Ectoparasitism in thrips and its possible significance for tospovirus evolution

Silvia M. J. Pinent[1], Laurence A. Mound[2] and Thiago J. Izzo[3]
[1]UFRGS, Porto Alegre, RS, Brazil; [2]CSIRO Entomology, Australia; [3]INPA, Manaus, Brazil
E-mail: carlospi@portoweb.com.br

Abstract: The significance is considered of thrips probing or feeding on other organisms, whether arthropods or vertebrates, to considerations of the origin of tospoviruses within the Bunyaviridae, in the light of the newly discovered ectoparasitic habits of *Aulacothrips dictyotus* in Brazil.

Introduction

Tospovirus workers and entomologists generally consider thrips to be essentially phytophagous, most individuals being found on green leaves or in flowers. However, several tospovirus vectors are amongst the most versatile of thrips species in terms of their feeding habits. Despite feeding primarily on leaf and flower tissues, *Frankliniella occidentalis*, *Fr. schultzei* and *Thrips tabaci* all will feed on other arthropods, particularly mites. Moreover, predation on small arthropods is the typical behaviour of several species of Thripidae. Therefore, although thrips seem to be adapted particularly to ingest materials of plant origin, some species are able to digest animal tissues. But it is not only invertebrates that thrips are known to probe with their mouthparts. People in widely separated countries have reported skin lesions caused by thrips, the species involved usually being one or more that is locally abundant (see references in Mound *et al*., 2002). In addition, it is not unusual to find thrips in the nests of birds, although the possibility that thrips probe on the skins of nestling birds or mammals has never been properly investigated.

Tospoviruses, because of similarities in their molecular structure, are grouped within the family Bunyaviridae, in which all other species are known only from arthropods and vertebrates. If Tospoviruses have evolved within the Bunyaviridae then the question arises as to how they made the transition from being animal parasites to being plant parasites. But tospoviruses apparently cannot exist in the absence of thrips. They seem to be entirely dependent for their continued existence on the feeding, breeding, and dispersive behaviour of thrips. Given the diverse feeding relationships among thrips, involving other arthropods and possibly even vertebrates, it is likely that thrips come into contact with other members of the Bunyaviridae from time to time. Given the lack of evidence of any evolutionary association between thrips and tospoviruses (Mound, 2003), the possibility that these plant diseases might have arisen by mutation from some animal parasite should probably be considered. The following report, concerning the first thrips species reported to be ectoparasitic on another insect, may thus have significance when considering the origin of the relationship between tospoviruses and thrips.

Thrips biological diversity

A wide range of biologies can be found amongst the 5000 or more described species of thrips (Mound & Heming, 1991). Members of the sub-order Tubulifera are particularly diverse, with different species feeding on leaves, flowers, fungal hyphae, fungal spores, mosses, and the tissues of other small arthropods (Mound & Marullo, 1996). However, members of the sub-order Terebrantia also feed on most of this range, despite the majority of the species being associated with flowers and leaves. The basal clades of Thysanoptera are found in this sub-order, and the plesiotypic life style is presumed to have involved fungus or detritus feeding (Mound et al. 1980). This habit is retained in the Merothripidae, in which family adults exhibit more characters in the plesiomorphic state than do any other thrips. Subsequent radiation amongst Terebrantia involved flower-feeding, and species in one basal clade have recently been demonstrated to breed only in the male cones of

a group of lower plants, the *Macrozamia* cycads (Mound & Terry, 2001). These *Macrozamia* thrips are members of the family Aeolothripidae, the sister-group to the Merothripidae. However, most Aeolothripids are facultative predators on other arthropods in flowers, with species in a few small tropical genera obligate predators on leaves and grasses (Mound & Marullo, 1998).

In contrast to these basal clades, the major advanced Terebrantia comprise the families Thripidae and Heterothripidae. The first, which includes most pest species and all of the tospovirus vectors, is found worldwide. At least 1700 species of Thripidae are described, feeding primarily in flowers or on leaves of higher plants including many on grasses, but with some species obligate predators and a few that feed on lower plants such as mosses or ferns. The family Heterothripidae is found only in the New World, and comprises four genera and rather more than 70 described species (Mound & Marullo, 1996). All but one of these species are placed in three of the genera, and field studies suggest that they are all flower-living, particularly on Malpighiaceae (Del Claro et al, 1997). The fourth genus, *Aulacothrips*, includes just one species, *A. dictyotus* Hood (1952), and until recently this has been known from just two adult females, collected in Sta Catharina State, southern Brazil.

Ectoparasitism in Aulacothrips dictyotus

A considerable population of *A. dictyotus* was discovered at Sao Jose do Rio Preto (Sao Paulo State, Brazil), during observations on interactions between *Camponotus crassus* (Formicidae), *Trigona hyllinata* (Meliponidae), and *Aethalion reticulatum* (Aethalionidae) on the leaves of *Bauhinia variegata* (Caesalpiniaceae). First and second instar larvae of this thrips, also propupae and pupae, were observed living on the abdominal tergites of *A. reticulatum* beneath the hind wings. The association appeared to be specific, because no thrips were found beneath the wings of a second, unidentified, species of *Aethalion* on the same plant at this locality (Izzo et al. 2002).

Of 212 nymphal *A. reticulatum* examined, 52 had larval thrips beneath the wing rudiments. Similarly, of 48 adult *A. reticulatum* examined, 13 were found with thrips under the wings. More than 10 larval thrips could be found beneath the wings of a single bug (Fig. 1). Even after being killed and transported long distances in alcohol, larvae of this thrips remained firmly attached by their head region at the base of the hind wing of a bug (Fig. 2). Two newly emerged first instar larvae of this thrips were found under the wings of one such bug preserved in alcohol. Moreover, the second larva spins a pupal cocoon, and these flat pupal cocoons (Fig. 3) were found under the wings of adult *A. reticulatum*. Pupal cocoons are also known in some Aeolothripidae (Hoddle *et al*., 2000), and have been seen recently in *Heterothrips arisaemae* Hood, courtesy of Ilke Feller. The life cycle of *A. dictyotus* thus seems similar to related thrips, except that it is spent entirely on the surface of these Homotera.

The *A. reticulatum* were found living gregariously in groups of 30 to 80 individuals. Presumably, transfer of immature thrips between individuals of *Aethalion* when the bugs moult is facilitated by this gregarious behaviour. The colony of bugs was observed to be disturbed by the presence of the thrips, their behaviour becoming agitated, and individuals were noted crawling over each other. The oviposition site of the thrips has not been determined, but the presence of very early first instar larvae under the wings of one bug suggests that the eggs are laid on the host. Moreover, the hind wings of several adult bugs were clearly deformed, and this damage might possibly be caused by the thrips oviposition.

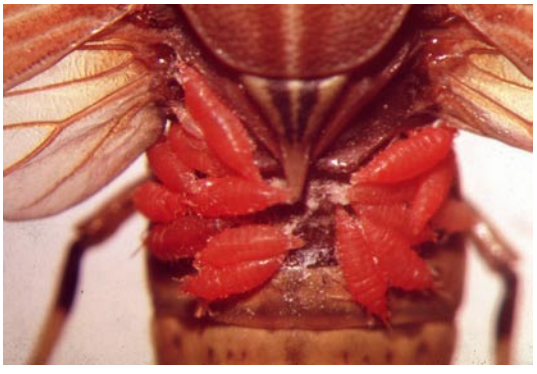

Fig. 1. *Aulacothrips dictyotus* 1st and 2nd instar larvae beneath wings of adult *Aethalion reticulatum*.

Fig. 2. *A. dictyotus* 2nd instar larva feeding in axillary region of adult *Aethalion reticulatum*.

Fig. 3. *Aulacothrips dictyotus* pupal cases on abdomen of adult *Aethalion reticulatum*.

Comments

The body structure of adult *Aulacothrips dictyotus* is remarkable within the Heterothripidae. The wings are held close together medially on the abdomen, protected when at rest by a series of spines. Moreover, the third and fourth antennal segments are grossly expanded with the sensorium convoluted, and the distal segments greatly reduced. Adults of this species have been observed walking over *Aethalion* adults and nymphs, and the curious reduction of the antennae and protection of the wings is probably related to the biology of the species. Future studies will hopefully examine the feeding behaviour of these remarkable thrips.

As indicated above, several unrelated thrips species have become predatory on other small arthropods, including mites and scale insects (Palmer & Mound, 1991). Many thrips species are remarkably opportunistic in their habits, changing from phytophagous to predatory depending on the available conditions (Mound & Teulon, 1995; Agrawal et al., 1999). Also, phytophagous thrips are well known to probe human skin at times, sometimes causing small lesions (Lewis, 1973). Recent studies on other Thysanoptera have emphasised the remarkable diversity of behaviour patterns within this group, including sociality (Crespi & Mound, 1997) and domicile construction (Mound & Morris, 2001). Thus there is no intrinsic reason to consider the ectoparasitic way of life as impossible for a thrips, from either the nutritional or the behavioural aspect.

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