

## So many thrips – so few tospoviruses?

Laurence A. Mound  
CSIRO Entomology, GPO Box 1700, Canberra, Australia,  
E-mail: [laurence.mound@csiro.au](mailto:laurence.mound@csiro.au)

**Abstract:** Tospoviruses are considered to be dependent on Thysanoptera for their existence in nature, but scarcely 0.15% of Thysanoptera species (9 of 5500) are known to be vectors. Moreover, these vector species are not closely related to each other, suggesting either that many thrips species have lost an association with tospoviruses or that each Tospovirus species has evolved an independent relationship with a thrips species. The lack of evidence for a long evolutionary relationship between thrips and tospoviruses, together with the lack of any evidence that tospoviruses are associated with any native Australian plant species nor any native Australian thrips species, despite that continent being where TSWV was first observed, raise questions concerning where, when, how, and how often the thrips/tospovirus associations originated.

### Introduction

From a crop protection point of view, the association between tospoviruses and thrips is all too evident. If a crop is suffering from a tospovirus attack, then it can safely be assumed that a species of thrips is involved. Indeed, tospoviruses are not known to exist in crops or in nature in the absence of thrips, although much of the experimental work by virologists is done without a thrips vector, transmitting these maladies by rubbing leaves together. Within a crop, the spread of a Tospovirus is, to a large extent, a function of the behaviour, dispersive activity, and rate of development of the local thrips vector species. Without thrips, tospoviruses cannot transfer from one plant to another, and without thrips tospoviruses survive from one season to another only in infected plants. This dependency of tospoviruses on the biology of thrips is so strong that it is surprising so little attention has been paid to the origin, or origins, of this dependence. The purpose of this article is to consider the available evidence concerning when, in their evolutionary history, thrips acquired the ability to transmit tospoviruses. The parallel problem remains for consideration by virologists, concerning when tospoviruses evolved their association with plants and thrips, given the assumption that they evolved within the Bunyaviridae whose members are known only from vertebrates and insects.

### Thysanoptera origin and radiation

Thysanoptera are presumed to have evolved from fungus-feeding detritus-living ancestors, a habit that is retained in the members of the Merothripidae, and also in the Psocoptera that presumably shared a common ancestor with thrips (Mound, Heming & Palmer, 1980). Presumably there was an early radiation onto floral structures, and thrips may even have been involved as pollinators during the early radiation of flowering plants (Terry, 2002, this volume), one basal clade thrips genus retaining an association with the reproductive structures of a basal clade plant group, the cycad genus *Macrozamia* (Terry, 2001). Subsequently three major food sources were adopted by thrips – fungal hyphae and spores, green leaves, and flowers with or without leaves as well. A few species are also predators, and a very few feed only on mosses (Mound & Marullo, 1996).

Currently, the 5000 recognised species of thrips are arranged into nine families, the largest of which is the Phlaeothripidae, the sole family in the suborder Tubulifera. The 3200 species in this family exhibit a wide range of biologies, but the 700 members of the subfamily Idolothripinae all feed by imbibing whole fungal spores, a few species being known to have a special spore-crushing apparatus in the fore gut (Mound & Palmer, 1983). In contrast, about half of the 2500

species in the subfamily Phlaeothripinae feed on fungal hyphae rather than spores, with most of the remaining species feeding on flower or leaf tissues, including a few on mosses, and a very few species predatory on other small arthropods. Some of the leaf-feeding Phlaeothripinae induce galls, particularly in tropical countries, but very few species in this subfamily attack any crops, and none are known to be associated with any tospoviruses.

The other eight families in the Thysanoptera are all included in the suborder Terebrantia (Table 1) (Moritz, Morris & Mound, 2001). Members of the Merothripidae and Uzelothripidae are all very small thrips associated with fungal hyphae in warm countries. In contrast, members of the Melanthripidae are usually large and robust, and they all breed in flowers in temperate areas. The Aeolothripidae is a rather larger family, but whereas the species of the two largest genera, *Aeolothrips* and *Desmothrips*, are commonly phytophagous in flowers or non-obligate predators on other arthropods, the species in the many small genera from the tropics are all obligate predators. The species of the next two families are rather poorly known, although all five species in one genus of Adiheterothripidae are known only from the flowers of date palms, *Phoenix dactylifera*. The seventh family, Heterothripidae, is found only in the New World and, with one exception, all the species are flower-living. The exception is of considerable biological interest, because it has recently been shown to be ectoparasitic on a species of Homoptera, a way of life that is unique amongst Thysanoptera (Izzo et al. 2001; Pinent et al. 2002, this volume).

The eighth family of Terebrantia is, with 1700 known species, by far the largest. The Thripidae is found worldwide, from Greenland to the southern oceans, and includes almost all of the pest species of thrips. The species of many genera are associated only with grasses, whereas others are associated only with dicotyledonous plants, some in flowers but others only on leaves. Pest species are commonly more adaptable in their habits, and many of them feed and breed both on leaves and in flowers.

### Thrips associated with tospoviruses

For Tospovirus workers, the important statistic in Table 1 is that only 9 of the 5500 known species of thrips have been shown to be

associated with any of these diseases. Thus less than 0.2% of Thysanoptera species are known to be associated with tospoviruses, and there is no evidence that many more thrips species are likely to be implicated. This immediately suggests that the probability of a long evolutionary history between these organisms is unlikely. More significantly, the few thrips species that are associated with tospoviruses are not closely related to each other (Table 2).

Only five of the 160 described species of *Frankliniella* are known to be vectors of tospoviruses, only three of the 280 species of the genus *Thrips*, and just one of the 90 species of *Scirtothrips*. Phylogenetically, the third of these thrips genera is widely distant from the first two (Mound & Marullo, 1996). Moreover, *Thrips* and *Frankliniella* are members of generic groups that cannot be considered closely related in view of their structural differences. *Frankliniella* genus-group is probably Gondwanan in origin, whereas *Thrips* genus-group is a relatively recent lineage, apparently evolving subsequent to the separation of the African and South American continents (Mound, 2002, this volume).

Even within the two genera, *Thrips* and *Frankliniella*, the vector species are not closely related, neither phylogenetically nor geographically (Table 3). The Eurasian species, *F. intonsa*, is similar in structure to the western USA species, *F. occidentalis*, but the species most closely similar to the western flower thrips is *F. panamensis* (Moritz, Morris & Mound, 2001). *F. fusca* and *F. zucchini* both differ considerably in structure from these species, and *F. schultzei* seems even more distantly related (Mound, 2002, this volume). Similarly, the structural differences between the three species of genus *Thrips* that are known as vectors are so great that these three cannot be considered as being closely related within this large and diverse genus.

### Origin of the thrips/Tospovirus relationship

Since the known vector species are not closely related to each other, two alternative evolutionary scenarios must be considered. Assuming that the thrips/Tospovirus associations had a single evolutionary origin, then this must have been early in the evolution of the Thripinae. This assumption involves the conclusion that the vast majority of thrips species subsequently

became resistant to these organisms thus losing the ability to act as vectors to plants. The alternative scenario is that the thrips/Tospovirus associations have had multiple origins, each of the unrelated vector species developing an association with a Tospovirus independently. The first of these scenarios seems, to a thrips worker, essentially unlikely. However, because the existence of each Tospovirus is considered to be dependent on the existence of its vector, the second scenario implies that each Tospovirus has itself evolved independently, a situation that virologists apparently consider impossible.

### Country of origin of Tospoviruses

Finally, when considering origins, it is essential to distinguish between the country where a Tospovirus is first recorded, and the country where it may have originated. The first of these is probably a function of the existence locally of a virologist sufficiently interested to discover the virus, and is likely to be of little evolutionary significance. Thus although Australia was where TSWV was first noted, and a further 10 years elapsed before this virus was found elsewhere, this cannot be taken as evidence that it originated there (Best, 1968).

Within Australia, tospoviruses are widespread, but they have been recorded in that

continent almost exclusively from non-native plant species, and are known to be vectored only by non-native thrips species. Evidence for the existence of these viruses in any member of the diverse Australian flora is very weak, despite the comment by Best (1968) that TSWV might be latent or symptomless in some native Australian plants. Latham & Jones (1997) reported examining 1590 specimens of 42 species of Australian native plants, but found Tospovirus in only one specimen (*Calectasia cyanea*; Xanthorrhoeaceae). In contrast, they tested 12,105 specimens of 70 different species of introduced weeds, vegetables and ornamentals, and found Tospovirus in 664 specimens. Moreover, high incidence of TSWV was related to the presence of the introduced thrips, *F. occidentalis*. Again, it must be stressed that no native Australian thrips species has been shown to be a vector, and the thrips breeding on crop plants in Australia are almost always species that have been introduced from overseas (Mound & Gillespie, 1997). Finally, we cannot assume that vector species, such as *F. occidentalis* or *F. schultzei* that are now widespread around the world, acquired an association with any particular Tospovirus before, rather than subsequent to being distributed widely around the world by human trading in plants.

FAMILIES	SUB-FAMILIES	Genera currently valid	Species currently valid	Species vectoring Tospovirus
Phlaeothripidae	Phlaeothripinae	350	2500	0
	Idolothripinae	80	700	0
Uzelothripidae		1	1	0
Merothripidae		3	15	0
Melanthripidae		4	65	0
Aeolothripidae		23	190	0
Fauriellidae		4	5	0
Adiheterothripidae		3	6	0
Heterothripidae		4	70	0
Thripidae	Panchaethripinae	35	125	0
	Dendrothripinae	10	90	0
	Sericothripinae	10	90	0
	Thripinae	235	1700	9

Table 1. Occurrence of Tospovirus vector species in the Thysanoptera

Thripinae genera	Described species	Recorded vectors
<i>Frankliniella</i>	160 species	5 species
<i>Thrips</i>	280 species	3 species
<i>Scirtothrips</i>	90 species	1 species

Table 2. Tospovirus vectors

<i>Frankliniella intonsa</i>	Europe to Asia
<i>Frankliniella occidentalis</i>	Western USA
<i>Frankliniella fusca</i>	Eastern USA
[ <i>Frankliniella bispinosa</i> ]	S.E. USA
<i>Frankliniella schultzei</i>	S. America
<i>Frankliniella zucchini</i>	S. America
<i>Thrips tabaci</i>	Eastern Mediterranean
<i>Thrips setosus</i>	Japan
<i>Thrips palmi</i>	S.E. Asia
<i>Scirtothrips dorsalis</i>	S.E. Asia

Table 3. Area of origin of Tospovirus vector species

The origin of tospoviruses, and the origin or their association with thrips, thus remains entirely conjectural, but further consideration of this evolutionary phenomenon might well yield economic benefits.

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