concepts, as well as the creation of the first rough draft of a global virus tree (35). Viruses have developed as a new kind of world, one with a highly connected gene-genome network that is in constant, dynamic interchange with the worlds of other MGEs as well as cellular host organisms (36).

There is not a single gene shared by all viruses, in contrast to cellular creatures which share roughly 100 homologous genes passed down from the LUCA. Therefore, viruses are undeniably polyphyletic, having emerged several times from separate gene pools (37). However, the virus's lifestyle is defined by two distinct sets of genes: those in charge of virion generation (morphogenetic modules) as well as those responsible for semiautonomous genome replication (replication modules). Viruses can be classified as either encoding no proteins required in replication or lacking a morphogenetic module (e. g., capsidless viruses) (38). The vast mainstream of viruses, however, possess both replicating along with morphogenetic modules, and deciphering their evolutionary histories is crucial to gaining insight into the emergence and development of viruses (39). The semiautonomous, semiparasitic genome replication mechanism of viruses is shared by a wide variety of selfish replicons or MGEs that don't form virions but encode at least some genes necessary in their propagation. DNA plasmids and self-replicating transposons (for example, eukaryotic retrotransposons) are the most common types of MGEs (40). Protein-primed DNA polymerase B (PolB), superfamily 3 helicase (S3H), rolling-circle replication endonucleases (RCREs) and reverse transcriptase (RT) are all required for the replication of the various MGEs. All of these enzymes, which are so characteristic of viruses, are extremely uncommon or nonexistent in cells (41). Furthermore, RNA viruses encode RNA-dependent RNA polymerases (RdRPs) identical to the RTs, whereas MGEs and cells do not. Whether or if the current viral RNA-dependent RNA polymerases are descended from ancestral

RdRPs that may have participated in the replication of RNA genomes in the hypothesized RNA-protein universe prior to the emergence of DNA genome is still up for debate (42).

The common ancestry of MGE and viral replication modules can be traced back to replication systems that existed long before LUCA, namely to the original RNA recognition motif (RRM). Accordingly, virus/MGE replication modules appear to evolve at the earliest stages of development, possibly even inside protocellular replication systems, supporting the concept of genetic parasite inevitability (43).

Proteinaceous capsids, unique to viruses, preserve and safeguard virus genomes amongst infections, allowing genome release to the host cell. Viruses with icosahedral capsids, then those with elongated helical capsids, exert an outsized degree of control over the virus morphosphere, despite the vast range of capsid morphologies. Many, if not most, virus morphogenetic modules have developed from cellular predecessors at various points in time, from the Late Universal Common Ancestor (LUCA) to the present day, as has been proven by recent investigations (44). Therefore, it can be deduced from the evolution of virus genome core components that viruses typically originated through ancient MGE-like elements stealing protocapsid proteins from cells and supplying replication-related proteins to newly emerging viruses (45).

Given the apparent prehistoric origins of MGEs, the evolutionary history of the corresponding virus hosts can be used to estimate the time of creation of genuine, encapsidated viruses. Viruses that have a capsid protein (CP) with either a single jelly roll (SJR) or a double jelly roll (DJR) structure can serve as a model for these early beginnings, perhaps during the LUCA period. These virion proteins have been proposed to have originated from repurposed cellular carbohydrate-binding homologs that have an SJR fold (46). DJR-CP is a putatively pre-LUCA virosphere-evolved protein that forms an icosahedral capsid for dsDNA viruses that infect bacteria, archaea, as well as a wide variety of eukaryotes. During this time, viruses encoding this capsid protein likely diversified to infect a wide variety of host organisms. Single jelly roll CPs are most prevalent in eukaryotic RNA as well as ssDNA viruses, although it is also used by several DNA bacteriophages and archaeal viruses. However, it appears that these virus families have independently recruited single jelly roll proteins from host cells on

multiple times (47).

While SJR-CPs as well as DJV-CPs are old and widespread, the zinc finger domain virion matrix Z protein is employed by only one family of vertebrate RNA viruses, Arenaviridae. Z-proteins have a fold that is strikingly similar to eukaryotic E3 ubiquitin ligases, suggesting that they were recruited by the ancestral arenavirus not too long ago, likely during the course of vertebrate evolution. So, from LUCA to vertebrates and perhaps still today (see ssDNA Viruses), viruses have emerged with innovative combinations of replication in addition morphogenetic modules (48).

Viruses with diverse encapsidated genomes (Baltimore classes) tend to be underrepresented in some cellular host evolutionary lineages. Archaea are the most specialized hosts since they only allow dsDNA and ssDNA viruses. All 7 Baltimore virus classes, including RNA, reverse-transcription and DNA viruses, are only found in animals, making them the sole known host for these viruses (49). In contrast to the virome of aquatic organisms, which is dominated by a wide variety of dsDNA viruses, the virome of land plants is liberated by +RNA viruses, with only a small number of RNA, reverse-transcribing, dsRNA and ssDNA viruses present. In contrast, the green algal virome is stuffed with enormous dsDNA viruses belonging to the Phycodnaviridae family. Fungal viromes are also devoid of dsDNA viruses but show a preference for dsRNA viruses (50).

The International Committee on Taxonomy of Viruses (ICTV) has accepted a new virus classification that does not use the Baltimore classes or virion morphology. This grouping, on the other hand, is based on a number of different criteria. Although the Baltimore classes offer a useful framework for comparing the components of viromes, this classification of viruses does not yet exist. This megataxonomy, on the other hand, is supported by virus phylogenomics, which is then reinforced by bipartite (gene-genome) network analysis, in addition to a comparison of the virion and capsid protein structures. There are four worlds in this evolutionary classification that are dedicated to viruses, and each of those realms is further subdivided into kingdoms, phyla, classes, orders, families, genera, and species (51). Riboviria and Monodnaviria are the two categories that can be used to split the virome of terrestrial plants. Riboviria refers to viruses that have the ability to reverse-transcribe RNA, while Monod-

naviria refers to ssDNA viruses (52).

Following this introduction, we will use phylogenomics as a lens through which to examine the makeup of the plant virome as well as its evolution on a broad scale. Due to the limiting sampling of lower plants such as lycophytes, bryophytes, green algae and ferns, in addition to gymnosperms, examination of the vegetation the majority of virome can only be found in blooming land plants, which are classified as angiosperms (53). In contrast, viruses found in lower plants receive just a cursory examination in the context of the evolution of plant viromes. Our primary take-away is that horizontal virus transfer (HVT), which frequently occurs between hosts with very different genetic make-ups, was a major force in shaping the plant virome. It appears that the HVT occurrences are caused by the close ecological ties that exist between a varieties of creatures. These ties include predatory and parasitic relationships, as well as commensal and symbiotic relationships. The more rapid development of viruses that can occur as a result of mutations is outside the purview of this particular article (54).

Composition of the angiosperm virome

When it comes to the classification of plant virome components, there are at least three metrics that are helpful: (a) evolutionary, which is defined based on phylogenomic and taxonomic diversity; (b) ecological, which is classed based on the virus host range in addition to the occurrences of infections within plant populations; as well as (c) economical, which is classified based on the virus disease's impact on agriculture, bioenergy, or decorative plants (55). Although the evolutionary approach is the primary emphasis of this article, we will also briefly discuss virus ecology associated disease consequences in areas where they are particularly pertinent. The replication as well as morphogenetic modules of plant viruses are, for the most part, united with other viruses of eukaryotes, and particularly with animal viruses (56). The processes that are determined by the particulars of plant biology are what differentiate plant viruses from their other relatives. This is accompanied by a two-phase systemic infection that includes both local cell-to-cell movement in addition to systemic transport through the vasculature of the plant. Transfer of the virus from one plant to another is the first step in this process. Plasmodesmata are responsible for the active transmission of the virus from one cell to another and tend to require particular movement proteins (MPs) that

are expressed by the virus in order to function properly (57). The most distinctive characteristic of plant viruses is represented by their extraordinarily variable movement proteins. Systemic transport is typically dependent on additional capabilities of viral proteins as capsid protein s, movement proteins, or counter-defense proteins. On the other hand, in certain viruses with larger genomes, this role is carried out by proteins that are specifically devoted to long-distance transport (58).

Vectors, which include plant-parasitic fungi, plant-feeding arthropods, nematodes, as well as plasmodiophorids (protists that belong to the phylum Cercozoa), are required for the transmission of viruses from one plant to another. The mechanism of transmission is unique to each virus and vector, also it frequently contains genetic determinants that are connected with the virions as well as extra transmission elements that are referred to as helper components (59). RNA interference (RNAi), often referred to as RNA silencing, is one of the powerful RNA-based defense systems that plants possess, which allows them to combat RNA as well as DNA viruses. A great number of plant viruses rely on either specified RNA interference suppressor proteins or the suppression activity of proteins with other functionality (for example, CPs, movement proteins, or transmission factors) so that they can more easily infect their hosts (60).

As a result, the genome of a prototypical plant virus includes modules for morphogenesis, transport, transmission, replication, as well as RNA interference suppression. A significant number of viral genes, particularly those found in viruses with relatively modest genome sizes, are involved in more than one of these processes (60). There are, on the other hand, plant viruses that have genomes that are either very small or none at all. These viruses either no longer possess the capability to transmit the disease or have never acquired it. These viruses have a latent existence, which can be determined by vertical transmission through seeds and/or pollen and an absence of pathogenicity as well as infectiousness (the ability to initiate infection in previously uninfected hosts through plant-to-plant propagation) (61). Vertical transmission occurs when the virus moves from plant to plant via pollen or seeds. Vertical transmission takes place when the virus is passed from one plant to another by the transfer of pollen or seeds. In this section, we will talk

about the taxonomic classification of the worldwide plant virome. Our decision to proceed in this manner is predicated, in large part, on the evolutionary history of the viral replication as well as the components of the morphogenetic module (62).

RNA Viruses: Realm Riboviria, Kingdom Orthornavirae

As was previously indicated, the majority of plant virome diversity is classified as Riboviria. The true RNA viruses that skip the DNA replication step altogether are found in the kingdom Orthornavirae. To be excluded of the rest of the global virome, the replication mechanisms of RNA viruses have been arranged around the RNA-dependent RNA polymerases gene, which is the only gene that is shared by all viruses belonging to this kingdom (63). Therefore, the RdRP phylogenetic tree is utilized as a framework to reconstruct the development of RNA viruses and to establish a taxonomy for them. This tree shows that Orthornavirae can be divided into five distinct groups at the phylum level (64) (Figure 1).

Phylum Lenarviricota.

Eukaryotic virus families Narnaviridae, Mitoviridae and Botourmiaviridae are thought to have descended from +RNA bacteriophages found in the most basal phylum Lenarviricota. Mitoviruses reproduce inside mitochondria and are RNA replicons that lack a capsid as well as encode solely the RNA-dependent RNA polymerases. While most mitoviruses have been discovered in fungus, there has been evidence of this viral family in plants in recent years (65). Noninfectious mitoviruses, Capsidless, are technically mobile RNA elements, with the RdRP as their sole claim to virusness. There are also fungal viruses in the family Botourmiaviridae, although the tiny genus Ourmiavirus comprises encapsidated, MP-encoding plant viruses. Furthermore, invertebrates have been reported as hosting a plethora of related but as-yet-unclassified viruses. Accordingly, plant ourmiaviruses are just a small branch within the Lenarviricota, a phylum that is likely to give rise to many novel viral taxa (66).

Phylum Pisuriviricota.

RNA viruses belong to this 2nd phylum is divided into three classes, each of which corresponds to a branch of the enormous lineage formerly known as the picornavirus supergroup. Simple icosahedral dsRNA viruses that typically encode only the RNA-dependent RNA polymerase as well as a unique type of

capsid protein belong to the class Duploviricetes (67). There are 2 families of plant viruses in this phylum, and they are called Partitiviridae and Amalgaviridae, respectively. Numerous fungal as well as as-yet-unclassified invertebrate viruses belong to the large Partitiviridae family. Alphapartitivirus and Betapartitivirus are the identified plant partitivirid genera, both of which are also shared by related fungi as well as unclassified invertebrates. These viruses have a remarkable propensity to HVT, as seen by their extraordinary host range variability among closely related viruses. Screening of a large collection of plant metaviromes has revealed that partitivirids are a common plant virome component found in many different species of wild plants (68). Partitivirids' nonpathogenic lifestyle is what made it easy to overlook their apparent ecological domination. There is a distant relationship between the nucleocapsid proteins (NCs) of RNA plant viruses in the Phenuiviridae family and the RNA-dependent RNA polymerase encoded by plant and fungal dsRNA amalgavirids (69).

Plant amalgavirids appear to have accepted their noninfectious, vertically transmitted fate, much like partitivirids. Amalgaviruses may or may not produce virions; either way, they appear to be an example of a dsRNA virus that has adapted the replication mechanism utilizing nucleocapsid proteins that is typical of -RNA viruses rather than transcribing its genome in virio, as is usual of dsRNA viruses (70).

Both Pisoniviricetes and Stelpaviricetes possess a chymotrypsin-like protease that is essential to polyprotein processing. This protease is known as the SJR-CP, and it is also associated with a protein (VP-g)-primed method of RNA synthesis, in addition to having a close phylogenetic link with the dsRNA. The Duplicate Viruses (71) (Figure 1). Two orders, *Picornavirales* and *Sobelivirales*, both under the class *Pisoniviricetes*, are home to their own families of icosahedral plant viruses: the Secoviridae as well as the Solemoviridae. The secovirids are common picornaviruses having a two-part genome as well as the S3H restriction enzyme found in other picornaviruses (Figure 1). The majority of the members of this family are spread by insects (such as aphids, beetles and whiteflies) or nematodes. Solemovirids, on the other hand, are transmitted by beetles in addition to a wide range of other insects, along with their genomes are much smaller as well as more densely packed (72) (Figure 1).

The Stelpaviricetes class concludes with the order Patatavirales, which contains the large and commercially significant Potyviridae family of plant viruses. The potyvirids, encode a unique superfamily 2 helicase (S2H), a divergent group of picorna-like viruses and two additional proteases that play separate roles in the process of viral replication, RNA interference suppression and vector transmission. Potyviruses have a unique capsid protein that creates flexuous filamentous virions of various plant +RNA viruses (fCP), in contrast to the majority of viruses in this phylum, which have icosahedral virions built by SJR-CPs (73). Structural study has demonstrated an unexpected evolutionary relationship between RNA viruses of various phyla, displaying that fCP is similar to phenuivirid (RNA viruses) nucleocapsid proteins. Most potyvirids transmit nonpropagatively by attaching to arthropod stylet or foregut receptors via the virus helper component. While the *Bymovirus* genus uses plasmodiophorid protists for virus transmission, the potyvirus genus has evolved an affinity for different vectors, for example whiteflies, aphids and mites (74).

Phylum Kitrinoviricota.

In contrast to other *Riboviria* phyla, where plant viruses are in the minority, the class Alsuviricetes is overwhelmingly composed of members of the phylum Kitrinoviricota. The capping enzyme (CapE), superfamily 1 helicase (S1H), as well as RNA-dependent RNA polymerase are all components of the viral genome that are shared by all members of this supergroup, previously referred to as the Alphavirus-like supergroup (75) (Figure 1). These viruses exhibit extraordinary variety in genomic architecture and virion shape beyond just one replication module (76). The archetypical member of the *Virgaviridae* family is the *Tobacco mosaic virus* (TMV), which has a 6.4-Kb genome and encodes just the capping enzyme -S1H-RdRP RNA replicase, movement proteins, along with a single CP generating rigid rod-shaped particles (rCP). TMV spreads in an unusual, vector-free way: by injuring host plants through natural or human-caused mechanical means like wind, animals, or farming (77).

Beet yellows virus (BYV), the prototypical member of the family Closteroviridae, has a ~15.5-Kb genome producing 10 proteins, five of which compose the morphogenetic module as well as assemble into intricate filamentous virions, making it one of the more

ornate members of the viral family. Alpha-, beta-, and gammaflexivirid CPs (all of which can be identified in the order Alsuviricetes) have homology with three of these CPs (78). Closteroviruses have a complicated virion architecture that comprises a specialized MP and the full morphogenetic module as part of their six-component transport module. One of the most striking examples of genomic complexity in RNA viruses is found in closteroviruses, which also encode powerful RNAi suppressors. Similar to potvirids, closterovirids are spread by a variety of insect vectors (including whiteflies, aphids as well as mealybugs) in a nonpropagative, semipersistent way (79).

Hepelivirales is one of the three taxonomic orders within *Alsuviricetes* and it is home to the plant virus family *Benyviridae*. The rod-shaped virions carried by plasmodiophorid vectors are formed by the rCP of benyvirids, which is identical to that of virgavirids. Furthermore to the *Virgaviridae* and *Closteroviridae*, the much larger order *Martellivirales* also contains the *Kitaviridae*, *Bromoviridae*, as well as *Endornaviridae* (80). The small, tripartite genomes as well as icosahedral virions of bromovirids are hallmarks of these nonpersistent viruses, which are transmitted by a wide range of insects. Aphid-transmitted Cucumber mosaic virus is the worst bromovirid. At least 1,000 plant species are infected (81). Kitavirids are the only plant viruses in this phylum with enveloped virions distributed by mites and are closely related to Negivirus insect viruses. *Endornavirids* are uncommon viruses because they lack the morphogenetic module but encode multiple enzymatic domains as well as the replication module of Alsuviricetes. In the *premeta-viromics* period, these capsidless viruses were largely ignored despite their prevalence in plants, where they generate asymptomatic, long-lasting, vertically transmitted infections (82, 83).

Tymovirales is the third order of the Alsuviricetes, and it contains five different families: the spherical Tymoviridae, which encode SJR-CPs; the filamentous *Betaflexiviridae*, *Alphaflexiviridae*, as well as *Gammaflexiviridae* (formerly combined in one family Flexiviridae); as well as the capsidless Deltaflexiviridae. Of these, the *Gammaflexiviridae* and *Deltaflexiviridae* infect plant-pathogenic fungi as well as the *Alphaflexiviridae*, *Betaflexiviridae*, and *Tymoviridae* infect plants (84). Many *Tymovirales* also contain a papain-like protease besides the highly conserved RdRPs, CapE, and S1H. *Alphaflexiviridae* have MPs that are triple

gene blocks, *Betaflexiviridae* have movement proteins that are 30K-like, as well as *Tymoviridae* have their own distinct movement proteins. However, alphaflexivirids among betaflexivirids are transmitted by a broad variety of arthropods including mites, aphids, as well as mealybugs. Viruses that belong to the genus Potexvirus as well as others appear to lack vectors along with are conveyed mechanically, but other viruses, such as others, are transported mechanically (85, 86). Mechanical transmission is the only known method of transmission for these viruses. This would imply that some tymovirids have this latter property, whereas other tymovirids are transmitted by beetles in a manner that is not propagative. It has been demonstrated that among the nonenveloped +RNA plant viruses, tymovirids in the genus Marafivirus are the ones that are transmitted by leafhoppers in a propagative fashion. This indicates that the viruses replicate themselves within the insect host. This is thought to be due to the fact that leafhoppers consume the leaves of infected plants as part of their diet (87).

Tombusviridae and *Luteoviridae* are 2 families of icosahedral plant viruses that make up the *Tolucaviricetes* subclass of the phylum *Kitrinoviricota*. The RdRP phylogeny is the primary link between this group as well as the Alsuviricetes; the short, densely packed genomes of tombusviruses and luteoviruses contain only SJR-CPs (which are unrelated to those in tymoviruses) and unique forms of MPs as well as RNA interference suppressors (88) (Figure 1). Some tombusvirids (including variables such those in the genus Tombusvirus) may be spread directly from soil to plants without the use of any vectors. Aphids transmit luteovirids in a unique, long-lasting, circulative and nonpropagative way: the viruses move from the insect's digestive tract to its salivary gland with no replication, as well as are then deposited through saliva when the aphid feeds on the phloem of a subsequent plant (89).

As of now, the order Amarillovirales, which contains the solitary family of enclosed viruses, entirely animal, *Flaviviridae*, belongs to the 3rd class of *Kitrinoviricota*, *Flasuviricetes* (Flavivirus supergroup). However, the Gentian Kobu-sho-associated virus (GKaV) is the only flavi-like virus found in Japanese alpine ornamentals. This virus's monopartite genome is the biggest of any plant virus we know of, clocking in at around 23 Kb. Most likely, GKAV was recently transmitted from invertebrates to plants, given the two

most closely related viruses [*Macrosiphum euphorbiae* virus 1 discovered in a potato aphid and soybean cyst nematode virus both infect plant-feeding arthropods (90, 91).

Phylum Duplornaviricota.

There are only 2 families of plant viruses that fall under this phylum of dsRNA viruses, as well as couldn't be more different from one another: Totiviridae and Reoviridae. The gene complement of totivirids is identical to that of partitivirids (Figure 1), making them one of the simplest RNA viruses. Even though these double strand RNA virus families are very distantly related to one another, their RdRPs nevertheless assemble into icosahedral virions composed of 60 capsid protein homodimers arranged on a pseudo T = 2 lattice. This particular capsid structure is only seen in diverse dsRNA viruses, which sets them apart from other virus types (92). However, the genomic organisation of partitivirids and totivirids is distinct from one another: In contrast to the former, which have two distinct genomes, totiviruses generally express both capsid protein and RNA-dependent RNA polymerases from a single mRNA that is the same size as the total genome. This is in contrast to the former, which have two separate genomes. Totivirids were first discovered to infect plants relatively recently, during the course of ecogenomics research. According to M. Roossinck's personal letter, it appears that the life cycle of plant totivirids, which are also known as plant partitivirids, is quite similar to that of plant partitivirids. This is despite the fact that there is still a great deal to learn about the ecology and biology of plant totivirids (93, 94). To date, the Totiviridae family has been shown to be home to a variety of viruses that are capable of infecting fungi, parasitic protists, as well as invertebrates. On the other hand, plant reovirids are viruses that are harmful and are spread by insects. These viruses have been investigated extensively. They are representatives of three separate genera within a family that is otherwise dominated by animal viruses but also includes a few fungal viruses and a virus that originates from a green picoplankton alga (95, 96). Although animal viruses make up the majority of this family, the other members include a virus that originates from a green picoplankton alga (97, 98). There is a large variety of plant diseases that are caused by plant reovirids, such as wilt, leaf curl, and scabies. Plant reovirids are the causative agents of these diseases (100, 101). In contrast to the +RNA viruses that were discussed previously and that are

transmitted by arthropod or nematode vectors without replicating (this type of transmission is typically referred to as nonpropagative transmission), plant reoviruses do replicate in their insect (leaf-for-plant-hopper) vectors. This is the type of transmission that is frequently referred to as propagative transmission (102, 103). This striking example of virus adaptability also provides potential clues to the pathways by which reoviruses have evolved (for more information on this subject, see the section of the article titled Origins as well as Diversification of the Plant Virome: Horizontal Virus Transfer along with Virus-Vector Associations). Plant reoviruses, which are closely related to animal reoviruses, also have huge genomes that are segmented as well as are made up of ten or twelve distinct dsRNA molecules. This is similar to the genome structure found in animal reoviruses (104) (Figure 1). These dsRNA molecules are then encased in an unusual double-shelled, concentric icosahedral virion. These genomes are responsible for the production of as many as seven different virion proteins, all of which are coencapsidated with the genome. These proteins include outer and inner capsid proteins, RdRP, as well as capping enzyme (104). Within infected cells, these virion proteins perform the functions of assembly of the virion, transmission of the vector (outer CP) and replication of the RNA. The nonstructural proteins have a role in the creation of the viroplasm (the location that appears to be responsible for genome replication and virion assembly), the inhibition of RNA interference, and the migration of viruses from plant cell to insect cell in both insects as well as plants (105).

Phylum Negarnaviricota.

In this phylum, RNA viruses encapsulate their RdRPs and other replication proteins similarly to dsRNA viruses. However, their virions have very different structures, often consisting of a helical, compact, filamentous nucleocapsid as well as a membrane envelope decorated with virus-encoded glycoproteins (104, 106).

Negarnaviricota primarily infects invertebrates, although it can sometimes infect vertebrates. Protists as well as fungi have both been found to host several RNA viruses in recent years. There are three families of plant viruses (*Fimoviridae*, *Tospoviridae* and *Aspiroviridae*) as well as many genera within two large families of predominantly animal viruses (*Rhabdoviridae* and *Phenuiviridae*), however these viruses are much less diverse than their animal counterparts (107, 108).

Many of these viruses, such as plant reovirids, are arthropod-plant hybrids that have the ability to replicate in plant as well as insect hosts. Therefore, members of the *Tospoviridae* family have three-component ambisense genomes that are packed into enveloped virions. These virions infect not only plants but also the microscopic insects known as thrips, which act as their transmission vectors (109, 110). Tomato spotted wilt virus is the prototypical member of the plant RNA virus family (1) because of its ability to infect a wide variety of crops and its widespread distribution (111). Mites, which are tiny spider arthropods, are vectors for the family *Fimoviridae*, which is characterized by enclosed virions that harbor four- to eight-component genomes. Lastly, hemipteran insects containing leafhoppers, plant hoppers, aphids (Nucleorhabdovirus and Cytorhabdovirus), in addition arachnid mites (Dichorhavirus) are responsible for transmitting the majority of plant rhabdovirids due to their monopartite genomes (112, 113). The virion and genome structures of RNA plant viruses are similar to those of their animal relatives, with the exception that the former encode movement proteins as well as RNA interference suppressors necessary for systemic infectivity in plants (114, 115). However, there are three separate genera of plant RNA viruses that each veer from this standard model in their own unique way. *Tenuiviruses* belong to the family *Phenuiviridae*, and their large, segmented RNA genomes (up to 8 segments, totaling up to almost 25 Kb) set them apart from all other known plant viruses. The ancestral membrane envelopes of the *tenuiviruses* appear to have been abandoned in favor of the filamentous nucleocapsids. Nonstructural glycoproteins were maintained by tenuiviruses as a means of mediating the virus's normal method of spread, which is through planthoppers (116, 117). Similarly, nucleocapsid-like CPs create the rod-shaped, envelope less virions of *Varicosavirus* members (*Rhabdoviridae*) (118). Another distinguishing feature of the varicosaviruses is that they are spread not by arthropods but by the zoospores of soil fungi. The aspivirids (formerly classified as Ophioviridae) are similar in that they lack envelopes but instead use nucleocapsids as fungus-transmitted virions. The emergence of these three viral species is a clear reflection of the adaptation of RNA viruses to a plant-specific lifestyle given the predominance of nonenveloped plant viruses (119).

Reverse-Transcribing Viruses

Viruses that encode a reverse transcriptase (RT)

protein that is homologous to RNA virus RdRPs make up the second kingdom, Pararnavira, in the superkingdom Riboviria. Therefore, RNA viruses and reverse-transcribing viruses are placed in the same highest-level taxon since they are thought to have descended from the same ancestor (120). Plants host members of the 6 officially recognized families within Pararnavira, including the +RNA-encapsidating *Metaviridae* as well as *Pseudoviridae* as well as the dsDNA-encapsidating *Caulimoviridae* (informally called *pararetroviruses*) (121). There is a phylum called *Artverviricota*, a class called Retravicetes, along with an order called Ortervirales for the *pseudovirids*, and *caulimovirids* (122) (Figure 1). RT as well as RNase H, a morphogenetic module (Gag polyprotein with the characteristic α -helical capsid protein as well as zinc-knuckle NC domains), as well as a polyprotein-processing aspartic protease are all components of the replication module shared by all orterviruses (123, 124). Plants are no exception to the rule that *metavirids* and *pseudovirids*, which are closely related to the Retroviridae of vertebrates, abundantly populate the genomes of many eukaryotes (125). However, in contrast to infectious retrovirids, the infectivity as well as intercellular spread of the majority of *metavirids* along with *pseudovirids* have not been explained, in spite of the conservation of the gene that encodes the structural Gag polyprotein as well as the occasional existence (including in plant viruses) of genes encoding putative envelope proteins responsible for virus entry. This is the case despite the fact that infectious retrovirids have been studied extensively (126, 127). As a result, *metavirids* as well as *pseudovirids* have traditionally been regarded as transposable elements. The Ty3/Gypsy and Ty1/Copia families' long terminal repeat (LTR) retrotransposons include *metavirids* and *pseudovirids* (128). Because of this, most LTR retrotransposons have not been included into the ICTV framework, making genus-level classification of these viruses unsuitable (129). Nearly 14,000 *metavirids* and *pseudovirids* were discovered in a recent investigation of 80 plant genomes. The presence of members of both families in all major divisions of green plants, including the most primitive *Chlorophyta*, suggests that they have always been part of the *Viridiplantae* family tree (130, 131). It is hypothesized that plant *metavirids* as well as *pseudovirids* do not infect other cells because they do not encode detectable movement proteins (132). It has been discovered that *metavirids/pseudovirids* are horizontally transferred frequently in plants despite the absence

of identifiable infectious particles. High resemblance between several fungal and plant metavirids indicates plant-pathogenic fungi might take part in their horizontal dispersion; however, the processes required are currently unknown (133, 134). Figure 1 depicts the replication besides morphogenetic modules shared by *metavirids*, *caulimovirids* as well as *pseudovirids*. They package their double strand DNA genomes into infectious virions that may be isometric or bacilliform. Phylogenetic analysis of the RT indicates that *caulimovirids* and *metavirids* share a common ancestor. Like metavirids and pseudovirids, petunia vein clearing virus expresses all proteins as a single polyprotein that the viral-encoded protease processes (135, 136). Caulimovirids replicate without host chromosome integration, unlike other orterviruses. Even though most caulimovirids do not express an integrase, endogenous virus elements (EVEs) from caulimoviruses are found in plant genomes and presumed to be integrated via non homologous end-joining during DNA repair (137, 138). Most EVEs are dormant, but when certain stressors set them up again, they can spread. Insect vectors such as aphids, mealybugs, and leafhoppers are responsible for the genus-specific spread of caulimovirids, which like many other plant viruses express a movement protein of the 30K superfamily (139). Two viral “helper factors,” which link viruses to their stylet-end receptor, are essential to the transmission process. Particularly, the reactivation-competent endogenous petuniavirus not has known insect vectors, which adds to the theory that it is a vivo transitional form among simpler metavirids along with more complicated caulimovirids. Therefore, it is likely that the integrase gene was lost during the evolution of caulimovirids from a metavirus-like ancestor as well as the movement proteins and vector transmission components were acquired (140, 141, 142).

ssDNA Viruses

Monodnaviria consist of ssDNA viruses with HUH superfamily rolling-circle replication endonucleases (RCREs). This domain has six virus-class phyla (143). In the phylum Cressdnaviricota, all eukaryotic viruses have circular single strand DNA genomes along with express homologous Reps with the N-terminal HUH endonuclease as well as C-terminal S3H domains. These viruses are known as cressdnaviruses. This phylum brings together 7 virus families as well as a large number of viruses found by metagenomics that are provisionally linked (clades CRESSV1– 6) (144). Within the phylum that encompasses all plant

viruses, the families *Geminiviridae* as well as *Nanoviridae* are where they all reside. *Cressdnaviricota* (Cressdna) (Figure 2). In contrast to plant viruses in this phylum, most members of *Cressdnaviricota* have extremely short virus genomes (approximately 2 kilobases) that only code for 2 proteins, namely Rep and capsid protein (144, 145). Plant viruses in this phylum also code for movement proteins also RNA interference suppressor in along with Rep and CP. The virions of geminivirids have a distinctive shape consisting of twinned, or geminate, icosahedra that encapsulate either monopartite or bipartite genomes (146, 147, 148). Insects (such as whiteflies, aphids and leafhoppers) are responsible for the genus-specific transmission of these virions. This transmission occurs through a circulative, nonpropagative method that is comparable to that of +RNA luteovirids (149, 150).

As a result, the genomes of nanovirids are fragmented into six to eight circular DNA molecules, both of which encodes a separate protein and is autonomously encapsulated into simple icosahedral virions. Each of these DNA molecules contains almost one kilobase of information (151, 152). Nanovirids are characterized by their small size and their ability to replicate rapidly. Remarkably, various genomic segments of nanovirids only rarely co-occur in the same plant cell. Instead, they separately accumulate in independent cells, which enables the virus to reproduce by complementation, a process in which the gene products are transferred from cell to cell. This is a remarkable fact (153). On contrary, several nanovirus particles enter each vulnerable aphid vector cell, which ensures that specific segments of the genome never split from one another. In addition, during circulative, nonpropagative aphid transmission, the frequencies of genome fragments alter, revealing more close connections with the insect than merely travelling from the insect's gut to its salivary glands (154, 155). In contrast to geminivirids, transmission of nanovirids requires a helper component in addition to the virus particles themselves. Geminivirids and nanovirids are both connected with a wide variety of satellite nucleic acids, such as alphasatellites (*Alphasatellitidae*), which encode their own Reps but not the capsid proteins and are therefore dependent on geminivirids in addition nanovirids (156, 157).

Statement of conflict of interest

The authors have declared no conflict of interest.

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