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Specificity of Retention and Transmission of Viruses by Nematodes[1]

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A central problem for anyone concerned with the transmission of viruses by vectors is to understand how it is that a given vector can transmit one virus but not another, and that a given virus can be transmitted by one species of vector though not by another species that may be closely allied to it taxonomically. With a few exceptions, there is still little indication of what features underlie this specificity between virus and vector, although there is enough information to suggest that the mechanism is probably not the same in all instances.

As with other vectors, so also with nematode vectors there is evidence of specificity between virus and vector. Thus, two major groups of nematode-borne viruses have been described, and two corresponding groups of vectors. The nepoviruses (8) have small isometric particles (Fig. 1) and are transmitted by nematodes in the genera *Xiphinema* Cobb and *Longidorus* (Micoletzky) Thorne and Swanger, which are both in the superfamily Dorylaimoidea. By contrast, the tobraviruses (8) (previously known as netuviruses) have straight tubular particles (Fig. 2) and are transmitted by species of *Trichodorus* Cobb, which are in the superfamily Diphtherophoroidea. With the exception of tobacco ringspot virus (17, 31), none of these nematode-transmitted viruses is known to have vectors in other phyla.

In each nematode genus there is further evidence of vector specificity. For example, *Longidorus elongatus* (de Man) Thorne & Swanger transmits two nepoviruses, raspberry ringspot virus (21) and tomato black ring virus (9), but does not transmit a third, arabis mosaic virus (22). *Xiphinema diversicaudatum* (Micoletzky) Thorne transmits arabis mosaic virus (7, 14), but not grapevine fanleaf virus (2), which serologically is distantly related to arabis mosaic virus. In *Trichodorus,* vector specificity seems somewhat less well-developed than in *Xiphinema* or *Longidorus.* For example, van Hoof (34) showed that several species of *Trichodorus* transmit tobacco rattle virus in the Netherlands. But specificity exists nevertheless, because *T. anemones* Loof will transmit a British, but not a Dutch, strain of pea early-browing virus (4). Also, van Hoof (34) reported that *Trichodorus pachydermus* Seinhorst transmitted only one of the five Dutch isolates of tobacco rattle virus that were tested.

Transmission of a virus by a nematode involves a sequence of processes: uptake of the virus particles from plants, survival of infective particles in the nematode, their inoculation by the nematode to other plant cells, and infection of the receptor plants by the virus. The probability of transmission is the product of the probabilities that each of these processes is successfully completed. Failure to complete any one of the processes will cause failure to transmit. In discussing vector specificity, we will therefore consider transmission, stage-by-stage.

Uptake of virus from plants: Sänger et al. (20) were the first to show that a plant virus could be directly detected in a nematode. They cut open *Trichodorus* nematodes that had been allowed to feed on plants infected with tobacco rattle virus, and showed that some of the extracts obtained in this way produced a few lesions when inoculated to suitable hosts of the virus. Although we now think that the virus particles detected by this method came from the nematodes' intestines and have nothing to do with transmission, such tests provide a convenient check of whether nematodes have taken up a virus from plants. Using this method, van Hoof (33) detected tobacco rattle virus in *Xiphinema diversicaudatum,* a nonvector, and Taylor (22) found that *Longidorus elongatus* acquires, not only the two viruses that it

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transmits (raspberry ringspot and tomato black ring), but also two viruses that it does not transmit, arabis mosaic and strawberry latent ringspot. In these instances at least, failure to transmit does not reflect a failure to ingest the virus particles.

Sites in nematodes where virus particles are retained: Taylor and Robertson (26, 27, 28) found, by means of electron microscopy of thin-sections of virus-carrying nematodes, that virus-like particles become associated with the cuticular lining of the buccal capsule

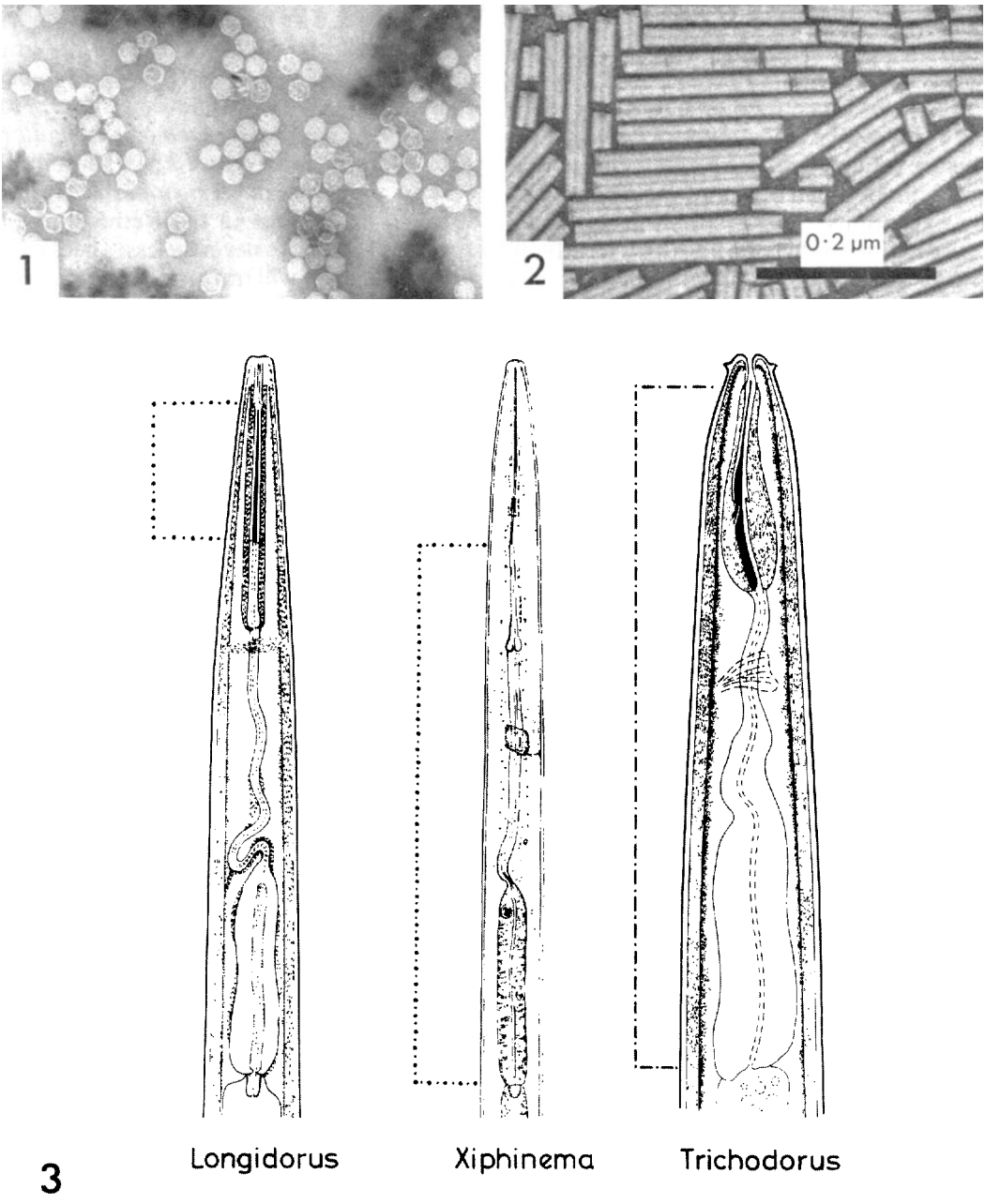


Fig. 1-3. 1 and 2. Electron micrographs of purified virus preparations mounted in 1% sodium phosphotungstate (Courtesy I. M. Roberts). **1)** Particles of arabis mosaic virus. **2)** Particles of tobacco rattle virus. **3)** Diagram of anterior portion of vector nematodes. Broken lines indicate portions of the alimentary tracts where virus particles are retained.

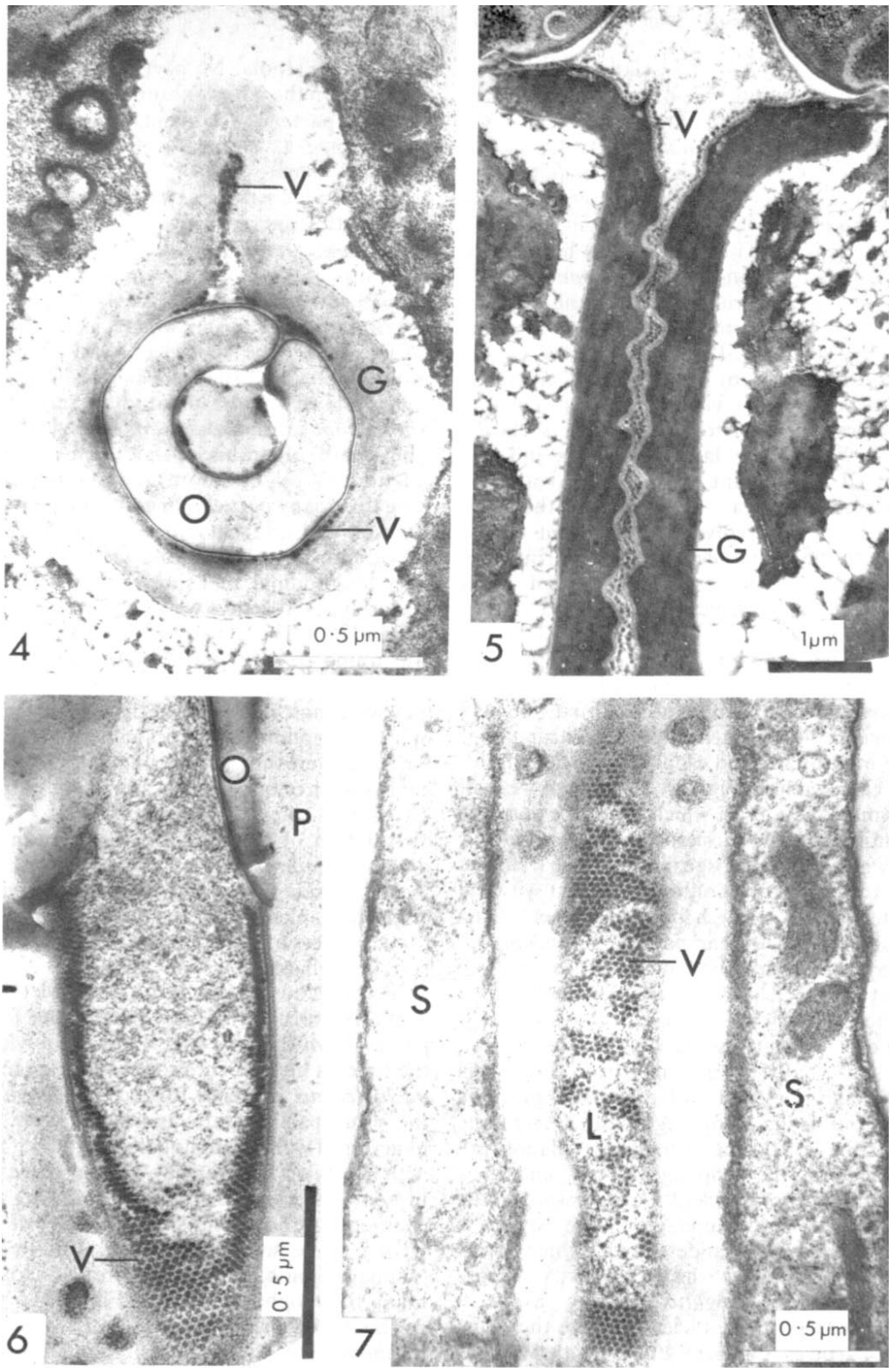


Fig. 4-7. **4)** Transverse section of buccal region of *Longidorus elongatus* carrying raspberry ringspot virus. Note virus-like particles (V) between odontostyle (O) and guide sheath (G). **5)** Longitudinal section of buccal region of *L. elongatus* carrying raspberry ringspot virus. Note numerous virus-like particles (V) lining guide sheath (G), and that none is associated with stoma cuticle (C). **6)** Oblique longitudinal section through odontophore and odontostyle of *Xiphinema diversicaudatum* carrying arabis mosaic virus. Many virus particles (V) are attached to wall of odontophore (P) lumen but not to structurally different odontostyle (O). **7)** Longitudinal section of odontophore of *X. diversicaudatum* carrying arabis mosaic virus. Virus particles (V) are seen where esophageal lumen (L) is cut tangentially. Odontophore sinuses (S) lie parallel to lumen.

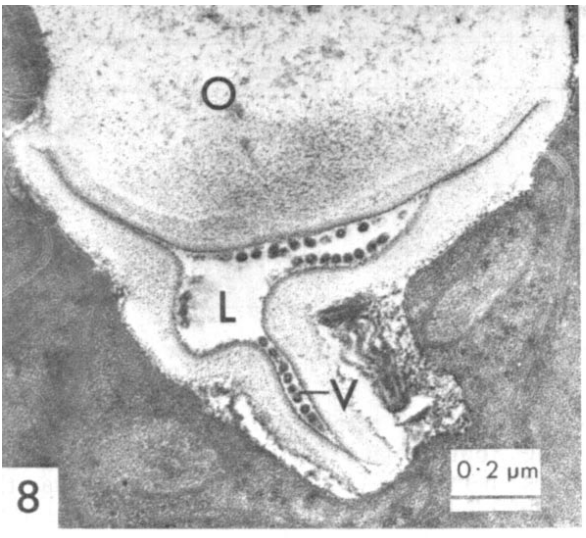
or of the esophagus. They studied *Longidorus elongatus* carrying raspberry ringspot virus, *L. elongatus* carrying tomato black ring virus, *Xiphinema diversicaudatum* carrying arabis mosaic virus, *X. index* Thorne and Allen carrying grapevine fanleaf virus, and *Trichodorus pachydermus* carrying tobacco rattle virus. McGuire et al. (16) have made similar observations on *X. americanum* Cobb carrying tobacco ringspot virus, and Raski et al. (19) have confirmed the behavior of strains of grapevine fanleaf virus in *X. index*. Taylor and Robertson (26) proposed that, in vector nematodes, the virus particles become specifically associated with these surfaces, from which they later dissociate and are injected into plant cells along with the nematodes' saliva. Transmission therefore seems not to involve multiplication of the virus in the nematode or passage through its gut wall or coelom. Indeed, plant virus particles have never been found inside nematode cells.

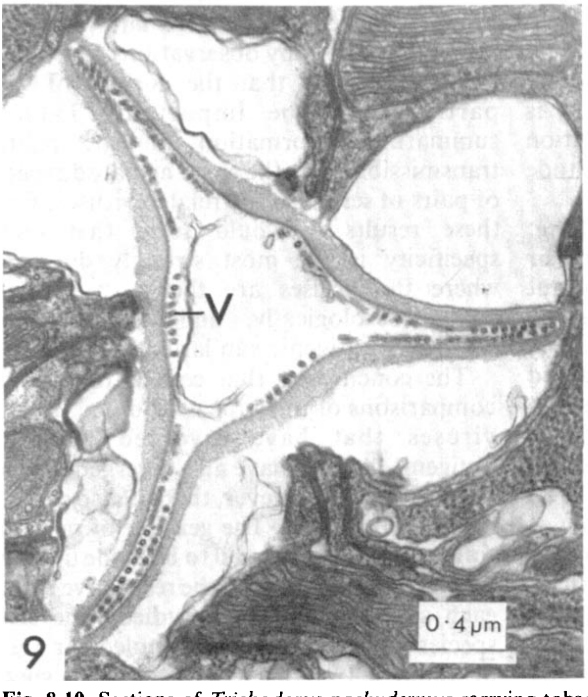
The sites of retention found by Taylor and Robertson (26) differ somewhat from one nematode genus to another. First, we will consider the main features of the structure of the mouthparts and esophagus of nematodes in each genus (Fig. 3), and then we will examine sections in which virus-like particles readily can be discerned. In *Longidorus elongatus,* the long spear is in two parts. The anterior part, or odontostyle, is cast with the outer cuticle of the nematode at each of the four molts. The rear part, or odontophore, apparently is not cast but is rebuilt at molting (Taylor and Robertson, *unpublished*), and is attached to the tubular part of the esophagus, which ends in a muscular bulb. At the rear end of this bulb is a nonreturn valve, the esophago-intestinal valve, which prevents material from being regurgitated from the intestine (30). The esophageal glands are situated in the esophageal bulb, and their secretions pass into and move forward in the lumen of the esophagus. The stylet is surrounded by a guide sheath, which forms the posterior part of the buccal cavity. A cross section of *L. elongatus* carrying raspberry ringspot virus (Fig. 4) clearly shows the virus-like particles lining the guide sheath, which is appressed to the retracted stylet. The longitudinal section (Fig. 5) shows the very many particles associated with the guide sheath, and the contrasting lack of particles associated with the structurally different lining of the stoma. No particles were found either within the odontophore lumen or lining any other part of the esophagus, or in any part of virus-free *L. elongatus*. In *L. elongatus* carrying tomato black ring virus, the distribution of particles was similar to that found with raspberry ringspot virus.

The general morphology of the feeding apparatus of *Xiphinema* is similar to that of *Longidorus,* but the guide sheath continues anteriorly beyond the guide ring, as a reflexed collar. Also, the posterior end of the odontophore has triradiate flanges (Fig. 3). Figure 6 is an oblique longitudinal section of *Xiphinema diversicaudatum,* carrying the type strain of arabis mosaic virus, at the junction of odontophore and odontostyle. Note that many particles line the lumen of the odontophore, and that none lines the lumen of the odontostyle. The second view (Fig. 7) is more longitudinal, and shows many particles in close-packed arrays where the lumen is cut tangentially. These virus-like particles were also found in other parts of the esophagus including the lumen of the esophageal bulb; they were most numerous at the anterior ends of odontophore and esophageal bulb. Particles were not found lining the stoma, guide sheath or odontostyle, nor in any part of virus-free *X. diversicaudatum*. The distribution of particles was the same in *X. diversicaudatum* carrying the hop strain of arabis mosaic virus, in *X. index* carrying grapevine fanleaf virus, and also, as shown by McGuire et al. (16), in *X. americanum* carrying tobacco ringspot virus.

In the genus *Trichodorus,* the stylet is a tooth-like structure (Fig. 3), and the food passes down the pharyngeal lumen, in which the stylet is housed, into the esophagus. In *T. pachydermus* carrying tobacco rattle virus, the virus particles are associated with the pharyngeal wall throughout its length, but not with the stylet (Fig. 3 and 8). They also line the lumen of the esophagus, where the characteristic long and short particles of the virus can be seen clearly (Fig. 10). In the esophageal bulb, the particles are again found lining the esophageal lumen (Fig. 9).

The behavior of tobacco rattle virus in *Trichodorus* is, therefore, more similar to that of viruses in *Xiphinema* than that of viruses in *Longidorus*. This difference seems to correspond to a difference in the length of time fasting, virus-carrying nematodes retain the ability to infect healthy plants with virus.





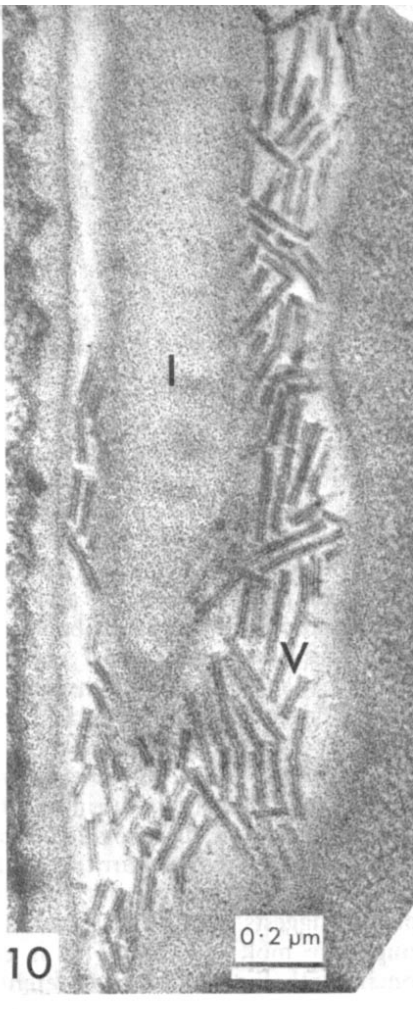


Fig. 8-10. Sections of *Trichodorus pachydermus* carrying tobacco rattle virus. **8)** Transverse section of pharynx, showing lumen (L) with attached virus particles (V) seen in cross section. Odontostyle (O) is embedded in pharyngeal wall. **9)** Transverse section of triradiate lumen of esophageal bulb. Virus particles (V) are mostly cut in cross section. **10)** Longitudinal section of esophagus. Virus particles (V) of both characteristic lengths are attached to esophageal wall, which is infolded (I).

This period lasts up to 12 wk for viruses transmitted by *Longidorus* (23), whereas durations of almost 1 yr are reported for *Xiphinema* (1), and of well over 1 yr for *Trichodorus* (35).

Specificity of retention: The evidence provided by electron microscopy of virus-carrying vector nematodes leads to the suggestion that the association of virus particles with a specific surface in the duct that carries the nematode's food from plant to intestine plays an important part in the transmission process. Let us now consider the evidence that specificity of transmission is determined by the specificity of association with a surface within the nematode. Table 1

TABLE 1. Specificity of virus transmission by nematodes, and site of virus retention.

Nematode	Virus			
	Raspberry ringspot (strain S)	Arabis mosaic	Grapevine fanleaf	Tobacco rattle
Longidorus elongatus	++[a](G)[b]	0(0)	---	0(0)
Xiphinema index	0(0)	---	++(E)	---
X. diversicaudatum	0(0)	++(E)	0(0)	---
Trichodorus pachydermus	---	---	---	++(PE)

[a]Symbols for transmission: ++ = much, 0 = none.
[b]Symbols for retention site: (E) = esophagus, (G) = guide sheath, (P) = pharynx, (0) = none, --- = not tested.

summarizes information on the vectors and also gives results for five nontransmitting combinations of the same viruses and species of nematode. In none of these nonvector situations have virus particles been found retained on any of the nematode surfaces with which virus particles become associated in vector situations. It seems probable that, at least in these instances, vector specificity is related to the specificity of the association between virus particles and nematode surfaces.

Fate of virus particles during molting: The retention of infectivity during molting, or the lack of retention, has provided important evidence on the way viruses are transmitted by insects. With nematode vectors, the available evidence suggests that virus is not retained through the molt (13, 25). This is easy to reconcile with the site of virus retention in *Longidorus*, because the guide sheath is cast with the nematode's outer cuticle. However, in *Xiphinema* and *Trichodorus* the lining of the esophagus is not cast with the outer cuticle. The probable fate of virus particles associated with the esophageal lining of *Xiphinema* is shown by electron microscopy (27). In larval and adult *X. index*, the particles of grapevine fanleaf virus are found in the triradiate lumen of the esophagus within the esophageal bulb (Fig. 11). In molting *X. index*, the lining of the esophagus is sloughed off and passes backwards into the intestine (Fig. 12). After each molt, therefore, *Xiphinema* has a new, virus-free lining in its food canal and so is unable to transmit until it has again acquired virus particles from plants.

Mechanism of retention and release of virus particles: The way in which virus particles are retained on specific nematode surfaces and later released is far from clear. Harrison (3) showed that serologically distinctive strains both of raspberry ringspot virus and of tomato black ring virus have different specific nematode vectors, and suggested that this might be because the surface of the virus particles is involved in the transmission process. Indeed, if we have interpreted the electron microscopy observations correctly, it seems inevitable that the surface of virus particles will be important. Table 2 summarizes information on the relative transmissibility by the same nematode species of pairs of serologically related viruses. From these results it would seem that vector specificity is the most strongly developed where the viruses are the most distantly related serologically, and decreases with increasing antigenic similarity.

The conclusions that can be drawn from comparisons of this type are limited, because viruses that have diverged the most antigenically may have also diverged the most in other ways. However, there is also evidence of a different kind. The genome of raspberry ringspot virus was found to be made up of two species of RNA (10) and the respective roles of each species have been studied. The larger species (called RNA-1) has a molecular weight of about 2.4×10^6, and the smaller species (called RNA-2) of about 1.4×10^6 (18). Hybrid isolates can be prepared by taking RNA-1 from one virus strain and RNA-2 from another. In this way it was shown that some characters of the virus are determined by RNA-1 and others by RNA-2; for example the cistron for the virus coat protein is in RNA-2 (11). Hybrids were made between two strains with different vector specificities, and different serological properties (Table 3); note particularly the difference in efficiency of transmission of these strains by *Longidorus elongatus* (24). Table 4 shows the relative transmissibility of isolates of the parental and

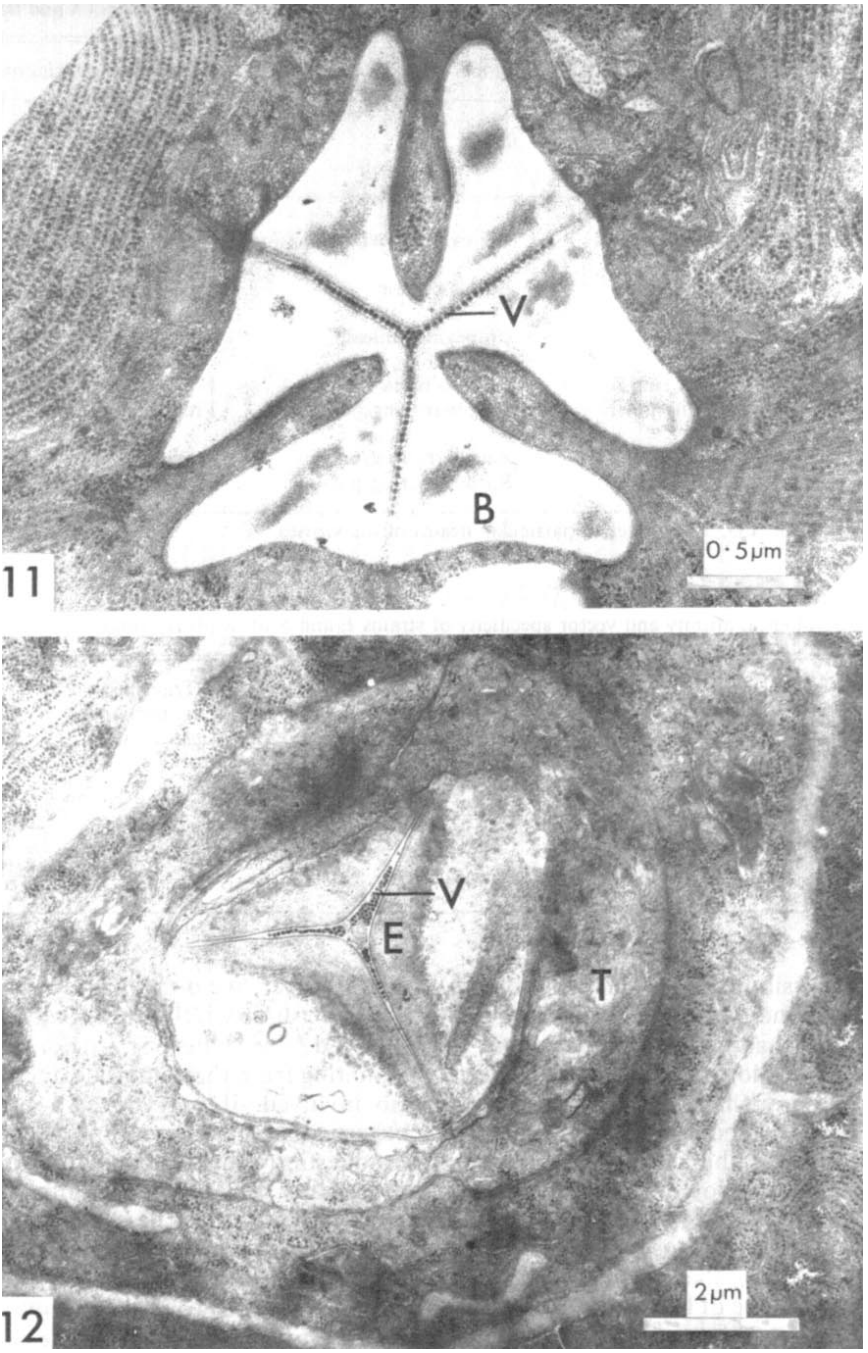


Fig. 11-12. 11) Transverse section of cuticular platelets (B) lining lumen of esophageal bulb of *Xiphinema index* carrying grapevine fanleaf virus. Virus particles (V) lie in triradiate lumen. **12)** Transverse section of esophago-intestinal valve of molting *X. index* carrying grapevine fanleaf virus. Note sloughed off esophageal lining (E) with virus particles (V) in its lumen. Esophageal lining is surrounded by valve tissue (T).

the hybrid types. Transmissibility by *L. elongatus* is determined by RNA-2; the source of the RNA-1 seems to make no difference. The RNA species carrying the coat protein cistron, therefore, also determines transmissibility and, although other explanations are not all excluded, we suppose this is because the coat protein critically

TABLE 2. Relation between nematode transmissibility and serological relatedness of pairs (A and B) of viruses.

Nematode	Viruses compared		Nematode transmission		Mean percentage cross-reacting antibody
	A	B	A	B	
Trichodorus anemones	Pea early-browning-B[a]	Pea early-browning-D	Frequent	None	1
Xiphinema index	Grapevine fanleaf	Arabis mosaic	Frequent	None	8
X. diversi-caudatum	Arabis mosaic	Grapevine fanleaf	Frequent	None	8
Longidorus elongatus	Tomato black ring-S	Tomato black ring-E	Frequent	Trace	12
L. macrosoma	Raspberry ringspot-E	Raspberry ringspot-S	Frequent	Trace	25
L. elongatus	Raspberry ringspot-S	Raspberry ringspot-E	Frequent	Less frequent	25
L. elongatus	Raspberry ringspot-S	Raspberry ringspot-LG	Frequent	Frequent	90

[a]The suffixes B, D, E, LG, and S refer to particular strains of the viruses.

TABLE 3. Serological affinity and vector specificity of strains E and S of raspberry ringspot virus.

Virus strain	Reciprocal of antiserum titer		Transmission by nematodes	
	RRV-E antiserum	RRV-S antiserum	*Longidorus elongatus*	*Longidorus macrosoma*
RRV-E	512	256	Less frequent	Frequent
RRV-S	128	1024	Frequent	Trace

affects transmissibility (12). This would seem to be an extra function for virus coat protein.

A point that has caused some concern is that although serologically distinctive strains of a virus may have different vectors, serologically unrelated viruses may have the same vector. We think this can happen because the features of the particle surface that are involved in serological specificity may not be identical with those that determine transmissibility, so that a major change occurring in one type of feature often, but not always, results in a change in the other type. To quote a possibly relevant analogy, a major change in an antigenic determinant might well lead to an alteration in the surface-charge density of virus particles, although a similarity in surface-charge density need not imply serological relationship.

For virus to be transmitted, virus particles must associate with, and later dissociate from, a site in the nematode. We have argued that the surface of the virus particle plays a critical role; however, we do not know whether the nematode surface is the only other component required, or whether other materials emanating from the nematode or the plant are also involved. If only the two surfaces are concerned, association and dissociation may be a question either of adsorption and elution, or perhaps of a more complex process involving the steric properties of the two surfaces. But we cannot rule out the possibility that the system has other components, and would point out that virus particles lining the guide sheath or esophagus seem mostly to be separated from these surfaces by a layer of electron-translucent material, possibly mucus.

Dissociation of the virus particles from their site of retention seems most likely to occur when saliva passes from nematode to plant, perhaps because the pH or ionic conditions then change, or because of some enzymic effect of the saliva either on the surfaces of nematode or virus particles, or on

TABLE 4. Transmission by *Longidorus elongatus* and serological specificity of hybrids between strains E and S of raspberry ringspot virus [data from Harrison et al. (Ref. 12)].

RNA constitution of isolates[a]	No. transmissions[b]		Serological specificity of isolates before and after transmission
	L. elongatus-containing soil	Steamed soil	
RNA-1 (S)/RNA-2(S)	21/24	0/12	S
RNA-1(E)/RNA-2(S)	21/24	0/12	S
RNA-1(S)/RNA-2(E)	7/24	0/12	E
RNA-1(E)/RNA-2(E)	6/24	0/12	E
None	0/24	-	-

[a]Hybrid isolates were made by using mixtures of purified samples of RNA-1 and RNA-2 as inoculum, and culturing isolates from single lesions.
[b]Numerator is the number of *Chenopodium quinoa* hypocotyls infected, denominator is the number of seedlings exposed to infection. Infected *C. quinoa* plants were used as virus sources.

materials involved in binding the virus particles to the nematode surface. But, however it occurs, dissociation seems unlikely to be rapid. The viruses can persist for weeks in their vectors, and some can be transmitted to several plants in a series when the nematodes are individually transferred from plant-to-plant every day or two. This kind of serial transmission is reported for at least one species of *Trichodorus* (32), one of *Xiphinema* (5), and one of *Longidorus* (6).

Lack of dissociation would presumably result in the failure of a nematode to transmit, and Taylor and Robertson (29) have preliminary results that might be interpreted in this way, although other explanations are also possible. Working with *L. macrosoma* Hooper, which transmits strain E of raspberry ringspot virus readily, but strain S rarely or not at all (3), they found that particles of both strains became associated with the odontostyle and the surface of the guide sheath. The distribution of particles of the two strains was the same.

Inoculation and infection of plants: Having dissociated from their site of retention, virus particles have still to be inoculated into plant cells. For virus to be transmitted, the particles must be infective, and the plant cells must not be so damaged or otherwise affected by the nematode that the virus is unable either to replicate in them or to pass into adjacent cells. With nematode-borne viruses there is no evidence that vector specificity is determined at this stage, although something analogous seems to have been described with the fungus-transmitted tobacco necrosis virus. Kassanis and MacFarlane (15) obtained results they interpreted as indicating that invasion of some plant species by some *Olpidium* strains resulted in changes that made virus infection unlikely. Something similar may occur with nematode-transmitted viruses, and in fact the description of feeding by *Trichodorus similis* Seinhorst suggests that most cells that have been penetrated are severely damaged, although cytoplasmic streaming resumes in a few of them (36).

Conclusions: Our main conclusions may be stated as follows. Considerable vector specificity exists in the transmission of viruses by nematodes. Transmission is the end result of a sequence of processes. Thus, failure to transmit, and hence vector specificity, may be caused by failure to complete any one of these processes. The particles of viruses that are transmitted are retained on the inner surface of the guide sheath or esophagus, the exact site depending on the nematode genus. Nontransmitted viruses are mostly not retained at these sites or, in one instance, possibly not released from them. The nature of the protein surface of the virus particles seems to determine vector specificity.

Finally, we would also emphasize that we have dealt only with the behavior of viruses in nematodes. The phenomena we have described also have important implications for the survival and spread of the viruses in nature, and this subject might make an interesting contribution on another occasion.

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