AN INTRODUCTION TO THE THYSANOPTERA
A SURVEY OF THE GROUP[1]

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I acknowledge with gratitude the invitation of Bruce L. Parker, Margaret Skinner and the organizers of this meeting to open the proceedings. It is a great pleasure to be asked to enthuse about a group of insects for which I have long had a particular affection - the Thysanoptera. My problem is that relatively few of the world's entomologists - less than 0.2% - appear to share this interest; it is therefore particularly gratifying to have an entire conference devoted to a thrips and to be able to meet with like-minded colleagues to focus on a serious economic problem.

I do not claim any special knowledge of pear thrips - indeed I expect many of you here to be more informed than I, but from my long experience of the biology and ecology of the order, I hope I might today provide a useful background to the group, and tomorrow highlight more specific thoughts and discussions relating to thrips and sugar maples. I believe it appropriate to open this conference with emphasis on the basic biology of the order, for without such knowledge applied work will not develop.

The recent impressive progress made by a few thysanopterists on a broad front over the last 20 years has raised the status and importance of the order from relative insignificance to one capable of providing excellent experimental techniques and material for a whole range of studies from fine structure to community structure relevant to the Insecta as a whole. Indeed, despite their small size and apparent

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[1] Adapted from the author's presidential address given to the Royal Entomological Society of London, 1987. Antenna 11:92-99.

unpopularity among entomologists, the thrips might reasonably be presented as a microcosm of progressive entomological thought in many fields. My aim is to convince you of this.

At the outset I acknowledge the generous help given by fellow thysanopterists in discussions, and particularly for providing photographs and slides without which the emphasis on "living" thrips and their habits would have been difficult.

Microtechniques, Functional Morphology and Anatomy

A major technical challenge is posed by the diminutive size of individuals; almost all the temperate Terebrantia are only 1-2 mm long and relatively few of the predominantly tropical Tubulifera exceed 10 mm. As for all insect orders, scanning electron microscopy (SEM), has transformed the appreciation of their fine structure (Fig. 1). In two recent studies, on feeding (Chisholm & Lewis 1984) and flight (Ellington 1980) using SEM on dead specimens and technically innovative cinematography on living individuals, there has been a leap forward in knowledge.

Perhaps more than any other feature, thrips are characterized by their unique mouthparts, consisting essentially of a single left mandible, paired maxillary stylets and labral pad. The static interrelationships between these structures has been clearly revealed by plasma-ashing (Thomas 1974) the mouthcone before SEM - a technique that might well be useful for examination of structures in many other orders (Chisholm & Lewis 1984). Cinematography of the mouthparts of individuals filmed as they fed in specimen chambers on clear liquid containing polystyrene marker particles, enabled rates of cibarial pumping and ingestion to be measured accurately (Chisholm & Doncaster 1982). Thrips filmed feeding on protoplasts in liquid suspension revealed how spherical chloroplasts are elongated by the suction pressure of cibarial pumping as they pass up the very narrow maxillary canal. In addition, Kirk's (1984) recent careful observations of eight species of thrips feeding on fresh pollen from 12 species of flowers have confirmed how widely exploited is this food source by the

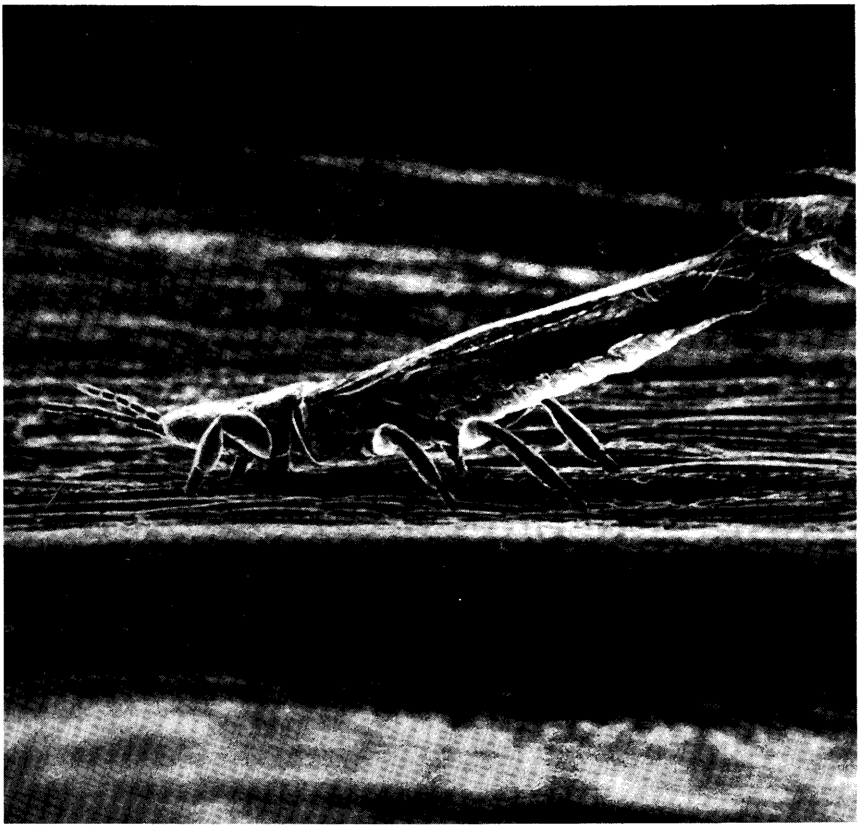

Figure 1. Cereal thrips in feeding position on leaf (photo by I. Chisholm).

order, the thrips rapidly piercing and sucking the contents of many individual grains per minute, then discarding the empty exine. Only one other insect, a ceratopogonid fly, *Atrichopogon pollinivorus*, is believed to remove the contents of individual grains rather than consume them whole (Downes 1955).

Thrips wings, too, are distinctive and pose intriguing questions about the mechanism and evolution of flight in small insects. In the Terebrantia, fore and hind wings consist of a membranous spar fringed with cilia, which when extended comprise about 80% of the wing area. The cilia on the trailing edge of *Thrips physapus* Linneaus wings are inserted into elongated, "figure of eight" sockets, whose shape and elasticity lock them into different positions at an angle to the membrane when the wings are folded or extended during flight. The extreme alignments of the cilia to the wing axis vary from 15-20° when the wings are folded along the back with cilia lying alongside the body, to 55-80° when unfolded (Ellington 1980). Ellington's elegant cine film records show that preparatory to take off the cilia are combed and locked into the extended position by abdominal flexing which draws them through combs and setae on the sides and posterior edges of several abdominal tergites. At the late stage in this process, which may be completed in 0.3-0.4 s or last up to a minute in some species, the fore and hind wings become coupled at an angle of 30° to their longitudinal axes when a hooked seta on each hind wing passes around two long setae from the posterior base of each forewing. The wings are then clapped together dorsally, the thrips raises the thorax and lifts off with a jump of the hind legs. During flight the wings clap together at the dorsal end of the cycle then fling open to begin the subsequent downstroke (Ellington et al., unpublished data). Because the hind wings lag behind the forewings in the cycle there may be a phase difference making the fling a two-stage process.

In the wider evolutionary context, one wonders why the smallest flying insects from the Thysanoptera, Coleoptera and Hymenoptera have converged on a wing design with a central membranous spar and long fringes. Ellington speculates that the enhanced circulation of air created by the fling is more persistent if a small amount of flow through the wing is possible; further study of thrips may provide answers to this broader entomological question.

In the early days of pheromonal studies, during the 1960s and 70s, various types of sternal glands in the Isoptera and Coleoptera were identified as sources of sex pheromones (Percy & Weatherston 1974). It is noteworthy, therefore, that 60 years ago (Klocke 1926) described sternal glands in male *Thrips physapus* believing they had a role in mating. More convincing evidence for the presence of a pheromone in thrips were provided by Bode (1978) who showed the ultra structure of the sternal glands of *Thrips validus* to be consistent with the likelihood of these being pheromone glands. Histochemical tests showed the secretions to consist principally of lipids with some acid mucopolysaccharides.

Another recently discovered glandular area in the dorsal region of the head of male *Merothrips* (Moritz 1984) is reminiscent, at least in position, of the alarm pheromone-producing gland in the head of soldier termites (Nasutiterminae) (Moore 1969). The ultrastructure of this gland resembles that of the abdominal sternal glands in thripid males; it has added interest because it appears to have displaced the brain completely from the head capsule into the prothorax. Its function remains unknown.

Many more excellent studies, comparable with those made on any other order, have been made on the ultrastructure of the rectal papillae, peritrophic membrane and spermatozoa by Bode (1977, 1979, 1983) and on embryogenesis by Moritz (unpublished data), but I would like to draw particular attention to an aspect of the microstructure of the chitin. Presumably such small creatures are at risk from prolonged submersion by dew or rainfall. The presence of elaborate cuticular arrays around and within many abdominal and thoracic stigma (Moritz 1985a, Palmer & Mound 1978) seem capable of trapping a film of air to produce at least local areas of plastron, permitting respiration whilst temporarily submerged. The one known species of aquatic thrips, *Organothrips bianchi* which lives in slime at the base of Taro stems, has no such arrays in its abdominal stigma, and only very simple ones in the mesothoracic stigma, but the cuticle of the II and IV abdominal segments is pale and only slightly sclerotised suggesting that cutaneous respiration supplements the more normal spiracular method.

Behavior and Ecology

I can best illustrate how thrips are contributing to the mainstream of modern ideas on behavioral ecology by reviewing a few aspects of their reproduction and the intraspecific relationships arising from it.

The Thysanoptera is the only insect order, apart from the Hymenoptera, to be entirely haplodiploid, the males being derived exclusively from unfertilized eggs (Whiting 1945, Stannard 1968). In the sub-order Terebrantia the eggs are inserted singly by the valved ovipositor into plant tissue and larvae emerge with the help of hatching spines on the embryonic cuticle over the head. Despite high population densities of adults on plants, particularly on flowers, the insects' behavior is essentially solitary showing minimal social interaction. Eggs are ignored by females after laying; individuals meet randomly for mating, then part; aggregation appears to be almost, if not entirely, a response to features of the habitat (odor, scent, moisture content) rather than to other individuals. By contrast, members of the sub-order Tubulifera have no ovipositor so lay their eggs on the surface of plants, often in clumps which may be guarded by the female or, in a few species, by both sexes. There are reported instances of such maternalism in at least seven tubuliferous species; in *Bactridothrips brevitubus*, an adult male usually, and sometimes a female, or both, sit close to the egg mass (Haga 1973). Sometimes two or more females contribute to the same egg batch which may eventually contain more than 200 eggs. Parents remate after eggs hatch and as hatching occurs sequentially instars from different parents are mixed. Other species such as *Gigantothrips elegans* guard the eggs more aggressively, the female displaying by waving her abdomen to produce a visual, or possibly olfactory, signal to deter other thrips and predators (Mani & Rao 1950).

A striking and distinctive feature of many tubuliferans is the sexual dimorphism in the size and complexity of the forelegs. The larger (oedymerous) males have massive, almost grotesque, fore-femora with pointed teeth at the tips of the fore tarsi, while smaller (gynaecoid) males, more like females, have relatively slender forelegs with less prominent teeth. Such dimorphism is most pronounced in gregarious species living in galls or under bark (Stannard 1957, Ananthakrishnan 1970) with strongly female-biased sex ratios. Furthermore in polymorphic species the large males are often wingless or short-winged and the short-winged individuals have the weaker forelegs. Crespi's (1986) patient observations on territoriality and fighting in *Haplothrips pedicularis*, a common British species living in *Stereum* shelf fungus, show vividly the use to which such strongly armoured forelegs are put. Several females contribute to communal egg masses and males fight in territorial defence of these oviposition areas, grasping and stabbing each other with their forelegs. Fights between males of similar size escalate into prolonged battles persisting for an average of 5 minutes before the loser moves away. In each combat the larger male usually wins and thereby secures 80% of the matings, taken most frequently during oviposition periods with a laying female. Smaller, subordinate males attempt "sneak" copulations and, after such, occasionally challenge the dominant males. Such fascinating behavior poses several intriguing questions in behavior ecology. Defence of oviposition sites is common among insects and often involves last male precedence. The increased rate of copulation by *H. pedicularis* males during oviposition and their success at mating last before eggs are laid, all suggest that the last male to mate before oviposition is likely to fertilize the eggs. There are as yet no data on sperm competition in thrips to confirm this but given that techniques are already developed to handle and study the ultrastructure of thrips sperm and histogenesis (Bode 1983) it should be possible to resolve this question.

Game theory models, which seek to characterize optimal fighting strategies, predict that contestants should be able to assess each others fighting ability, so the more vigorous fighter can escalate his effort (Parker 1974, Maynard Smith 1982). The substantial escalation of battles between *H. pedicularis* males of similar size and the lower frequency of challenges by small subordinates suggest that potential contestants do indeed assess their opponents size. Whether they do this visually, by the intensity of stabs or abdominal waggings, or even audibly (Hood 1950) is unknown. If the first, do fights occur in the dark situations in which many polymorphic species live? Furthermore, why do males with large forelegs tend to be wingless? Does this allow nutritional resources to be diverted towards weaponry and increased sperm production? Suffice to say that speculation on these points (Hamilton 1964, 1979) contributes to the important debate on the genetical evolution of social behavior.

Another thrips that contributes to an understanding of the interactions between intrinsic genetic and extrinsic ecological factors in the evolution of sociality is the Panamanian *Anactinothrips gustaviae* (Kiester & Strates 1984). "Colonies" of 15-75 individuals of this species occupy a permanent resting site on the bark, from which they move out on apparently well co-ordinated foraging missions, each lasting about an hour, before returning to the same site. Adults and I and II instar larvae move together in a closely knit group up the trunk of the host tree, pausing to browse among lichen patches. When the main group moves on, any stragglers scurry to rejoin it. Eventually the colony descends the trunk and returns to the original site. When moving, the adults wave their raised abdominal tips to and fro continuously. Contact is probably maintained by scent perhaps dispersed from the waving abdomen, which may be a supplementary visual signal. Insofar as the "group" behavior appears to cover care for the young, an overlap of generations, and a possibility of a division of reproductive labor between oedymerous and gynaecoid individuals, the species seems to be on the fringe of being truly social. Such diversity of complex behavior within the order was barely imagined even 20 years ago, other perhaps, than by the far-sighted J. D. Hood.

Of course, thrips have the usual wide range of interspecific interactions with other invertebrates, including many predators and hymenopterous parasites, and allantonematids causing ovarian degeneration (see Lewis 1973). Nor are thrips free from infection by pathogenic fungi. In glasshouses *Entomophthora thripidum* causes epizootics in populations of *Thrips tabaci*, infected individuals dying as the fungus breaks through the abdominal integument (Samson et al. 1979). The aquatic Taro thrips may carry as a symbiont a sessile ciliate *Propixidium moritzi*, similar to species found on the cuticle of hydrophilid beetles and water bugs (Moritz 1985b).

Some species are themselves predatory on other thrips, and particularly the eggs, instars and adults of mites, eggs of small moths and immature coccids and aleyrodids. One puzzling relationship occurs in Malaysia between the cacao thrips, *Selenothrips rubrocinctus*, a *Psilogaster* sp. (Eucharitidae) and ants. All species of this family of tropical chalcids are believed to be parasitic on the larvae and pupae of ants, and lay their eggs remote from the ant host. This species of *Psilogaster* lays 50 to 100 eggs in a circle around a single egg of a cacao thrips. When the thrips hatches, it tries to escape from the surrounding palisade of *Psilogaster* eggs, thereby stimulating some of them to hatch, and the emerging planidia attach themselves to the young thrips larva (Kirkpatrick 1957). It is not known how this behavior enables them to reach their ant host but some ants do occasionally carry larvae of cacao thrips in their jaws (Callan 1943), and this might provide an opportunity for the planidia of *Psilogaster* to transfer.

Applied Aspects

The pest status of thrips which can cause serious damage to crops in dry environments centers on their feeding and the effects this has on plant tissue. Members of both sub-orders probe vegetation with their stylets and suck sap from the pierced cells, though by a somewhat different muscular action in each sub-order (Heming 1978, Chisholm & Lewis 1984). Many tubuliferans cause galls but most pests are terebrantians, with relatively short maxillary stylets which probably penetrate not more than 60μm after a hole has been punched into the tissue by a thrust of the mandible. Radiographic studies of ingestion from artificial diets and vegetation by *Thrips tabaci* (Day & Irzykiewicz 1954) and *Limothrips cerealium* (Haliday) (Chisholm & Lewis 1984), species that normally feed respectively on di- and monocotyledonous plants, suggest that phytophagous thrips ingest 10-20% of their body weight per hour, presumably losing water by respiration and excretion at a comparable rate. The gross external effects on plants of such feeding are easily detectable and well known; silvered patches develop under areas of concentrated punctures, and damaged leaves and petals eventually become discolored, distorted and brittle, sometimes falling from the plant in hot dry weather. The external and internal microscopic effects on plants are less obvious and appreciated. SEM reveals that surface leaf wax is removed around probing sites by the adpressed labral pad and the leaf cuticle, so exposed, wrinkles due to plasmolysis of the underlying epidermal cells (Fig. 2). The holes made by the stylets in the leaf tend to be "figure-of-eight" shaped presumably to accommodate the mandible and maxillary tube.

Internally, cells lying just beneath the epidermis, are emptied of their contents by light infestations, and after feeding there is little seepage from them indicating that each cell is emptied completely before the thrips probe again. After intensive feeding over a small area, the internal cell structure becomes completely disrupted. Epidermal cells, and especially the bulliform cells likely to be involved with water conservation in cereals, shrivel; many mesophyll cells disappear completely, others retain no cytoplasm or cell contents. The direct effects of such heavy attack are desiccation and death of the plant. In Britain, there has been considerable concern recently about the appearance and spread of *Frankliniella occidentalis* in glasshouses, where ornamentals, particularly chrysanthemums, can be made unsalable by relatively light infestations.

Kirk (1987) has estimated that a single pollen feeding thrips could destroy 0.2-0.7% of a flower's pollen in a day, and extrapolation of these daily feeding rates using the numbers of thrips likely to occur on flowers and estimates of pollen production, suggest that damage to pollen by thrips may reduce the yield and fitness of some crop plants.

Figure 2. External appearance of feeding lesions. Surface leaf wax removed; "figure of eight"-shaped hole reveals point of insertion of single mandible and linked maxillary stylets (photo by I. Chisholm).

Five species of thrips have so far been identified with virtual certainty as virus vectors, the principal virus being tomato spotted wilt virus (TSWV) which produces a range of symptoms on crop plants worldwide, often causing serious losses. Tobacco ringspot virus has also been transmitted in laboratory conditions (Messiaha 1969).

Not all plant feeding by thrips is disadvantageous. In 1930 *Liothrips urichi* Karny was introduced into Fiji from Trinidad to control the weed Koster's curse (*Clidemia hirta*) (Simmonds 1933) and the thrips has provided control ever since over wide areas - not by killing the weed directly, but by inhibiting its growth so that it cannot compete with the surrounding vegetation. More recently attempts have been made to control alligator weed (*Alternanthera philoxeroides*) in Florida by *Amynothrips andersoni* imported from Argentina. The weed forms dense mats of interwoven stems that block drainage canals, impede navigation and crowd out wildlife. Feeding by the thrips produces scarred lesions along the margins of terminal leaves which curl to provide further protection for feeding thrips. There are hopes that the thrips will prove useful along with a flea beetle and phyticid stem borer (Maddox et al. 1971).

My last example of the economic impact of the order arises from the strongly thigmotactic behavior of cereal thrips, mainly *Limothrips cerealium*. Clusters of this species forming behind the glass of framed pictures are a common household nuisance in Britain and Europe, and there are even records of watches being stopped by their ingress. But the newest problem is associated with automatic fire detection systems now widely installed in hospitals, institutional homes, offices and industrial premises. When female thrips fly from drying cereals in late summer to seek hibernation sites, they are blown into buildings and in seeking crevices may find their way into smoke detectors. Many thousands of false fire alarms occur annually, especially in arable farming areas. For example, over a four-day period in July in Suffolk in 1985, insects were responsible for 70% of false alarms. As fire brigade units may charge £100 for a false turnout, the problem is clearly expensive on a national scale, as well as making the systems unreliable and thus dangerous and inconvenient to occupants of buildings. One private hospital in southeastern England claims to have had about 100 false alarms in a single summer.

Twenty-five triggered detectors examined after incidents all contained *Limothrips* with up to a maximum of about 300 individuals in a single device. Detectors that respond to optical scatter by smoke are most susceptible, and probably a single thrips in the right position will trigger some of these models, but ionization types are also at risk. Woven gauze covers, fine enough to exclude thrips also tend to exclude smoke particles, so one possible solution to the problem depends on changing the geometry of covers to prevent entry, or the internal configuration to prevent thrips triggering a sensor even if they enter it.

Resumé

The evidence presented clearly shows the immensely diverse range of entomological science at basic, technical and applied levels encapsulated in the study of the Thysanoptera. For such a small order, with only 5,000 or so named species, and one which has received relatively little attention from entomologists, this is remarkable. It is for these reasons that I suggest the thrips can be regarded as a -- "microcosm" of the Insecta, worthy of much wider study. Thysanopterists are not "beyond the fringe", and there is much beyond the "fringes!"

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Discussion Period

Comment: I have had trouble with insects getting into my smoke detector, and I put Tanglefoot inside so they couldn't crawl in. Have you considered that?

Lewis: Yes, I didn't mention solutions to the smoke detector problem. There are several possibilities. One is to put a sticky material around the outside because the thrips tend to enter the detector by climbing up the walls and crawling across the ceiling. The trouble with this solution is the detector gets very mucky after a while. Another possibility is to incorporate a repellant or a slowly vaporizing insecticide in the plastic. All of these alternatives have been investigated and in some cases incorporated. However, the best solution is to change the detector design itself so there isn't a gap that a thrips can crawl into that would set off the alarm.

Question: I'm from Pennsylvania and we've had pear thrips damage there even longer than Vermont. We have noticed an apparent direct correlation between thrips damage and the flowering of the maple trees. It seems almost cyclic in nature in relation to the flowering of the tree. Do you think there is a direct relationship between the increase in thrips populations and the flowering of the tree?

Lewis: I don't know if there is a correlation or not, but this basic question should be investigated. In the last 4 to 5 years much research has been done on pollen feeding by thrips, predominantly by one person, Dr. W. D. J. Kirk, who is now in England. He claims there could be a significant decrease in fertility of attacked plants due to aborted flowers.

Comment: Considering all the pollen grains that most plants produce, it is hard to believe that thrips can seriously affect flowering. The insect would have to be a good scavenger to deplete the entire pollen crop. However, I admit I don't know much about the fundamentals of pollen and pollen dispersal, particularly in relation to maple trees, to know whether a 10, 15, 50 or 80% reduction of pollen would be enough to make any difference in seed set.

Comment: In response to this, I've been working on western flower thrips and we have definitely found a strong correlation between the number of flowers in blossom, the number of open flowers and the number of western flower thrips. I think it is mostly the effect of dispersal. The thrips come from the coast, and move into the apples at that time.

Question: Just for clarification, one fact I remember from past literature on thrips is that they rasp the leaf tissue. Based on your presentation, this is not the case. Would you say that the past information is incorrect?

Lewis: Yes, it is. They do not rasp in the traditional sense of the word, though it depends on your definition of rasp. Rasping to me means that something is scraped. Thrips don't scrap the leaf surface, they puncture the leaf and suck the plant juices out. I brought a film that shows thrips punching a hole in the leaf, inserting the stylet and sucking out the plant fluid. You can see the liquid pulsing within the thrips head. They certainly do not rasp. This belief emanates from work on thrips by Wardle & Simpson published in 1927. Thrips feeding looked like rasping, until more sophisticated high power magnification techniques showed what was really occurring. The literature needs to be updated. Unfortunately, I propagated the myth further. When I wrote my book, I copied diagrams from Wardle & Simpson, but they were wrong.

Question: Is the appearance of the rasping-like damage due to the feeding on the embryonic tissue whereby a lot of damage on the smaller leaf parts gives the appearance of a rasping like action?

Lewis: I suppose very young plant tissue that has been fed upon by thrips, could, once expanded, develop into a hole. Aphid damage sometimes appears as holes in the leaf, not because aphids make holes but because when they feed on very young buds with delicate tissue, pierced areas eventually die resulting in a hole in the expanding leaf.

Question: Based on your feeding studies did you ever find any thrips injecting substances into the leaf tissue, or do you think it's possible, based on your previous studies?

Lewis: Yes, I think it is. Tomorrow you will see a sequence in the film on thrips feeding that suggests that saliva enters feeding punctures.

Question: At what stage in the life cycle of the thrips is it attacked by pathogenic fungi?

Lewis: I know of evidence that all stages, except eggs, can be attacked, depending on the species.