The biology of thrips is not the biology of their adults: a developmental view

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Abstract: Ontogenesis of two thrips species, *Frankliniella occidentalis* and *Suocerathrips linguis*, is described to show the wide range of biology during larval and adult phases. *F. occidentalis* feeds on more than 500 plant species in over 50 families; *S. linguis* only on two *Penicillium* species. The piercing-and-sucking mouthparts of the larval stages need powerful cibarial muscles, and displacement of the brain into the pro- and mesothoracic region is inevitable, although in adults the brain shifts again into the head capsule. During the larval period, the visceral muscle cells of the mid gut come into tight contact with the lobed salivary glands. In virus vectors this situation facilitates the entry of virus particles into the salivary glands. The duration of the second larval stage varies, thus increasing the chance of finding an optimal pupation site. Social behaviours of these two thrips species are very different, and *S. linguis* shows a typical subsocial status with parental care for developing larvae. Larval stages in this species survive only if close contact to their adults is maintained. The fungus feeding of *S. linguis* is discussed as a protection strategy against microorganisms such as *Wolbachia.* From this background diploid parthenogenesis in thrips is in reality a masked haplo-diploid parthenogenesis with *Wolbachia*-infected females.

Introduction

Larvae are a characteristic feature of all thrips life histories. But what is the evolutionary significance of larvae in this order? In most insects the pre-adult developmental instars provide the species with a means of obtaining nutrition and sometimes of dispersal (Wolpert et al., 1998). These allow a population to exploit new and different habitats or environments for feeding. From this view selection strategies are clear and understandable. But what of larval and adult thrips, that feed either on the same green plants, fungi, or on the same mosses (Mound and Palmer, 1983a). The distribution of a thrips population is strongly influenced by climatic conditions, and the individuals have more or less no control over their flight path and destination (Lewis, 1997). The important factors are those that influence flight take-off.

In recent decades, the worldwide trade in plants has led to the extensive spreading of some thrips species worldwide (Mound, 1983). *Frankliniella occidentalis* was localised in western USA until 1980 (Mound, 1997), but then quickly spread worldwide as a major pest (Kirk, this volume; Brødsgaard, 1994; Bryan and Smith, 1956; Gaum et al., 1994; Rijn et al., 1995; Wolpert et al., 1998; Yudin et al., 1986). In contrast, the monophagous *Suocerathrips linguis* (Mound and Marullo, 1994) cultivates and feeds on two *Penicilium*-species that live on the surface of *Sansevieria* leaves. This thrips is known only from England, on cultivated *Sansevieria* plants in greenhouses, although it probably originated somewhere in Africa.

These two thrips species differ widely in their behavior, ranging from non-social to subsocial. It seems that the more or less uncontrolled dispersive flight activity, and the common nutritional resources of larvae and adults matche successfully together, independent of which behavioral status they have. However, these circumstances play an important role in the co-evolution of several microorganisms, such as plant pathogens and entomopathogens. Less is known about these interactions, such as why some species become vectors of tospoviruses (German et al., 1992) but others do not, and why the first larval stage is the important phase for virus acquisition (Wetering et al., 1996). However, three years ago *Wolbachia* was discovered in two thelytokous thrips species, *Heliothrips haemorrhoidalis* and *Hercinothrips femoralis* (Pintureau et al., 1999), and last year in the predatory thrips *Franklinothrips vespiformis*

(Arakaki et al., 2001). Perhaps we must reconsider everything once again, and the conclusion might be that diploid parthenogenesis in several thrips species is only a *Wolbachia* driving arrhenotoky, as in other insects (Bourtzis et al., 1998).

Material and Methods

Insect rearing methods

The *F. occidentalis* stem culture (originally from Switzerland) was kept in a breeding room. The insects were reared on beans (*Phaseolus vulgaris*) under a temperature of 23 C " 1 K, a relative humidity of 80%, and a light regime of LD=16:8 (light on: 6.00 am). *S. linguis* was cultured on *Sansevieria trifasciata* (different cultivars) under a constant light regime of LD = 16 : 8 (light on: 6.00am), a temperature of 23 C " 1 K, and a relative humidity of 80%.

Embryonic stages

F. occidentalis: It is difficult to collect eggs of *F. occidentalis* laid in plant leaves because they are embedded in the plant tissue. Adults were kept in acrylic glass cages. After transferring thrips females to a cage, each cage was enclosed with parafilm. An agar-block was placed on the top of the parafilm. Females laid their eggs within the agar from which these eggs could be removed easily with a fine brush. *S. linguis*: Females of *S. linguis* lay their eggs at ground level on the host plant, making egg collection difficult. Therefore, young *Sansevieria trifasciata* leaves were dissected from whole plants. They were moved to plastic beakers, glued to the bottom of a beaker, and surrounded by moist cotton. About 20 adult thrips were transferred to one leaf and kept in cylindrical glass containers covered with gauze. Egg laying began after two weeks.

Postembryonic stages

F. occidentalis: All postembryonic stages were reared in chambers made from Greiner-plates with glass lids in a climatic cabinet at a temperature of 23°C, 80% relative humidity, and a light regime of LD = 16 : 8. Chambers were filled with 0.4% agar to a height of 2 to 3 mm. A bean leaf disc was placed on top of the agar on which the eggs were positioned. *S. linguis*: Larvae were kept with adults on *S. trifasciata* leaves. Leaves were glued in a plastic box containing moist absorbent cotton. The plastic box with the *S. trifasciata* leaf was placed in a glass cylinder covered with gauze.

Slide preparation

Light microscopy - whole mounting: Embryonic stages of *F. occidentalis* and *S. linguis* could be examined *in-vivo*. Once eggs were enclosed in paraffin oil, their chorion became transparent making *in-vivo* observation possible (Moritz, 1997). Larval, propupal, and pupal stages were incubated with lactic acid at a temperature of 45°C**,** dehydrated with ethanol, and embedded in canada balsam for mounting onto microscope slides. Adults were treated in AGA (60% ethanol: glycerol:acetic acid = 10:1:1), dehydrated and after transferring in isopropanol and xylene, mounted in canada balsam on microscope slides. Pictures of different depth and focus level were taken with a Coolpix 950 (Sony) connected with a zoom microscope (Leica MZ 12.5) and computerized with Automontage (Syncroscopy).

Histology

Paraffin: Carnoy (1 h, ethyl alcohol : chloroform : acetic acid = 6:3:1) was used as a fixation fluid for all developmental stages. After fixation, the samples were dehydrated in an ethanol series, gradually infiltrated with isopropanol, and embedded in paraffin. Serial sections were cut on a microtome in three different directions. Each section was 6 – 8 µm thick. For overview pictures the animal was cut medially and deparaffined with xylene, and assembled on an SEM-specimen holder.

Scanning electron microscopy

All ontogenetic stages were killed in modified Carnoy´s fluid (ethyl alcohol : chloroform : acetic acid = 3 : 1 : 1) and dehydrated in an ethanol series and finished in Hexamethyldisilazan (Nation, 1983). In special cases, animals were fixed in acetone and dehydrated with the critical point drying technique. The material was coated with a layer of gold in a Blazer sputtercoater in argon. Prepared specimens were examined with a scanning electron microscope (Hitachi SEM 2400), and the observations recorded on a digital printer or on Ilford plus-FP4 125 roll film.

Video techniques

Video recordings were made with a time-lapse recorder, respectively a Digital Handycam (Sony DCR-TRV-620E) and a 3CCD color video camera (JVC KY-F55B) in combination with a TV zoom lens (18-108 mm, F 2,5). The evaluation of the video tapes was carried out with the Observer package 3.0 (Noldus).

Results

Early embryogenesis and katatrepsis

Our knowledge of thrips embryogenesis is very poor and limited to less than 10 species. The successful culture of the phlaeothripid *Suocerathrips linguis*, and investigation of its embryogenesis, gives us some understanding of how different development can be in different thrips. In terebrantian species (*Frankliniella tenuicornis*, *Frankliniella occidentalis*, *Hercinothrips femoralis* and *Parthenothrips dracaenae*) eggs are deposited in plant material. These eggs do not move during embryonic development, although they are surrounded by degenerated and deformed plant cells, indicating some special reaction by the plant tissues. However, the embryos show a typical katatrepsis, which occurs after disruption of the amnion-serosa-membranes as the only extra-embryonic active part of these movements (Fig. 1). Normal water uptake and respiration is not essential, because eggs will develop in paraffin oil and the hatching procedure occurs after 48 hours. In contrast, the eggs of *S. linguis* lay on the plant surface, and the egg shells have typical hexagonal structures including aeropyles (Fig. 2). Isolated eggs of this species will not hatch. Video observations demonstrate that, to develop satisfactorily, the eggs of this thrips must be accompanied by adults. It seems to be important for each egg to be moved regularly. Adults of this phlaeothripine species transported the eggs to a collecting site, each egg being pushed with the adult's head, fore legs and abdomen (Fig. 3). Similar behavioural and developmental relationships between adults and eggs have not been reported for any other Phlaeothripidae. The eggs of many species in this family are found in groups, although it is not certain that they are always laid in those groups.

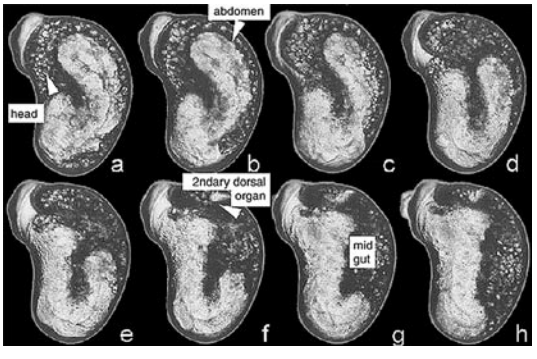

Figure 1: Katatrepsis of a terebrantian species (*Hercinothrips femoralis*) starting with amnion-serosa-fusion and rupture of the serosa. The amnion forms after katatrepsis the primary closure of the gut and the extraembryonic secondary dorsal organ fuses with the embryonic cell material of the head.

Determination procedures and the fate of cell clusters:

As in the embryonic development of most animal species, the structures that a cell may form become progressively more limited during development. When the potency of a cell cluster is restricted to its fate, the structure is said to be determined. We found paired clusters of cells in thrips embryos shortly after katatrepsis that build epidermal structures in adults. UV-light

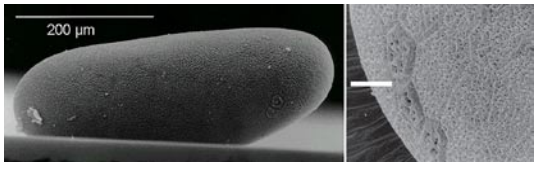

Figure 2: Egg of a tubuliferan species: *Suocerathrips linguis* with typical hexagonal structures and aeropyles.

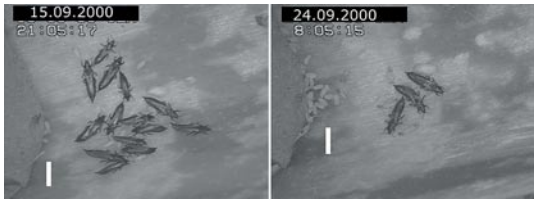

Figure 3: 7 days time-lapse record of an egg collecting point of *Suocerathrips linguis*

treatments of these cell clusters during embryonic development led to imperfect and deformed body segments in the subsequent adult stages. During larval development no aberrations are visible, thus the aberrant adult structures following destruction of embryonic cell groups prove the existence of imaginal discs. These results do not fit with our general understanding of development in hemimetabolous insects (Fig. 4).

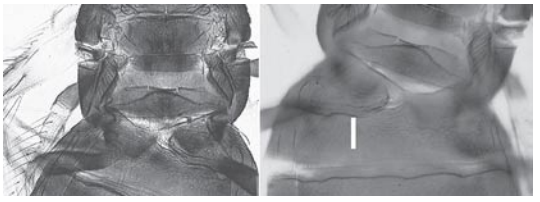

Figure 4: Aberrant first abdominal segments of *Frankliniella occidentalis* with missing imaginal discs of the right side.

The circle of life – stages of thrips development

Frankliniella occidentalis (Terebrantia): The developmental times of two different populations of Western Flower Thrips, from Halle (Germany) and Perth (West-Australia), were tested in March, September and November 1996. Eggs of both populations were collected at the same time intervals and deposited in Greiner chambers filled with agar and a disc of a bean leaf. The cultures were held under constant conditions (temperatures: 23°C ± 1K, relative humidity: 75% ± 10%; LD=16:8, 6 am light on). Genetic plasticity and variability leads to different durations of all ontogenetic stages and seems not to be important (Fig. 5). But three things are remarkable – a) the duration from egg hatching to the adult stage decreased in both populations from spring to autumn, b) the first larval stages of the Australian population moulted 10 to 20 hours later in comparison with the European population, and in a potential virus vector this could be important for plant protection strategies, and c) in general, the duration of the second larva stage has the highest standard deviation, and this presumably guarantees enough time to find a favorable

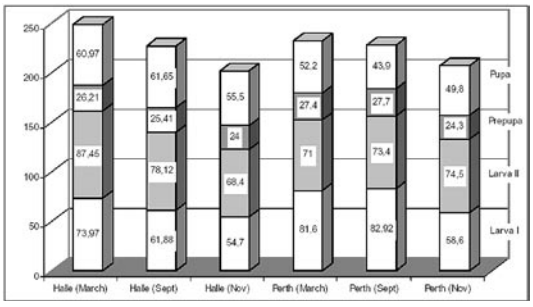

Figure 5: Life table of *Frankliniella occidentalis* populations from Halle (Germany) and Perth (Australia)

pupation site. Two further interesting phenomena are 1) the occurrence of a few second stage larvae that did not moult but survived up to 20 days, and 2) unmated females produced mostly male progeny although a few females hatched from unfertilized eggs under different temperatures.

Suocerathrips linguis (Tubulifera):
The study of the life history parameters of this species is not possible in a classical way. This species lives on *Sansevieria* plants and feeds in two fungi, described as RIV = *Penicillium* cf. *Corylophilum* Dierckx and SI = *Penicillium expansum* Link. Hatched first stage larvae were held on pieces of *Sansevieria* leaf. If such larvae were held alone, or in groups of 5 to 10, they failed to grow, and died at the latest after 5 days, with an average of 3.3 days. This abnormal mortality was not affected by varying the rearing conditions, including temperature and relative humidity, or the use of other leaves or rearing chambers. However, the abnormal mortality did not occur if the larvae were kept together with adults. Under these conditions all larval stages developed normally to adults, and the duration times of all pre-adult stages are given in Table 1. The whole duration from egg to adult emergence is about 43.5 days.

Particularly remarkable in this thrips is the variation in wing length: males with shorter wings, females with longer wings, and de-alate females with the fore and hind wings uniformly cut off (Fig. 6). After a female has survived several copulations, each followed by typical grooming and wing combing behaviour, the distal two thirds of each wing break off. These de-alate females

Egg	Larva I	Larva II	Propupa	Pupa I	Pupa II
10,8	10,5	13,2	2,3	3,5	3,2

Table 1: Developmental times of pre-imaginal stages of *Suocerathrips linguis* (in days)

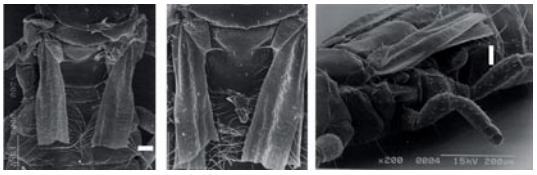

Figure 6: Fore and hind wings of mature females of *Suocerathrips linguis*

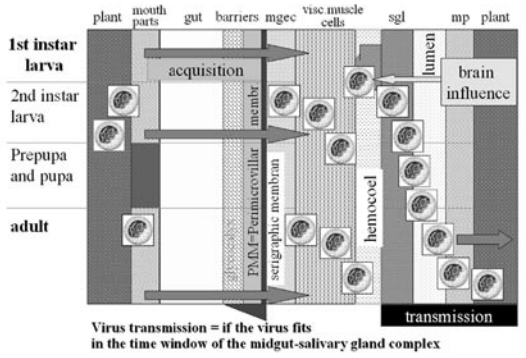

Figure 7: Virus pathways during ontogenetic development of the vector. Note the brain movement into the thorax and the tight contact between visceral muscle cells and the salivary gland (mgec = mid gut epithelial cells, visc. = visceral, sgl. = salivary gland, mp = mouth parts)

are then not available for further copulations, and become in effect a non-dispersive reproductive morph. Mound & Morris (2001) reported similar de-alation in several unrelated, domicile-creating Australian Phlaeothripidae, but this behaviour is not otherwise known amongst Thysanoptera.

Anatomy and tospovirus pathways in larval Terebrantia

In first and second instar larvae, the small head capsule contains only the large groups of cibarial muscles that operate the sucking mouthparts. The supra-oesophageal ganglion is displaced far into the pro- and mesothoracic region, the gut is filled totally with food, and the loop of the mid gut region is deeply extended into the thoracic segments. In this phase, there is tight contact between the lobed salivary glands and the visceral muscle cells of the mid gut. This complex exists only for a few hours. In later second instar larvae, with the reposition of the brain into the head, the salivary cells loose this tight contact to the muscle cells. This simple anatomical description is probably of great economic significance, because the transmission of tospoviruses to plants is limited by acquisition during thrips larval stages. The latent period of thrips becoming viruliferous is temperature dependent, and the ability of adult thrips to transmit tospoviruses decreases rapidly with the increasing age of larvae. The development of the pterothorax and the wing muscles separate the salivary glands and mid gut, and blocks further virus uptake (Fig. 7). It seems logical to conclude that virus migration through a vector is possible only if the virus is available during the time when the larval visceral muscle and salivary glands form a complex. But the tight contact between gut and muscle cells is only the base for effective virus uptake into the salivary gland, it is not the only factor. From this view, the next steps are the search for special adhesive and attractive substances that allow virus particles to pass several entry borders.

Discussion

Ontogenesis: As we can see, generalisations and interpretations of immature life stages, in the sense of a description of a generalised thrips development, are not possible. The individual ontogenetic stages have been described for some interesting or easy to culture species (Heming, 1995; Moritz, 1995), and we have a basic framework of life tables and data concerning environmental influences on thrips populations (Brødsgaard, 1994; Gaum et al., 1994; Hoddle et al., 2000; Kawai, 1990; Opit et al., 1997). However, we have no explanation for second instar larvae that live more than 20 days and do not moult, as reprted above. Again, we do not know why we have, between larval and adult stages

that share several nearly identical inner and outer structures, such a level of metamorphosis that is clearly comparable to secondary embryogenesis in holometabolous insects (Moritz, 1988b).

Two evolutionary strategies seem possible. The larvae are secondarily adapted to their host plant, or the adults are secondarily adapted to the plant on which they deposited their eggs. From the molecular (basic genetic information for punch and suck mouthparts available), physiological (reduced flight activity and difficulties of flight control (Lewis, 1997), and reduced wings due to the Reynold number (Moritz, 1989), the second strategy seems likely. Few embryological studies exist for thrips species; Tubuliferan embryogenesis has been examined by several authors (Ando and Haga, 1974; Bournier, 1966; Heming, 1979, 1980), but less is known about terebrantian species (Moritz, 1988a).

Sex control: Thrips show all three types of parthenogenesis (Lewis, 1997), and the mode of sex determination in thrips is thought to be haplodiploidy or arrhenotoky. *Parthenothrips dracaenae* is permanently thelytokous. However, males sometimes occur in very low numbers. Hymenoptera have two forms of thelytoky, revertible or microbe-associated thelytoky and non-revertible thelytoky (Stouthamer and Kazmer, 1994). In microbe-associated thelytoky, the *Wolbachia* bacterium causes parthenogenesis, and removal of these microbes by antibiotic or high-temperature treatments induces the production of males (Stouthamer and Werren, 1993). In thrips species, some indication exists for geographical differences in the occurrence of males. *Thrips tabaci* is cosmopolitan, but large numbers of males have been collected primarily in the eastern Mediterranean on its native host *Allium* (Mound, 1991). *Aptinothrips rufus* males are common in Europe, but not so in other temperate parts of the world, for example only three males were recorded from New Zealand amongst 682 females (Mound, 1982). Production of females from unfertilized *F. occidentalis* eggs occurs rarely, but initial trials indicate no temperature dependency (Kumm, 2002).

Virus acquisition and transmission: It has been known for many years that successful tospoviruses transmission is possible only if virus is acquired during larval feeding on infected plants (Amin et al., 1981; German et al., 1992; Ullman et al., 1992; Van de Wetering et al., 1996). A ligament between the mid gut and the lobed salivary glands was described in larvae of Tospovirus-vectors (Nagata et al., 1999), with the suggestion that this might be involved in virus migration. However, after sectioning several terebrantian species this ligament seems to correspond with the terminal filaments of the developing ovarioles. As in other insects with piercing-and-sucking mouthparts the head capsule is filled with powerful cibarial muscles, and this leads in all cases to a transposition of the brain into the thoracic region (Staub, 1979). As a result of these movements an effective virus pathway is available for some hours between the mid gut epithelial cells, the visceral muscle cells and the lobed salivary glands. All known investigations of virus acquisition by the early larval stages seem to fit our concept (Wijkamp et al., 1996). From this viewpoint, the longer duration of the first instar larvae in Australian *F. occidentalis* reported above is a danger to growers, because virus acquisition possibilities are increased. However, this is not the only factor in effective virus uptake and transport to the salivary gland, and the mechanisms that allow virus particles to react with and enter cell boundaries require further study (Bandla et al., 1998; Kikkert et al., 1998; Medeiros et al., 2000).

Behaviour: Thrips species show a wide variety of different behaviours, ranging from non-social to eusocial forms (Terry, 1997), although few species exhibit a eusocial lifestyle (Crespi, 1990; Kiester and Strates, 1984; Kranz et al., 2001; Kranz et al., 1999; Mound and Palmer, 1983b). In *S. linguis*, females often possess cut off wings, this resulting from copulatory bouts that sometimes last for up to 10 hours. After a few hours a fold line can be seen on the wings, indicating where this wing will subsequently fracture. Such long copulations may have the objective of avoiding or reducing sperm competition (Parker, 1970), they may prevent females from further matings (Alcock, 1994), or

they may involve removal of the sperm of rivals or reduce quantitatively the sperm of previous ejaculates. *S. linguis* is considered as subsocial, because of the dependence of the development of the larval stages on the presence of adults. The record here of *Penicillium* species as the only food source is new for thrips species. Further investigations are necessary to understand the advantages or effects of such antibacterial food. Presumably, this thrips species cannot acquire *Wolbachia*, and therefore male-killing and/or cytoplasmatic incompatibility leading to a female biased population is blocked. Possibly these fungus feeding specialists have developed a preventative strategy against bacterial infections, comparable to the male killing *Wolbachia* group?

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References

Alcock J. 1994. Post-insemination associations between males and females in insects: the mate guarding hypothesis. *Ann. Rev. Entomol*. **39**, 1-21.

Amin PW, Reddy DVR and Ghanekar AM. 1981. Transmission of tomato spotted wilt virus, causal agent of bud necrosis of peanut, by *Scirtothrips dorsalis* and *Frankliniella schultzei*. *Plant. Disease* **65**, 663-665.

Ando H and Haga K. 1974. Studies on the pleuropodia of Embioptera, Thysanoptera and Mecoptera. *Bull. Sugadaira Biol. Lab., Tokyo Univ*. **6**, 1-8.

Arakaki, N, Miyoshi T and Noda H. 2001. *Wolbachia*-mediated parthenogenesis in the predatory thrips *Franklinothrips vespiformis* (Thysanoptera: Insecta). *Proc. R. Soc. Lond*. B **268**, 1011-1016.

Bandla MD., R., C. L., E., U. D., and Sherwood JL. 1998. Interaction of tomato spotted wilt tospovirus (TSWV) glycoproteins with a thrips midgut protein, a potential cellular receptor for TSWV. *Phytopathology* **88**, 98-104.

Bournier A. 1966. L´embryogenèse de *Caudothrips buffai* Karny (Thysanoptera). *Ann. Soc. Entomol. Paris* **2**, 415-435.

Bourtzis K, Dobson SL, Braig HR and O´Neill SL. 1998. Rescuing *Wolbachia* have been overlooked. *Nature* **391**, 852-853.

Brødsgaard HF. 1994. Effect of photoperiod on the bionomics of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). *J. Appl. Entomol*. **117**, 498-507.

Bryan DE and Smith RF. 1956. The *Frankliniella occidentalis* (Pergande) complex in California (Thysanoptera: Thripidae). *Univ. Calif. Publ. Entomol*. **10**, 359-410.

Crespi BJ. 1990. Subsociality and female reproductive success in a mycophagous thrips: an observational and experimental analysis. *J. Insect Behaviour* **3**, 61-74.

Gaum WG, Giliomee JH and Pringle KL. 1994. Life history and life tables of western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), on english cucumbers. *Bull. Entomol. Res*. **84**, 219-224.

German TL, Ullman DE and Moyer JW. 1992. Tospoviruses: diagnosis, molecular biology, phylogeny, and vector relationships. *Ann. Rev. Phytopathol*. **30**, 315-348.

Heming BS. 1979. Origin and Fate of Germ Cells in Male and Female Embryos of *Haplothrips verbasci* (Osborn) (Insecta, Thysanoptera, Phlaeothripidae). *J. Morph*. **160**, 323-344.

Heming BS. 1980. Development of the mouthparts in embryos of *Haplothrips verbasci* (Osborn) (Insecta, Thysanoptera, Phlaeothripidae). *J. Morph*. **164**, 235-263.

Heming BS. 1995. History of the germ line in male and female thrips, pp. 505-535. In B. L. Parker, M. Skinner, and T. Lewis (Eds): *Thrips Biology and Management*, NATO ASI Series, Series A, Life sciences, New York and London.

Hoddle MS, Robinson L, Drescher K and Jones J. 2000. Developmental and reproductive biology of a predatory *Franklinothrips* n. spec. (Thysanoptera: Aeolothripidae). *Biol. Control* **18**, 27-38.

Kawai A. 1990. Life cycle and population dynamics of *Thrips palmi* KARNY. *JARQ* **23**, 282-288.

Kiester AR and Strates E. 1984. Social behaviour in a thrips from Panama. *J. Nat. Hist*. **18**, 303-314.

Kikkert M, Meurs C, van de Wetering F, Dorfmüller S, Peters D, Kormelink R and Goldbach R. 1998. Binding of tomato spotted wilt virus to a 94-kDa thrips protein. Phytopathology 88:63-69. *Virology* **88**, 63-69.

Kranz BD, Chapman TW, Crespi BJ and Schwarz MP. 2001. Social biology and sex ratios in the gall-inducing thrips, *Oncothrips waterhousei* and *Oncothrips habrus*. *Insectes soc*. **48**, 315-323.

Kranz BD, Schwarz MP, Mound LA and Crespi BJ. 1999. Social biology and sex ratios of the eusocial gall-inducing thrips *Kladothrips hamiltoni*. *Ecological Entomol*. **24**, 432-442.

Kumm S. 2002. Reproduction, progenesis, and embryogenesis of thrips (Thysanoptera, Insecta), pp. 140: Developmental Biology, University of Halle-Wittenberg, Halle.

Lewis T. 1997. *Thrips as crop pests*. CAB International Oxon, New York.

Medeiros RB, Ullman DE, Sherwood JL and German TL. 2000. Immunoprecipitation of a 50-kDa protein: a candidat receptor component for tomato spotted wilt tospovirus (Bunyaviridae) in its main vector, *Frankliniella occidentalis*. *Virus Research* **67**, 109-118.

Moritz G. 1988a. The ontogenesis of Thysanoptera (Insecta) with special reference to the Panchaetothripine *Hercinothrips femoralis* (O. M. Reuter, 1891) (Thysanoptera, Thripidae, Panchaetothripinae) I. Embryongenesis. *Zool. Jb. Anat*. **117**, 1-64.

Moritz G. 1988b. The ontogenesis of Thysanoptera (Insecta) with special reference to the Panchaetothripine *Hercinothrips femoralis* (O. M. Reuter, 1891) (Thysanoptera, Thripidae, Panchaetothripinae) III. Praepupa and Pupa. *Zool. Jb. Anat*. **118**, 15-54.

Moritz G. 1989. Zur Morphogenese des Flugapparates von *Hercinothrips femoralis* (O. M. REUTER, 1891) (Thysanoptera, Insecta). Verhandlungen des XI internationalen Symposiums fur die Entomofaunistik Mitteleuropas (SIEEC), pp. 374-378.

Moritz G. 1995. Morphogenetic Development of some species of the order Thysanoptera (Insecta), pp. 489-504. In B. L. Parker, M. Skinner, and T. Lewis (Eds): *Thrips biology and management*, Plenum Press & NATO Scientific Affairs Division, New York, London.

Moritz G. 1997. Structure, growth and development, pp. 15-63. In T. Lewis (Ed.): *Thrips as crop pests*, CAB International, Wallingford, Oxon.

Mound LA. 1982. Terebrantia (Insecta: Thysanoptera). *Fauna of New Zealand* **1**, 1-113.

Mound LA. 1983. Natural and disrupted patterns of geographical distribution in Thysanoptera (Insecta). *J. Biogeogr*. **10**, 119-133.

Mound LA. 1991. Patterns of sexuality in Thysanoptera. The 1991 conference on thrips (Thysanoptera): Insect and disease considerations in sugar maple management., pp. 2-14.

Mound LA. 1997. Biological Diversity. In T. Lewis (Ed.): *Thrips as crop pests*, CAB International. Oxon, New York.

Mound LA and Marullo R. 1994. New thrips on mother-in-laws tongue. *Entomologist's Monthly Magazine* **130**, 95-98.

Mound LA and Morris DC. 2001. Domicile constructing phlaeothripine Thysanoptera from *Acacia* phyllodes in Australia: *Dunatothrips* Moulton and *Sartrithrips* gen.n., with a key to associated genera. *Systematic Entomology* **26**, 401-419.

Mound LA and Palmer JM. 1983a. The generic and tribal classification of spore-feeding Thysanoptera (Phlaeothripidae: Idolothripina). *Bull. Brit. Mus. (Nat. Hist.) Entomology* **46**, 1-174.

Mound LA and Palmer JM. 1983b. Spore-feeding Thysanoptera of the genus *Anactinothrips* with a new sub-social species from Panama. *J. Nat. Hist*. **17**, 789-797.

Nagata T, Inoue-Nagata AK, Smid HM, R., G., and Peters D. 1999. Tissue tropism related to vector competence of *Frankliniella occidentalis* for tomato spotted wilt tospovirus. *J. General Virology* **80**, 507-515.

Nation JL. 1983. A new method using Hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. *Stain Technol*. **58**, 347-351.

Opit GP, Peterson B, Gillespie DR and Costello RA. 1997. The life cycle and management of *Echinothrips americanus*. *J. Entomol. Soc. brit. Col*. **94**, 3-6.

Parker GA. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev*. **45**, 525-567.

Pintureau B, Lassabliere F, Khatchadourian C and Daumal J. 1999. Parasitoides oophages et symbiotes de deux *Thrips* European. *Ann. Soc. Entomol. Fr*. **35**, 416-420.

Rijn PCJ, Mollema C and Steenhuis-Broers GM. 1995. Comparative life history studies of *Frankliniella occidentalis* and *Thrips tabaci* (Thysanoptera: Thripidae) on cucumber. *Bull. Entomol. Res*. **85**, 285-297.

Staub RF. 1979. Die postembryonale Entwicklung des Nervensystems von *Parthenothrips dracaenae* Heeger (Thys., Terebrantia). *Revue Suisse de Zool*. **86**, 367-394.

Stouthamer R and Kazmer DJ. 1994. Cytogenetics of microbe-associated parthenogenesis and its consequences for gene flow in *Trichogramma* wasps. *Heredity* **73**, 317-327.

Stouthamer R and Werren JH. 1993. Microbes associated with parthenogenesis in wasps of the genus *Trichogramma*. *J. Invert. Pathol*. **61**, 6-9.

Terry I. 1997. Host selection, communication and reproductive behaviour. In T. Lewis (Ed.): *Thrips as crop pests*, CAB International. Oxon, New York.

Ullman DE, Cho JJ, Mau RFL, Hunter WB, Westcot DM and Custer DM. 1992. Thrips-tomato spotted wilt virus interactions: Morphological, Behavioral and cellular components influencing thrips transmission, pp. 195-240. In K. F. Harris (Ed.): *Advances in disease vector research*, Springer-Verlag, New York.

van de Wetering E, Goldbach R and Peters D. 1996. Tomato spotted wilt tospovirus ingestion by first instar larvae of *Frankliniella occidenlalis* is a prerequisite for transmission. *Phytopathology* **86**, 900-905.

Wijkamp I, van de Wetering E, Goldbach R and Peters D. 1996. Transmission of tomato spotted wilt virus by *Frankliniella occidentalis*; median acquisition and inoculation access period. *Ann. appl. Biol*. **129**, 303-313.

Wolpert L, Beddington R, Brockes J, Jessell T, Lawrence P and Meyerowitz E. 1998. *Principles of development*. Oxford University Press. Oxford, New York, Tokyo.

Yudin LS, Cho JJ and Mitchell WC. 1986. Host range of western flower thrips, *Frankliniella occidentalis* (Thysanoptera, Thripidae), with special reference to *Leucaena glauca*. *Env. Entomol*. **15**, 1292-1295.