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ORIGIN AND EVOLUTION OF AUCHENORRHYNCHA-TRANSMITTED, PLANT INFECTING VIRUSES

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ABSTRACT

The Auchenorrhyncha transmit 38 plant viruses from among six distinct virus groups: reoviruses, rhabdoviruses, filaviruses, (rice stripe virus group), rafiviruses (maize rayado fino virus group), geminiviruses and the maize chlorotic dwarf virus group. Viruses from the first three groups multiply in their vectors, are transovarially transmitted and are postulated to have originated as insect viruses that secondarily adapted to plant hosts. The rafiviruses replicate in their vectors (the smallest plant viruses to do so), but are not transovarially transmitted; it is uncertain if these viruses originated as plant viruses or as insect viruses. Geminiviruses are circulative and neither replicate in their vectors nor are transovarially transmitted. The maize chlorotic dwarf virus group viruses are noncirculative and neither replicate nor are transovarially transmitted in their vectors. Viruses in these latter two groups likely originated in plants as seed-borne viruses that later lost this property after they evolved relationships with insect vectors. Insects from more than one homopteran family can transmit reoviruses, rhabdoviruses and geminiviruses although no particular virus is transmitted by vectors from more than one family. These distributions among vector families are best explained by association by descent of viruses with vectors for reoviruses and geminiviruses, and by colonization (horizontal transfer) of viruses from one homopteran family to another via a common host plant for rhabdoviruses.

INTRODUCTION

The Auchenorrhyncha are vectors of a variety of primarily phloem-associated plant pathogens as well as a few xylem-restricted bacteria. The phloem-associated pathogens include an unknown number of mycoplasma-like organisms (MLO), two spiroplasmas, a bacterium and viruses belonging to six groups recognized by the International Committee on Taxonomy of Viruses (ICTV). This review focuses on the relationships between these six virus groups and their Auchenorrhyncha vectors, although viruses transmitted by other arthropods will be discussed as appropriate.

In addition to their close association with plant phloem, the Auchenorrhyncha-transmitted plant viruses usually have grassy hosts, and most are not transmissible by artificial, mechanical methods. Aside from these common traits, the viruses vectored by the Auchenorrhyncha are diverse and encompass at least three distinct types of vector-virus relationships. In this

review I shall discuss each of the principal taxa of Auchenorrhyncha, their importance as virus vectors, and aspects of their phylogeny, biology and behavior pertinent to virus transmission. I will also review the virus groups vectored by the Auchenorrhyncha, emphasizing those characteristics that contribute to an understanding of vector relationships such as mode of virus transmission and vector specificity. For each virus group I will argue for an insect versus plant origin. Also, I propose two hypotheses, association by descent and colonization, to explain the occurrence of more than one vector family for three of the virus groups.

TERMINOLOGY

As noted in the Introduction, the Auchenorrhyncha exhibit at least three distinct vector relationships with plant viruses. Because of the many terms used to describe these relationships, I found it necessary to survey, then choose from among several possible terms those I use in this review. For example, non-persistent, semi-persistent and transitory transmission have all been used to describe the transmission of members of the maize chlorotic dwarf virus group by its leafhopper vectors. The rationale for my choices, non-circulative, circulative, and propagative, follows.

Non-circulative

Common to all viruses transmitted non-circulatively is the loss of vector inoculativity following a molt. Homopterans shed the stylets and lining of the foregut during a molt. Non-circulative viruses are thought to attach and detach from sites located on the stylets or foregut. These viruses are also characterized by retention by their vectors for several hours to several days. Retention time is influenced by temperature (high temperature decreases retention time) and vector feeding (feeding after acquisition decreases retention time). Non-circulative viruses include those previously referred to as non-persistent, semi-persistent, stylet-borne and transitory.

Circulative

Circulatively-transmitted viruses can be recovered from vector hemolymph, can be transmitted following injection into the vector's hemocoel, are not lost after a molt, and can be transmitted for weeks, sometimes for the life of the vector. A latent period of several hours to several days must pass before vectors become inoculative. The latent period is presumably the time it takes for ingested virus to pass through the gut wall, be transported to the salivary glands via the hemolymph and become incorporated into salivary secretions. Circulative viruses do not replicate in their vectors and none are known to be transovarially transmitted. The ability of vectors to transmit circulative viruses often declines with time, but can be restored by allowing vectors to reacquire from infected plants. Circulative viruses are referred to elsewhere as persistent or persistent, non-propagative viruses.

Propagative

Similar to the circulative viruses, propagative viruses can be recovered from vector hemolymph, can be transmitted following injection into the vector's hemocoel, are not lost after a molt and can be transmitted for weeks, sometimes for the life of the vector. However, unlike the circulative viruses, propagative viruses multiply in their vectors as shown by serial passage, quantitative serology or electron microscopic observation of sites of viral

synthesis and/or assembly within vector cells. Propagative viruses usually undergo latent periods of one or more weeks in their vectors. Ingested virus replicates in midgut cells prior to passage into the hemolymph and distribution to other organs. Virus then replicates in the salivary glands prior to transmission to plants, and, in those propagative viruses transovarially passed by females to their progeny, virus also replicates in the ovaries. Some viruses initially classified as circulative (persistent) subsequently were shown experimentally to replicate in their vector and hence have been reclassified as propagative. I prefer not to use the term circulative-propagative for propagative viruses, as this implies an evolutionary relationship between circulative and propagative viruses for which none has been established.

VECTOR TAXA

In assessing the Auchenorrhyncha as virus vectors, two points should be kept in mind. First, knowledge of plant viruses is greatly biased toward those affecting annual crops, particularly major food crops. Thus, we know a great deal more about viruses of rice, wheat and corn, for example, than we do about viruses of roses, rhododendrons, and oaks. Second, knowledge of Auchenorrhyncha-transmitted viruses in temperate regions far surpasses our knowledge of tropical viruses (notable exceptions are the rice and maize viruses). This bias exists and is likely to be perpetuated largely because most plant virologists are located in temperate regions in Europe, North America and Asia.

Among the five principal Auchenorrhyncha superfamilies, four contain families having vectors of plant pathogens. Cicadas, the only group not implicated as vectors, have soil-dwelling, root-feeding larvae, and adults that are xylem feeders. Host plants are woody trees and shrubs. The xylem-feeding cercopids (spittlebugs) vector plant pathogenic bacteria that reside in these plant vessels. It is not unexpected, that the cicadas and spittlebugs are not represented as virus vectors, because no plant viruses are known to replicate in or be transported by the xylem. The other families, all of which have phloem-feeding species that transmit viruses, are the Cicadellidae (leafhoppers), Delphacidae (planthoppers) and Membracidae (treehoppers) (Table 1).

The leafhoppers vector bacteria, mollicutes (spiroplasmas and MLO's) and 20 plant viruses. Among the ca. 60 recognized cicadellid subfamilies, eight are vectors of plant pathogens (Nielson 1985), but only two of these are virus vectors, the Agallinae and Deltocephalinae. The xylem-feeding Cicadellinae transmit xylem-residing bacteria, one of which (Pierce's disease bacterium) is also vectored by the cercopids. It is surprising that no leafhopper-borne viruses of woody dicots have been reported since many MLO's infecting these hosts are vectored by leafhoppers. Of the ca. 2,000 described leafhopper genera (Nielson 1985) only 19 have been reported as vectors of plant viruses (Tables 2,3,5,6).

The planthoppers vector 17 plant viruses (Table 1), four MLO's (O'Brien and Wilson 1985) and one bacterium. Three planthopper families are involved; the delphacids are virus vectors, the cixiids are MLO vectors, and a flatid is reported as one of the vectors of the fireblight bacterium. All delphacid-transmitted viruses infect the Gramineae, many on wheat, rice, maize or barley. Of the 137 described delphacid genera (O'Brien and Wilson 1985), only 16 are virus vectors (Tables 4,5,6). Although most planthoppers have tropical

distributions, delphacids are well-adapted to colder high altitudes and latitudes (O'Brien and Wilson 1985). The delphacid planthoppers are the most numerous among the Fulgoroidea, with 15.7% of described species. It is reasonable to assume that new vectors and viruses, including those that infect dicots, will be found among the planthoppers as more attention is focused on tropical plants and tropical planthopper families.

TABLE 1

Mode of transmission and viruses vectored by the Auchenorrhyncha.

Virus group [a]	Transmission Mode [b]	Number of viruses vectored		
		Cicadellidae	Delphacidae	Membracidae
Reovirus	propagative*	3	4	0
Rhabdovirus	propagative*	6	8	0
Filavirus	propagative*	0	5	0
Rafivirus	propagative	3	0	0
Geminivirus	circulative	6	0	1
MCDV group	noncirculative	2	0	0
TOTAL		20	17	1

[a] Abbreviation is maize chlorotic dwarf virus (MCDV).
[b] * indicates some group members are transovarially transmitted.

Like the planthoppers, most treehopper species have tropical distributions. Tomato pseudo-curly top virus is the only treehopper transmitted virus known (Simons and Coe 1958). The hosts of most treehoppers, as their name suggests, are woody species. As our knowledge of tree viruses increases, particularly in tropical regions, it is expected that additional treehopper vector species will be discovered.

VIRUS GROUPS VECTORED BY AUCHENORRHYNCHA

Maize Chlorotic Dwarf Virus Group

Maize chlorotic dwarf virus (MCDV) has been designated as the type member of the group (Gingery 1986a) with the rice tungro spherical virus (RTSV) as a probable member (Table 2). Both viruses are leafhopper transmitted to grassy hosts. The rice tungro disease is associated with a second, distinct, leafhopper transmitted virus, the rice tungro bacilliform virus (RTBV) which will be briefly discussed in this section. MCDV and RTSV have isometric particles, ca. 30-33 nm in diameter, containing single-stranded RNA. They differ from other viruses of similar morphology and size by having rapid sedimentation rates and high buoyant densities in CsCl. Examination of phloem and phloem parenchyma of MCDV-infected maize reveals a dense, granular inclusion that contains 31 nm diameter virus-like particles. Similar so-called "currant bun" inclusions have been observed in *Anthriscus* infected with the aphid-borne anthriscus yellows virus (AYV) (Harrison and Murant 1984).

MCDV, RTSV and RTBV are the only Auchenorrhyncha transmitted viruses that have non-circulative relationships with their vectors (Gingery 1986a). They differ from most non-circulative, aphid-borne viruses in that they are acquired

from and inoculated to the phloem and phloem parenchyma rather than plant epidermal cells as is characteristic of the potyviruses, carlaviruses, caulimoviruses, cucumoviruses and alfalfa mosaic virus. However, the Maize Chlorotic Dwarf Virus group viruses resemble the aphid-borne closteroviruses in this feature of the tissue where acquisition and inoculation occur. Neither MCDV nor RTSV is mechanically transmitted.

TABLE 2

Maize Chlorotic Dwarf Virus group (MCDV) Viruses, Rafiviruses (Maize Rayado Fino Virus Group), their host plants, and their Cicadellidae leafhopper vector genera.

MCDV Group	Host Plants	Cicadellid genera
Maize chlorotic dwarf	Monocot	*Graminella, Exitianus*
Rice tungro spherical	Monocot	*Nephotettix*
Rafiviruses		**Cicadellid genera**
Maize rayado fino	Monocot	*Dalbulus, Baldulus, Stirellus, Graminella*
Oat blue dwarf	Monocot, dicot	*Macrosteles*
Bermudagrass etched-line	Monocot	*Aconurella*

Harrison and Murant (1984) recently suggested that MCDV might require a helper factor for its vector transmission, analogous to the helper proteins that assist in the aphid transmission of potyviruses and caulimoviruses. Recent evidence suggests that a helper factor is involved in the leafhopper transmission of MCDV (R. E. Hunt, L. R. Nault, and R. E. Gingery, unpublished). Normally, *Graminella nigrifrons* (Forbes) will not transmit purified virus acquired through membranes. However, if leafhoppers are given prior access to plants infected with a mild MCDV strain, they will subsequently transmit a purified severe strain acquired through membranes. We speculate that a helper factor (protein?), acquired from plants infected with the mild strain, attaches to the leafhopper foregut or stylets and later serves as a reversible binding site for purified particles of the severe strain.

The spherical RTSV appears to function as a helper factor in the transmission of RTBV (see references in Gingery 1986a). RTBV is 35 nm in diameter and 150-350 nm in length. Nothing is known about its nucleic acid chemistry. *Nephotettix* vectors can transmit RTBV from plants coinfected with RTSV and RTBV, or from plants singly infected with RTBV if leafhoppers are given prior access to RTSV-infected plants. There is no evidence that the maize chlorotic dwarf disease is associated with a bacilliform or any other dependent virus (R. E. Hunt, L. R. Nault, and R. E. Gingery, unpublished).

Geminiviruses

Geminiviruses have isometric particles, ca., 16-18 nm in diameter, that occur in pairs, hence the name of the group. Geminiviruses are unique in that they contain single-stranded, circular DNA molecules. The definitive and

provisional members of the group can be subdivided by host relationships, symptoms, and vector taxa (Harrison, 1985, Francki *et al.* 1985). Members of one subgroup cause striate mosaics in Gramineae and are vectored by leafhoppers (Table 3). Members of a second subgroup cause stunting, yellowing, and leaf curling in dicots and are leafhopper borne (Table 3). The remaining two subgroups cause diseases in dicots and are vectored by whiteflies. Tomato pseudo-curly top virus is similar to members of the second subgroup except that its vector is a treehopper, *Micrutalis mallifera* Fowler (Harrison 1985). An aphid transmitted geminivirus is also suspected (Harrison 1985). No single geminivirus is transmitted by homopterans from more than one family taxa.

TABLE 3

Geminiviruses, and their host plants and leafhopper (Cicadellidae; Deltocephalinae) vector genera.

Geminivirus	Host plants	Cicadellid genera
Beet curly top	Dicot	*Circulifer*
Tobacco yellow dwarf	Dicot	*Orosius*
Chloris streak mosaic	Monocot	*Nesoclutha*
Maize streak	Monocot	*Cicadulina*
Wheat dwarf	Monocot	*Psammotetix*
Paspalum striate mosaic	Monocot	*Nesoclutha*

Several of the whitefly-transmitted geminiviruses are antigenically related, and are transmitted by the same whitefly species, *Bemesia tabaci* Gen. In contrast, the leafhopper-transmitted geminiviruses all have different vector species and are antigenically unrelated or, at best, distantly related.

The leafhopper- and treehopper- transmitted geminiviruses, as well as the whitefly-transmitted ones have a circulative relationship with their vectors. No evidence has been forwarded suggesting that any are propagative. In this regard, the geminiviruses share a relationship with their vector similar to that of the better studied luteoviruses and their aphid vectors. In leafhoppers, the geminiviruses have minimum latent periods as short as three hours and persist for several days or for the life of the vector.

Rafiviruses (Maize Rayado Fino Virus Group)

The maize rayado fino virus (MRFV) is the type member of the group which also includes the serologically-related oat blue dwarf virus (OBDV) and Bermuda grass etched-line virus (BELV) (Table 2). The name rafivirus has been proposed by Gamez (this volume) and will be used in this review. Rafiviruses have spherical particles ranging in size from 28 nm in diameter (BELV) to 33 nm in diameter (MRFV) that contain a single-stranded RNA molecule. The three viruses are transmitted by different deltocephaline leafhopper species. Much more is known about the relationship of *Dalbulus maidis* (DeLong & Wolcott) with MRFV (Gamez 1980) and *Macrosteles fascifrons* (Stal) with OBDV (Banttari & Zeyen 1976a), than is known for that between the recently-discovered BELV and its vector, *Aconurella prolixa* (Lethierry) (Lockhart *et al.* 1985). MRFV and OBDV have mean latent periods in their vectors of ca. two weeks and then are transmitted intermittently for several weeks. Neither virus is passed

transovarially by female vectors. The long latent period suggests that both viruses replicate in their vectors. This was confirmed by Gingery *et al.* (1982) and Rivera and Gamez (1986) for MRFV and by Banttari and Zeyen (1976b) for OBDV. These are the smallest viruses known to replicate in both plants and insects.

Filaviruses (Rice Stripe Virus Group)

Members of this group are the type member, rice stripe virus (RSV), maize stripe virus (MStpV), rice hoja blanca virus (RHBV), rice grassy stunt virus (RGSV), and European wheat striate mosaic virus (EWSMV) (Gingery 1986b) (Table 4). All have grassy hosts. These viruses have particles composed of fine filaments, 3 nm in diameter, that may assume a variety of configurations. They have a RNA genome and are associated with the accumulation of large amounts of a low molecular weight noncapsid protein in infected tissues. The group name, "Filaviruses" has recently been proposed (Gingery 1986b) and will be used in this review.

TABLE 4

Filaviruses (Rice Stripe Virus group), their host plants and their Delphacidae planthopper vector genera.

Filaviruses	Host plants	Delphacid genera
Rice stripe	Monocot	*Laodelphax*, *Unkanodes*, *Terthron*
Rice grassy stunt	Monocot	*Nilaparvata*
Rice hoya blanca	Monocot	*Sogatodes*
Maize stripe	Monocot	*Peregrinus*
European wheat striate mosaic	Monocot	*Javesella*

The filaviruses are vectored by delphacid planthoppers, in which they have mean latent periods of two or more weeks, are persistent for the life of the vector and are transovarially passed by females, except for RGSV. Inoculative males do not venereally transmit virus to females. Multiplication of filaviruses in their vectors has been demonstrated for RSV, RHBV and MStpV and likely occurs for all members of the group (Gingery 1986b). MStpV invades and multiplies in all organs of female *Peregrinus maidis* (Ashmead) and all male organs except perhaps for the testes (L. R. Nault, D. T. Gordon, W. E. Styer, and R. E. Gingery, unpublished). Invasion of the salivary glands by MStpV is prerequisite to transmission by *P. maidis*, but does not insure that a delphacid will be a vector. Although the MStpV noncapsid protein occurs in high concentrations in infected plants, no trace of the protein can be found in viruliferous *P. maidis* (Falk *et al.* 1985) and there is no evidence it plays a role in virus transmission.

Plant Reoviruses

Plant reoviruses have a two-layered or double-shelled capsid of icosahedral symmetry, 65-70 nm in diameter, containing either 10 or 12 segments of double stranded RNA. Virus particles mature in the cytoplasm of phloem cells, and form inclusions that contain virus particles in crystalline arrays.

The plant reoviruses can be divided into two genera recognized by the ICTV, the *Phytoreoviruses* which have 12 ds-RNA genome segments and cicadellid leafhopper vectors and the *Fijiviruses* having 10 ds-RNA segments and delphacid planthopper vectors (Table 5). Rice ragged stunt virus remains unclassified but it is more similar to the *Fijiviruses* than to the *Phytoreoviruses*. The number of *Fijiviruses* has been reduced recently by the demonstration that several previously recognized viruses are strains of the three listed in Table 5 (Francki *et al.* 1985).

TABLE 5

Plant reoviruses, host plants and their Cicadellidae leafhopper and Delphacidae planthopper vector genera.

Phytoreoviruses	Host plants	Cicadellid genera
Wound tumor	Dicot	*Agallia, Agalliopsis*[a]
Rice dwarf	Monocot	*Nephotettix, Recilia*
Rice gall dwarf	Monocot	*Nephotettix, Recilia*
Fijiviruses		**Delphacid genera**
Fiji disease	Monocot	*Perkinsiella*
Maize rough dwarf	Monocot	*Laodelphax, Delphacodes, Javesella, Sogatella, Dicranotropis Ribautodelphax, Unkanodes, Chilodelphax*
Oat sterile dwarf	Monocot	*Javasella, Dicranotropis, Delphacodes*
Unclassified		
Rice ragged stunt	Monocot	*Nilaparvata*

[a] Agallia and Agalliopsis are in the subfamily Agallinae. The other leafhopper genera are in the subfamily Deltocephalinae.

All plant reoviruses propagate in their leafhopper or planthopper vectors (Conti, 1985). High rates of transovarial transmission have been reported for wound tumor virus in selected *Agallia constricta* Van Duzee vectors and for rice dwarf virus in *Nephotettix cincticeps* (Uhler). In contrast, low transovarial rates are reported for the delphacid transmitted *Fijiviruses* (Shikata 1981). With the exception of the hosts of the wound tumor virus, reovirus hosts are all in the Gramineae.

Plant Rhabdoviruses

Rhabdoviruses infect and cause diseases in plants (monocots and dicots) and vertebrates, and also multiply in their invertebrate vectors (Francki *et al.* 1985). The plant rhabdoviruses have a distinctive structure, either bacilliform or bullet-shaped measuring 45 to 94 nm in diameter and 180 to 380 nm in length. The particles are enveloped and contain four to six structural

proteins and a single molecule of single-stranded RNA. A wide array of invertebrate vectors transmit rhabdoviruses including leafhoppers, planthoppers (Table 6), aphids, a lacebug (Hemiptera:Tingidae) and a false spider mite (Acarina:Tetranychidae). No official groups have been established for the plant rhabdoviruses, but it has been suggested that they be divided into two subgroups based on the properties of their proteins, kinetics of their transcriptases, and site of maturation of their particles within plant cells. A recent serological study found several planthopper-transmitted rhabdoviruses to have identical or similar nucleocapsids, thus reducing the number of viruses recognized in this group (Milne *et al.* 1986).

TABLE 6

Rhabdoviruses, host plants and their Cicadellidae leafhopper and Delphacidae planthopper vector genera.

Rhabdovirus	Host plants	Cicadellid genera
Cereal chlorotic mottle	Monocot	*Nesoclutha*
Oat striate mosaic	Monocot	*Graminella*
Potato yellow dwarf	Dicot	*Agallia*[a], *Agalliopsis*[a], *Aceratagallia*[a]
Rice transitory yellowing	Monocot	*Nephotettix*
Wheat striate mosaic	Monocot	*Endria, Elymana*
Winter wheat mosaic	Monocot	*Psammotettix, Macrosteles*
		Delphacid genera
Barley yellow striate mosaic	Monocot	*Laodelphax, Javesella*
Colocasia bobone disease	Monocot	*Tarophagus*
Digitaria striate	Monocot	*Sogatella*
Finger millet mosaic	Monocot	*Sogatella*
Maize mosaic	Monocot	*Peregrinus*
Northern cereal mosaic	Monocot	*Laodelphax, Unkanodes, Muellerianella, Terthron*
Shiraz maize rhabdovirus	Monocot	*Ribautodelphax, Peregrinus*
Cynodon chlorotic streak	Monocot	*Toya*

[a] Agallinae, all other genera are Deltocephalinae.

The plant rhabdoviruses have mean latent periods of 2 weeks or longer in their vectors, propagate in their vectors, and many are transovarially transmitted. Plant rhabdoviruses bud from nuclear or cytoplasmic membranes of cells of their leafhopper or planthopper vectors or plant hosts. At least one, maize mosaic virus, also buds from the plasma membrane of its delphacid vector (Ammar and Nault 1985). The plasma membrane is a major assembly site for vertebrate rhabdoviruses.

Other Auchenorrhyncha Transmitted Viruses

Several other leafhopper and planthopper transmitted viruses have been reported in the literature, but are insufficiently characterized to place them among recognized groups. Some may represent new plant virus groups. Two are discussed here.

African cereal streak virus (ACSV) has been associated with a phloem-limited, 24-nm diameter spherical virus transmitted by the delphacid planthopper, *Toya catilina* (Fennah) (Harden and Bakker, 1973). Nothing is known of the relationship between vector and virus. Thus, few clues are available for grouping the virus. The symptoms of ACSV are typical of those caused by filaviruses. Could ACSV be a filavirus? It is worth noting that early reports for four of five filaviruses erroneously indicated that spherical viruses were involved in the disease before the causal filamentous viruses were discovered (Gingery 1986b). If the 24-nm particles are the genuine causal agents of African cereal streak disease, they very likely represent a new virus group.

Maize mottle chlorotic stunt virus (MMCSV) was discovered while screening corn lines in Africa with MSV-inoculative *Cicadulina triangula* Storey (Rossel and Thottappilly 1983). Some of the leafhoppers happened to be coinfected with MMCSV. Once separated from MSV, MMCSV produced symptoms distinct from MSV and had spherical particles ca. 40 nm in diameter. A minimum latent period of three hours and persistence for two weeks in the vector suggest a circulative relationship. The virus particles are too large to be confused with members of the maize rayado fino virus group and the short latent period precludes the virus from consideration as propagative. MMCSV is clearly not a geminivirus and may be representative of a new group.

EVOLUTION OF PLANT VIRUSES

Plant Versus Insect Origin for Plant Viruses

Matthews (1981) remarks that the rhabdoviruses and reoviruses are of special evolutionary interest since members infect vertebrates, invertebrates or higher plants. Regardless of host, members of a particular virus group have many characteristics in common and are likely to share a common ancestor. A common feature of rhabdoviruses and reoviruses is their replication in insects. Matthews (1981) considers the rhabdoviruses and reoviruses, and I will add to this the filaviruses, to have most likely originated in insects and to have secondarily adapted to plants. No viruses from these three groups are seed-borne, thus plants are dead-end hosts. In contrast, most viruses from these groups can survive in their vectors by transovarial passage. Purcell (1982) argues that unless propagative phytopathogens are transmitted to 100% of vector offspring, they cannot be maintained indefinitely in their vectors without horizontal (insect to plant to insect) transmission. Since no maternally transmitted reoviruses, rhabdoviruses and geminiviruses are transmitted to all their progeny, it can be concluded that plants have become an integral part of their perpetuation. For those viruses in these groups that are not transovarially transmitted by their vectors (e.g., dead-end insect hosts), it is assumed that selection for this characteristic has been entirely replaced by dependence on alternate plant hosts.

A key step in the evolution of an insect virus into a plant-adapted virus is suggested by a recent study showing that leafhopper A virus (LAV), which is

normally transmitted vertically through leafhoppers eggs, can be transmitted horizontally through virus-immune plants (Ofori and Francki 1985). The plant, in this case maize, can serve as a transient reservoir of the LAV virus. The next step, albeit a very large one, would be the ability of such a virus to replicate in plants.

It is difficult to propose a plant or insect origin for the rafiviruses, since they multiply in both plants and vectors and are neither seed-borne nor transovarially passed. Nevertheless, Gamez and Leon (1985) favor a plant origin for MRFV and maintain that the virus secondarily adapted to an insect host and vector as a mechanism of viral perennation from one maize crop to the next. Further, if Rossman and Erickson (1985) are correct in their assumption that many, if not most, spherical plant viruses derive their icosahedral structure from the same ancestral fold, then the rafiviruses would have originated as plant rather than insect viruses. That spherical plant viruses may have had an insect origin should not be entirely discounted. LAV is only one of several isometric insect viruses accidently discovered in the Homoptera by investigators searching for plant pathogens in their vectors. While examining aphids for luteoviruses, D'Arcy et al (1981) discovered the aphid infecting *Rhopalosiphum padi* virus. The virus has a spherical particle 27 nm in diameter, a single-stranded RNA, and, like MRFV, has more than one protein species in its capsid. Its other properties, however, are dissimilar to rafiviruses (Gamez 1980). Purcell *et al.* (1981) reported 50 nm diameter virus-like particles in *Macrosteles fascifrons* (Stal) coinfected with the Western X disease MLO. An isometric latent virus having a 54 nm diameter was reported from *P. maidis* (Herold and Munz 1967). Unfortunately, nothing is known about the nucleic acid of this virus or its possible relationship to plant viruses. Similar-sized particles were observed in maize plants diseased with maize hoja blanca (maize stripe) and at one time were erroneously thought to be the causal agent of this disease (Lastra and Carballo 1983). The discovery of LAV and the *P. maidis* virus in the phloem of the host plants of these insects underscores the opportunities that insect viruses likely have had in establishing plants as alternate hosts.

It is easier to support a plant rather than an insect origin for the geminiviruses although they too, like the rafiviruses, are dependent on vectors for survival since they are not seed-borne. They may have originated from seed-borne ancestors that later abandoned this transmission strategy in favor of more efficient insect vectors. This is not to suggest that the evolution of characteristics prerequisite to circulative transmission is not complex, particularly attributes of the protein coat that allow virus to be recognized by and pass through membranes of the gut and salivary glands, but only that such an evolutionary scenario is more parsimonious than one favoring an insect origin. For the latter, geminiviruses would have begun as transovarially-transmitted, propagative viruses, then have become adapted to plants by first using plants as reservoirs and later as propagative hosts. Finally, steps had to occur whereby the viruses lost their transovarial and propagative capabilities in insects and adopted a circulative mode of transmission with a shorter latent period.

It is even more difficult to support an insect origin for the maize chlorotic dwarf virus group in which no vestige of these viruses originating from insect viruses is evident.

My proposals for an insect origin for certain plant viruses or a plant origin for others is largely predicated upon transovarial transmission in

vectors for those viruses proposed to have an insect origin and an absence of multiplication of viruses in vectors for those proposed to have a plant origin. My proposals do not consider it probable that insect viruses lost their ability to propagate in their ancestral hosts following adoption of alternate plant hosts, nor that plant-originating viruses spontaneously arose with the capacity for insect transmission. Such viruses must have had seed-borne ancestors. By the logic used here, the origin of the rafiviruses remains an enigma. If they arose as plant viruses, they would be the only group with a plant origin to adopt a propagative relationship with insect vectors. If they originated from insect viruses, no tell-tale vestige of transovarial transmission has been left behind.

Association by Descent and Colonization

In his summarizing statement on the evolution of plant viruses, Matthews (1981) proposes that "existing virus families are probably of ancient origin, and have co-evolved with their host organisms and arthropod vectors." Matthews also considers some virus groups to have probably had separate origins based on distinctive particle morphologies and intracellular replication strategies. Included among these are the reoviruses, rhabdoviruses and geminiviruses, since they are so different from the members of other virus groups. I will refer to these groups in the following discussion examining Matthews' proposal that viruses have coevolved with their vectors. In his earlier treatment of the subject, Matthews' (1981) examples were drawn from the tymoviruses and their beetle vectors.

Central to the arguments to be presented here is an understanding of vector specificity and transmission mode specificity. Matthews (1981) considers vector type (taxa) to be a stable character useful in delineating major virus groups. With no well-documented exception, homopterans from a single family are the sole vectors of any given virus. Another stable character is the transmission mode. If a virus is transmitted, for example, circulatively by one vector species, it is always transmitted circulatively by other vector species. Even in virus groups that have some members transmitted by one homopteran family and others by a second or third family, the transmission mode is the same. As noted earlier, the planthopper- and leafhopper-transmitted reoviruses are all propagative in their vectors as are the aphid-, planthopper-, leafhopper-, and lace bug-transmitted rhabdoviruses. Similarly, leafhopper-, whitefly-, treehopper- and aphid-transmitted geminiviruses are all circulative.

I propose two hypotheses to account for the occurrence of more than one family of vector homopterans for a plant virus group. I borrow the terms and concepts of Mitter and Brooks (1983) from their discussion of the evolution of parasite-host associations. To explain how related parasites occupy different hosts, they propose that parasites either speciate in concert with their hosts (association by descent) or the parasite of one host transfers to another (colonization). Association by descent may or may not involve coevolution. Coevolution implies reciprocal evolutionary change in interacting species (Janzen 1980, Thompson 1982). Because reciprocal evolutionary change has not been demonstrated to occur between plant viruses and their vectors, I will consider the broader concept of association by descent rather than coevolution in this discussion. Association by descent predicts that a virus-insect or virus-vector-plant association occurred prior to the evolutionary divergence that gave rise to different vector groups (Fig. 1). As viruses diverge with their vectors, new traits in the viral genome that arise in viruses in one

vector group will be isolated from the traits that arise in viruses in other vector groups, resulting in parallel vector and virus phylogenies.

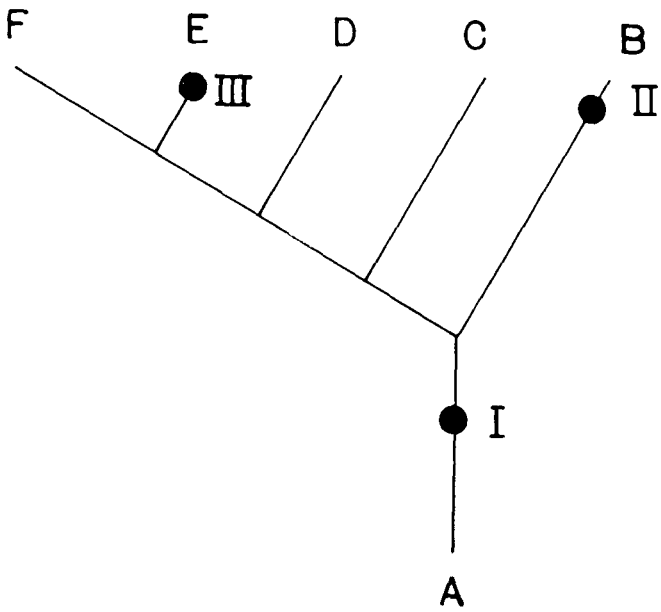

Fig. 1. Phylogeny of hypothetical extant insect vector taxa B-F with common ancestor A. Virus I (viruses shown as solid circles) associated with insect ancestor A and associated by descent with taxa B and E, resulting in divergence of virus I into subgroups II and III. C, D, and F represent taxa whose vectors and viruses have not been discovered or that have lost their ability to transmit virus, for example, by specializing as xylem feeders. This example could represent evolution of plant reoviruses with their vectors.

The colonization hypothesis is predicated upon the ability of a plant virus to transfer from one vector to another in a plant host common to both vectors and virus (Fig. 2). I predict that colonization occurs frequently in nature among closely related vector taxa (species in the same genus or related genera) based upon experimental colonization of plant virus vectors in the laboratory. Investigators studying the range of potential vectors of a plant virus are in reality conducting colonization experiments. For example, in my laboratory the ability of the *Dalbulus*-transmitted MRFV to colonize other deltocephaline vectors (and hosts) was demonstrated when species of *Baldulus*, *Graminella* and *Stirellus* transmitted the virus (Nault *et al.* 1980). The colonization hypothesis predicts that as the phylogenetic distance between vector taxa increases, the chances of colonization decreases. Thus, transfer of virus from one vector family to another may be a rare event, particularly for circulative and propagative viruses, even when the vector species and potential colonist vector feed in the same tissue of the host plant. To colonize a new vector family, circulative viruses would have to be preadapted to pass through the gut wall and salivary gland membranes of the new vector, and propagative viruses would have to be capable of replication in cells of the new vector among other physiological adaptations.

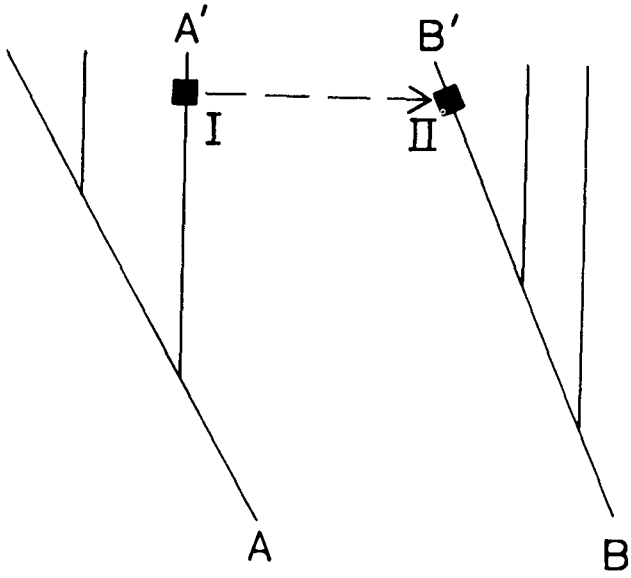

Fig. 2. Phylogenies of two unrelated arthropod vector taxa A and B. A member of virus group I (viruses shown as solid squares) associated with vector taxon A′, transfers to (colonizes) vector taxon B′ via a common host plant of the vectors and virus. Virus evolves into subgroup II with vectors from taxon B′. This example could represent transfer of rhabdoviruses between vector families.

Assuming association by descent and an insect origin, reoviruses would have associated with the Homoptera prior to the divergence of the Fulgoroidea from the rest of the Auchenorrhyncha (Fig. 3). Fossil records indicate that major taxonomic groups of the Homoptera diverged by the Upper Triassic ca. 180 million years ago (Evans 1963, Hennig 1981) and likely were early herbivores of the grasses as the grasses evolved from ca. 70 million years ago (Gould and Shaw 1983). This is ample time for the reoviruses transmitted by leafhoppers and planthoppers to diverge and acquire unique traits. This seems to be the case, for the leafhopper-transmitted *Phytoreoviruses* have 12 genome segments. Ten genome segments is likely the ancestral condition, for this is the number of genome segments that occurs in all other plant, insect and vertebrate reoviruses. The planthopper-transmitted *Fijiviruses* and rice ragged stunt virus have 10 genome segments, but have spikes on both the inner and outer virus capsids. Spikes on the inner and outer capsids are found only in the *Fijiviruses* and insect cytoplasmic polyhedrosis viruses (Francki *et al.* 1985).

Comparisons of leafhopper- and whitefly-transmitted geminiviruses in their plant hosts reveal no consistent differences among the two groups in terms of aggregation of virus particles or cytopathological effects (Francki *et al.* 1985), however, recent evidence suggests important differences in the genomes of members of these two groups (Francki *et al.* 1985, Harrison 1985). Two leafhopper-borne geminiviruses, maize streak virus and chloris streak mosaic

virus, appear to be monopartite, that is, each geminate pair contains a copy of the same genome. On the other hand, the genomes of three whitefly-transmitted geminiviruses are bipartite, that is, each geminate pair contains different genome segments with both segments being necessary for the infection of plants. Speculating on the origin of the geminiviruses, Harrison (1985) suggests that the bipartite condition evolved from an ancestral monopartite form. Further investigations showing consistent differences in the genomes between leafhopper- and whitefly-transmitted geminiviruses would support association by descent between these viruses and their homopteran vectors. This hypothesis predicts that the geminiviruses associated with the Homoptera prior to divergence of the Auchenorrhyncha and Sternorrhyncha (Fig. 3) ca. 230 million years ago (Hennig 1981) and is consistent with recent findings suggesting that an aphid-borne virus and a treehopper-borne virus are suspected to be members of this group (Harrison, 1985). If the association by descent model and a plant origin for the geminiviruses is correct, it may be possible that these viruses will be discovered in extant gymnosperms. Ancestral gymnosperms evolved (Gould and Shaw 1983) at the time of divergence of the Homopteran families.

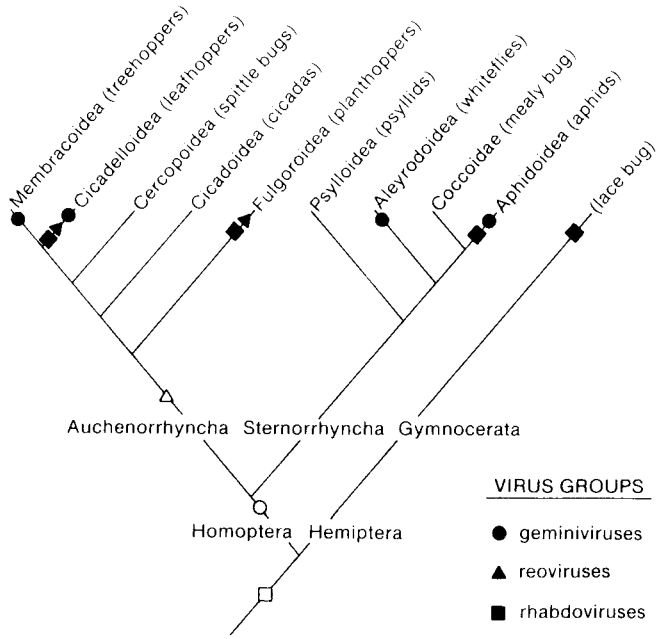

Fig. 3. Phylogeny of superfamilies of Homoptera with common names of groups in parentheses. Shown are Homopteran groups (and one Hemipteran) that vector the geminiviruses, reoviruses and rhabdoviruses. Assuming these plant viruses associated by descent with the Homoptera, open symbols show the latest point in time at which associations could have taken place. The phylogenetic tree was constructed after reviewing and accepting arguments presented by Evans (1963), Hennig (1981), and Strumpel (1983).

No other plant virus group has members vectored by as many arthropod family taxa as does the Rhabdoviruse group (Francki *et al.* 1981). As noted earlier, rhabdoviruses are complex, and possess several characters of potential

use for classification, including several structural proteins, varying transcriptase activities and different sites of particle maturation in plant cells. Using these characters, two plant rhabdovirus subgroups have been suggested (see review by Francki *et al.* 1985). Such a partitioning of the plant rhabdoviruses does not divide these viruses among vector families and thus does not support evolution of plant rhabdoviruses by the association by descent hypothesis.

Another problem with association by descent to explain the distribution of rhabdovirus vector families is that this would date the first rhabdovirus-vector-plant association prior to separation of the Insecta from the Acarina. This event would have occurred prior to the emergence of higher plants. Thus, assuming association by descent, rhabdovirus adaptation to plants would have taken place more than once, with both insects and mites, and perhaps also separately with the Homoptera and Hemiptera (Fig. 3). The colonization hypothesis offers a better explanation for the distribution of the several insect (and mite) families that vector plant rhabdoviruses. The multiplication of a rhabdovirus in phylogenetically distant groups may not be a formidable barrier. Lastra and Esparza (1976) experimentally demonstrated that the vertebrate vesicular stomatitis rhabdovirus will multiply in *P. maidis*. Thus the multiplication of, for example, a leafhopper transmitted rhabdovirus in a planthopper or aphid does not seem improbable. Although colonization may best explain the spread of rhabdoviruses among vector families, association by descent could explain some further evolution of rhabdoviruses within family groups. For example, it is interesting to note that only leafhoppers among the cicadellid subfamily Agallinae are vectors of potato yellow dwarf virus. All other leafhopper transmitted rhabdoviruses are vectored by leafhoppers in the subfamily Deltocephalinae.

CONCLUSIONS

Our awareness of Auchenorrhyncha-transmitted plant viruses currently is centered on those that infect the Gramineae and are vectored by cicadellid leafhoppers and delphacid planthoppers. I anticipate that many more exist, particularly those that infect dicots, have tropical distributions, and are transmitted by species in other Auchenorrhyncha families. Vector species from planthopper families other than the delphacids are likely to be discovered, particularly as more attention is paid to the tropical fulgoroids. Treehoppers, like the majority of leafhoppers and planthoppers, are phloem feeders and are potential vectors of rhabdoviruses, reoviruses, and plant viruses from other groups. Such treehopper-borne viruses could be discovered in tropical tree species, particularly minor crops that heretofore have received little attention from plant virologists and vector specialists. While newly-discovered Auchenorrhyncha-transmitted plant viruses will be included among the six groups covered in this review, others likely will be members of undescribed virus groups.

As the modern tools of molecular biology are brought to bear on the genomes of Auchenorrhyncha-transmitted plant viruses, more convincing evidence will be forwarded concerning their insect or plant origins. Additional insect viruses infecting the Auchenorrhyncha will be discovered, perhaps including some making the biochemical adjustments necessary to become plant-adapted viruses.

The association by descent and colonization hypotheses that I propose to explain the evolution of viruses with their vector taxa are subject to

experimental validation. The colonization model assumes, for example, that transmission success is directly proportional to the phylogenetic distance between the natural vector and the colonized vector species. The model is testable, but with some difficulty. Limitations for testing a broad spectrum of Homopteran vectors are the finding of species that will feed in the phloem of the virus host plant and, once selected, the difficulty in terms of labor and facilities of maintaining colonies of test species. The association by descent model will be strengthened if studies on geminiviruses and reoviruses reveal additional stable characters that can be used to construct phylogenies for these virus groups. Only after the construction of well-accepted virus phylogenies can the association by descent model be properly evaluated. If we learn that reciprocal genetic changes have occurred (or can occur) between plant viruses and their insect vectors, as could be the case for the reoviruses, then the association can be interpreted as coevolution. The concepts of association by descent or coevolution can be of help to plant virologists speculating on the evolutionary history of plant viruses. Unlike plant viruses, some insect vector groups have left behind a rich fossil record (Evans 1963, Heie 1967, Hennig 1981), thus the antiquity of plant viruses and their vector relationships can be placed on a geological time scale.

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