Location of Tobacco Rattle Virus in the Nematode Vector, *Trichodorus pachydermus* Seinhorst

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Tobacco rattle virus (TRV) has been detected in its natural vectors (*Trichodorus* spp.) by cutting up batches of infective nematodes in a drop of water and inoculating the suspension to herbaceous test plants (Sänger, Allen & Gold, 1962); the characteristic rod-shaped particles of TRV have also been seen in such preparations with the aid of the electron microscope. However, these results merely show that infective sap is ingested and are not necessarily indicative of any specific relationship between virus and vector as TRV has similarly been detected in *Xiphinema* and *Pratylenchus* nematodes which do not transmit the virus (van Hoof, 1967). *Longidorus elongatus* likewise ingests viruses which it does not transmit (Taylor, 1968) but in *L. elongatus* carrying raspberry ringspot or tomato black ring, two viruses of which it is the natural vector, we have found virus-like particles apparently specifically adsorbed on to the cuticular stylet guiding sheath (Taylor & Robertson, 1969). This led us to examine *Trichodorus pachydermus* Seinhorst to see whether we could find evidence of specific retention of TRV in association with the feeding apparatus, i.e. virus which might be transmitted as distinct from that which, ingested, passes into the intestine and becomes non-transmissible by the nematode.

Fig. 1. (a) Diagram of the oesophageal region of *Trichodorus pachydermus* (× 300). (b) Cross-section of the lumen of the pharynx, in the region where the stylet is attached, showing sectioned particles of tobacco rattle virus.
Fig. 2. (a) Longitudinal section through the lumen of the glandular part of the oesophagus with particles of tobacco rattle virus. (b) Cross-section of the lumen of the glandular part of the oesophagus, showing the association of tobacco rattle virus particles with the nematode cuticle and within the mucus layer.
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Infective *T. pachydermus* were obtained from a site in Fife where spraing disease (caused by TRV) of potato was prevalent. After extraction from the soil samples, the nematodes were fixed in 3% (v/v) glutaraldehyde and post-fixed in 1% osmium tetroxide, dehydrated in a graded ethanol series and, after transferring through two changes of 1:2 epoxypropane, were embedded in Araldite (Taylor et al. 1969). Transverse sections, about 60 nm. thick, were cut at 1 μm. intervals from the head end to the beginning of the intestine; they were stained on collodion-coated grids with alcoholic uranyl acetate and lead citrate and examined in a Siemens IA electron microscope at magnifications up to ×40,000. Rod-shaped particles occurred throughout the length of the lumina of the pharynx and of the oesophagus and were mostly orientated lengthwise in close association with the cuticle lining the digestive tract (Fig. 1a, b, 2a, b). There were more particles in the glandular part of the oesophagus than elsewhere and this may be associated with the presence of a layer of mucus overlying the cuticle in this region which possibly isolates and protects the particles from the flow of sap during feeding (Fig. 2b). Random measurements of particles from photographic plates showed that they were of uniform width (22 nm.) with the lengths distributed about three distinctive modes, 170, 90 and 45 nm. respectively, which accord with the particle length distributions of several English isolates of TRV (Harrison & Woods, 1966).

The transmission process by *Trichodorus* species is envisaged as a mechanical contamination of the stylet. The nematodes feed on the root tips of their host plants by puncturing the epidermal cell wall with thrusts of the solid stylet and by sucking out the cytoplasmic contents by the pumping action of the oesophagus (Chen & Mai, 1965; Hirumi et al. 1968). TRV particles ingested with the cytoplasm appear to accumulate in the lumen of the digestive tract by selective adsorption on to the cuticle. Subsequent transmission of the virus particles would presumably take place when the salivary secretions released from the glands of the oesophageal bulb flow forward to the stoma as the nematode thrusts out its stylet.

Although most of the *Trichodorus* species described from Europe and the U.S.A. are vectors of tobacco rattle virus, there is some evidence of specificity of transmission, a single nematode species transmitting only a particular isolate of the virus (Ayala & Allen, 1968; van Hoof, 1968). If the surface charges on the virus particles (Harrison & Roberts, 1968) are the means whereby they are adsorbed on to the cuticle of the digestive tract, differences in surface charges between virus isolates or possibly differences in the nature of the cuticle between nematode species could account for specific relationships between virus and vector.

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