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Biological control of thrips pests

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Introduction

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Frankliniella occidentalis and other thrips harmful to vegetable and ornamental crops in Europe

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Predators of *Frankliniella occidentalis* and *Thrips tabaci*

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Introduction

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During the last decade thrips pests have become key pests in many cultivated crops throughout Europe and elsewhere in the world. Untill the early eighties *Thrips tabaci* Lind. was the most prevalent thrips pest, but caused problems only occasionally. Since its accidental introduction in 1983, western flower thrips (*Frankliniella occidentalis* (Pergande) became the number one key pest in European greenhouses. In the late eighties it invaded vegetables and ornamentals grown in plastic tunnels and the field as well as fruit trees in the Mediterranean area of Europe. To control thrips pest outbreaks, growers were forced to apply chemical treatments intensively, thus upsetting commercially successful greenhouse IPM programmes. By then no adequate method for biological control of thrips was available. Research on predatory mites of thrips had not yet resulted in a satisfactory solution and studies with predatory bugs were still in an experimental phase.

In 1990 a research project was initiated between the Department of Entomology of the Wageningen Agricultural University (The Netherlands) with IRTA Cabrils (Spain) and University of Bologna/Bioloab Cesena (Italy), to enhance the development of biological control programmes for thrips pests. The project is financially supported by the Commission of the European Communities, Directorate General VI, within the CAMAR programme. The overall general scientific objective of the project is to collect, evaluate, massproduce and commercial apply natural enemies of thrips pests, especially western flower thrips, *F. occidentalis*. To reach the goals of the project, a detailed plan of work was conducted:

1. evaluation of literature information on thrips pests and the control capacity of natural enemies already known;
2. performing a field survey for native natural enemies in Europe and collection of parasitoids (worldwide);
3. development of a (laboratory) rearing method for thrips and its enemies; evaluation of new natural enemies of thrips in laboratory experiments;
4. evaluation of natural enemies selected in the third step in experimental greenhouses;
5. testing of natural enemies in commercial greenhouses and field;
6. assist in development of a mass production and distribution methods and the design of advisory material.

Tasks were divided among the participants: Italy concentrated on the evaluation of

Orius species, Spain on a study of native predators and Wageningen on parasitoids of thrips. Criteria developed earlier in Wageningen were used as parameters for pre-introduction selection.

This paper first gives an extensive overview of *Frankliniella occidentalis* and other thrips harmful to vegetable and ornamental crops in Europe, then provides information about the predators of *Frankliniella occidentalis* and *Thrips tabaci*, and finally summarizes the present state of affairs on thrips parasitoids, in particular their potential towards controlling *F. occidentalis*.

Frankliniella occidentalis and other thrips harmful to vegetable and ornamental crops in Europe

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Contents

Abstract

In this review the status of the thrips pest species in Europe and in particular of *Frankliniella occidentalis* (Western Flower Thrips), the most important pest thrips in Europe nowadays, is reported based on literature information up to December 1992. Different genera are mentioned amongst the Terebrantia suborder and of the Thripidae family: *Thrips*, *Taeniothrips*, *Heliothrips*, *Parthenothrips*, *Hercinothrips* and two genera of the sub-order Tubulifera, family Phlaeothripidae: *Liothrips* and *Haplothrips*. Some information regarding the biology, distribution and host plants (bionomics) is summarized. In general the damage induced by thrips, in relation to the different parts of the plant attacked, is discussed. The indirect damage like transmission of viruses, bacteria and fungi is described too. Regarding *F. occidentalis*, also systematic notes and an accurate study of the biology, its distribution in Europe, of the plants damaged worldwide and in Europe in particular, are represented. The typical damages induced by Western Flower Thrips on different crops are discussed. A short presentation of methods of sampling is indicated.

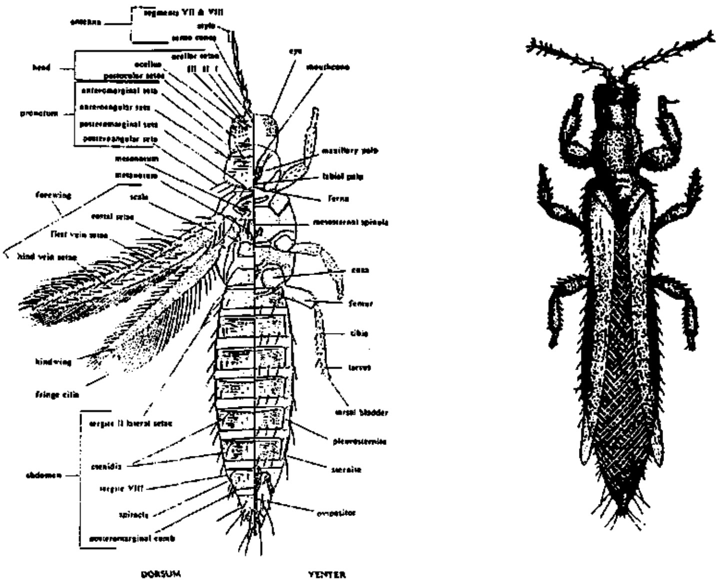
1. Introduction

Thrips is the common name given to insects of the order of Thysanoptera (*thusanos*, a fringe; *pteron*, a wing). The order includes over 5,000 species, most of which are small in dimension and slender in body (in temperate regions the length generally ranges from 1-2.5 mm) with a distinct head (Palmer et al., 1989). Morphology of the mouthparts differs from one family to another but feeding behaviour is generally similar, being characterized by rasping, puncturing and sucking (Borden, 1915). One oddity of the behaviour of some thrips species is that occasionally they can attack man by piercing the skin (Bailey, 1936). The front and hind wings are very slender, featuring a wide fringe of hairs and only a few veins or none at all. Wing length varies according to group, species and sex; macropterous, brachypterous and sometimes apterous adults can all be encountered. In the sub-order of Terebrantia the wings lie parallel to each other while in the Tubulifera sub-order they are overlapping so that only one is completely visible (Figure 1). The mouthparts of these insects are typically asymmetrical, presenting maxillary and labial palps (Mound, 1971). The antennae are short and usually comprise from six to nine segments. The eyes are compound and three ocelli are present on the top of the head. The legs feature single- or double-segmented tarsi ending in a vesicle (or bladder).

The abdomen is divided into eleven segments but only ten are visible. The end segments of Terebrantia usually taper to a cone in females and are bluntly rounded-off in males, whereas in both sexes of Tubulifera the tenth segment forms a tube ending in a terminal whorl of setae. Details of the structure of external genitalia have been described by Melis (1935), Doeksen (1941), Jones (1954) and Priesner (1964). Terebrantia feature a more marked sexual dimorphism than Tubulifera, with males being smaller and of paler colour.

Thrips reproduction is either partially or totally parthenogenetic. Either way, the various species are all either arrhenotokous or thelitokous and, according to most authors, females are always diploid and males haploid (Lewis, 1973). As in all typically bisexual species, adults usually mate within two or three days after the last pupal moult, each male being capable of fertilizing more than one female. The sexes locate each other by means of a sensory cone situated at the top of the antennae. Most thrips are oviparous. The white or yellowish coloured eggs are cylindrical and bean shaped and large with respect to the size of the female body. The eggs of Tubulifera are larger than those of Terebrantia, each sub-order also featuring a different egg-laying behaviour. While the Terebrantia, either zoophagous or phytophagous species, insert isolated eggs into the plant tissue by means of an ovipositor, the Tubulifera species, which have no saw-like ovipositor, generally attach the eggs onto plant surfaces by means of gelatinous substances. Egg mortality is usually greater in Tubulifera than in Terebrantia.

Sub order TEREBRANTIA



Sub order TUBULIFERA

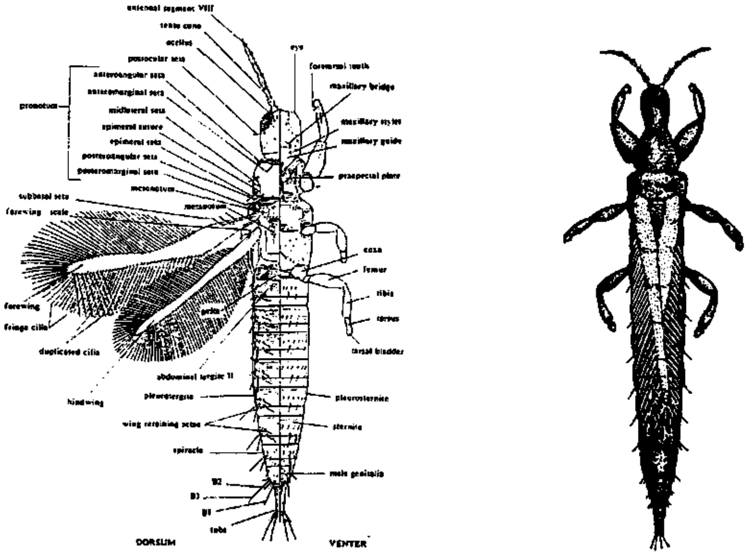


Figure 1: Living (right-hand side) and mounted (left-hand side thrips of the two sub-orders compared (from Lewis, 1973 and Palmer et al., 1989).

There are four or five instars between egg and adult; generally four in Terebrantia and five in Tubulifera, as shown in Figures 2 and 3. Usually, the first two feeding instars are called larvae and the subsequent, non-feeding ones, pupae. There are various objections to the use of this terminology to describe the growth of these insects, as some aspects of the development of thrips resemble more that of hemimetabolous insects (i.e. exopterygote), whose young are called nymphs, rather than that of holometabolous ones, (i.e. endopterygote), whose young are called larvae. Nevertheless, the term larvae is generally used and has therefore become well established, so adoption of a new term runs the risk of generating more confusion (Lewis, 1973). The subsequent stages of development are: egg, larvae I, larvae II, prepupa, pupa I, pupa II (only for Tubulifera) and adult. It should be noted that in French the developmental instars are indicated as *I stade larvaire*, *II stade larvaire*, *pronymphe*, *nymphe* and *adulte* (Bournier, 1983), in Italian: *neanide I*, *neanide II*, *prepupa* or *preninfa*, *pupa* or *ninfa*, *adulto* (Grandi, 1951), in Spanish: *larva I*, *larva II*, *proninfa*, *ninfa* and *adulto* (Lacasa, 1990).

Pupation normally takes place in the soil or under fallen and decayed plant tissues near host-plants, within which the insect usually builds a pupal cell, while several Terebrantia species dwell in leaves.

The life history of the reported species is summarized in chapter 2.

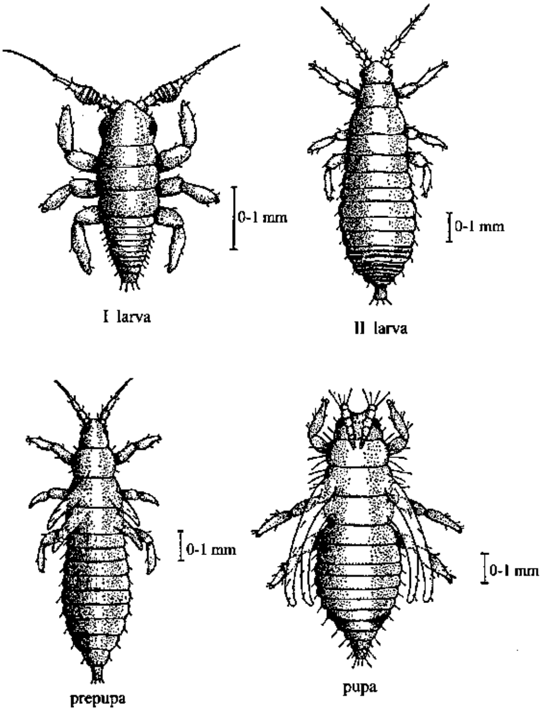


Figure 2: Immature stages of the bean thrips (*Caliothrips fasciatus* Perg.), a typical Terebrantia (from Lewis, 1973).

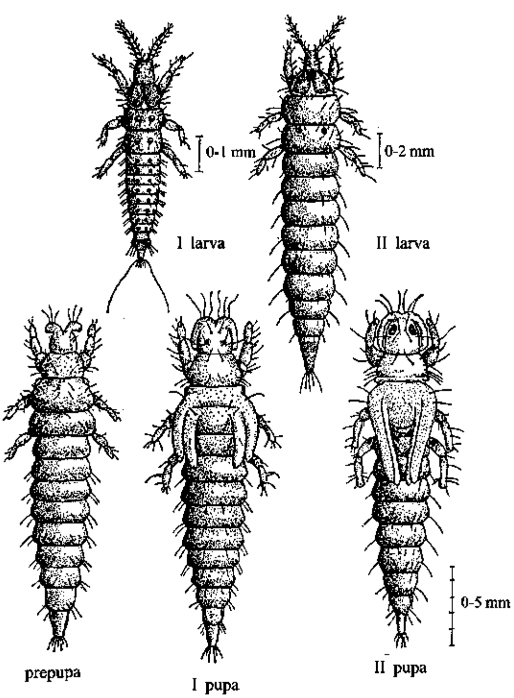
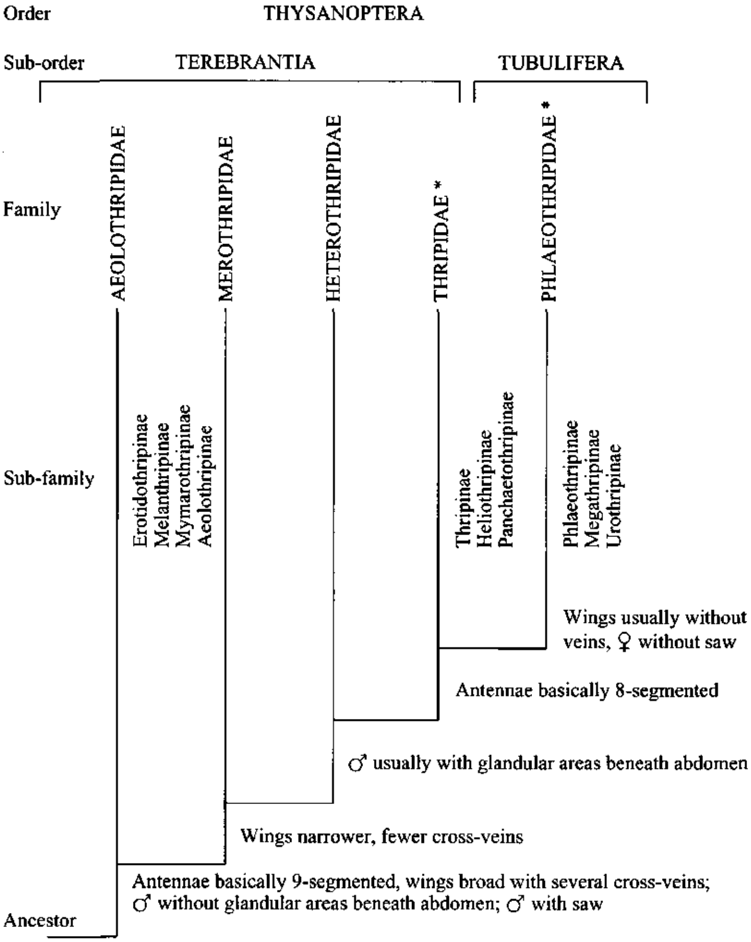


Figure 3: Immature stages of *Haplothrips leucanthemi* (Schrank) = *niger* (Osborne), a typical Tubulifera (from Lewis, 1973).

2. Thrips pest species in Europe

As stated above, the Thysanoptera order includes over 5,000 species. The order is subdivided into two sub-orders, namely Tubulifera, which only includes a single family (Phlaeothripidae) and Terebrantia, which comprises four families (Aeolothripidae, Thripidae, Merothripidae and Heterothripidae) (see Table 1) (Lewis, 1973).

Table 1: Summarized classification of the order Thysanoptera based on Priesner (1964), with the main characteristics of families and affinities of sub-families (from Lewis, 1973; Palmer et al., 1989); *: Family which includes some thrips species encountered in protected crops.



Most crop damaging Thysanoptera belong to the family Thripidae of the sub-order Terebrantia. These include, for example, *Frankliniella occidentalis* (Perg.), *Thrips tabaci* Lind., *Heliothrips haemorrhoidalis* (Bouché), *Parthenothrips dracaenae* (Heeger), *Thrips simplex* Morison, *Thrips meridionalis* Pr., *Taeniothrips dianthi* Pr., *Thrips fuscipennis* Haliday, *Hercinothrips femoralis* (Reuter) and *Thrips palmi* Karny. Amongst the most common phytophagous thrips harmful to vegetable and ornamental crops, only *Haplothrips cottei* (Vuillet) and *Liothrips vaneeckei* Pr. belong to the Phlaeothripidae family of the Tubulifera sub-order. In particular, with regards ornamental crops, *Thrips calcaratus* Uzel, *Dendrothrips ornatus* (Jabl.), *Gynaikothrips ficorum* (Marchal) and *Thrips laricivorus* (Kratochvil and Farsky) should be noted for the damage they cause to lime, laurel, *Ficus microcarpa* L. and larch, respectively.

2.1 *Frankliniella occidentalis* (Pergande) (Terebrantia, Thripidae, Thripinae)

2.1.1 Systematic notes

The bibliography of *F. occidentalis* was reviewed by Mantel (1989) and covers all the references, supplied with keywords, until September 1st, 1988. Integration of this survey regarding this chapter are taken from Brødsgaard (1989a).

The *Frankliniella* genus was described by Karny in 1910. It had initially been classified as *Thrips* by Linnaeus in 1758. In 1881, Targioni-Tozzetti introduced the name *Euthrips* and in 1895 Uzel called the genus *Physopus*, until its current name, which is still generally accepted (Bryan and Smith, 1956), was established by Karny (1912). Synonyms which have been employed over the years for *Frankliniella occidentalis* include, as reported by Oliver and Baker (1987):

Euthrips occidentalis Pergande, 1895
Euthrips tritici Crawford, 1909
Euthrips tritici var. *californicus* Moulton, 1911
Euthrips helianthi Karny, 1912
Frankliniella helianthi Karny, 1912
Frankliniella tritici var. *moultoni* Hood, 1914
Frankliniella tritici occidentalis Watson, 1919
Frankliniella tritici californica Watson,1923
Frankliniella moultoni Morgan, 1925
Frankliniella claripennis Morgan, 1925
Frankliniella canadensis Morgan, 1925
Frankliniella trehernei Morgan, 1925
Frankliniella californicus Moulton, 1929
Frankliniella californica Moulton, 1931
Frankliniella venusta Moulton, 1936
Frankliniella obscura Moulton, 1936
Frankliniella chrysanthemy Kurosawa, 1941
Frankliniella californica f. *trehernei* Moulton, 1948
Frankliniella dahliae Moulton, 1948

In the U.S.A., *F. occidentalis* is commonly called 'Western Flower Thrips'

(WFT) and 'alfa-alfa thrips', but the latter name was not approved by the Entomological Society of America.

2.1.2 Origin and Distribution

F. occidentalis is a species of nearctic origin, first reported by Pergande (1895) in California on apricot and potato leaves, on orange flowers and various weeds. It was subsequently reported in Florida on mango and bean crops (Morgan, 1913; Watson, 1918), and on citrus flowers recently (Childers and Beshear, 1992), Canada (Treherne, 1923), Utah (Pack, 1930), Alaska (Bryan and Smith, 1956), Hawaii (Sakimura, 1972) and in Texas (Stewart, 1985) and can currently be found throughout the United States (Beshear, 1983; Frantz and Mellinger, 1990).

Elsewhere, it has been encountered in New Zealand (Zur Strassen, 1973; Mound and Walker, 1982), Korea (Woo, 1974), Peru (Ortiz, 1977), Colombia and Costa Rica (Baker, 1988), South Africa (Giliomee, 1989), Japan (Barletta, 1986; Anonymous, 1989b) as well as Israel, where it has been detected since mid-1987 (Argaman et al., 1989; Gokkes, 1991), recently it was found in Australia too (Goodwin, pers.comm.).

In Europe its first appearance dates back to 1983, when it was found in *Saintpaulia ionantha* Wendl. nurseries in the Netherlands (Van de Vrie, 1987; Mantel and Van de Vrie, 1988; Vierbergen and Ulenberg, 1988). Since its initial detection in Europe, it has spread rapidly to protected crops throughout the continent (Figure 4). It has been found in Sweden (Pettersson, 1986; Nedstam, 1987), in Norway (Taerum, 1988), in Finland in August 1987 (Brax and Lindqvist, 1989; Tiitanen and Markkula, 1989; Kurppa, 1989), in Germany in 1985 (Zur Strassen, 1986) and in the United Kingdom (Anonymous, 1986). In the United Kingdom it is no longer considered as a new pest to be absolutely eradicated, as it has definitely established itself in protected agroecosystems (Bartlett, 1991). Other European countries in which *F. occidentalis* is found, include Ireland (Dunne and O'Connor, 1989); France (Bournier and Bournier, 1987), where it has also been detected in open fields by Fougeroux (1988), as well as Belgium since 1987 (De Clercq, 1991) and Poland since 1987 (Labanowski, 1991), Denmark since 1985 (Brødsgaard, 1989a), Spain (Lacasa et al., 1988; 1990), Portugal since 1989 (Leite, 1990) Switzerland since mid-1987 (Anonymous, 1989b; Ebener et al., 1989), Hungary since 1989 (Jenser and Tusnadi, 1989; Szabo and Ceglarska-Hodi, 1991) and in Greece in 1991 (Podikakis, pers. comm.). Finally, it has also been reported by Postolovski (pers. comm.) in ex-Yugoslavia in 1991.

It was first reported in Italy by Rampinini in 1987, when it was detected in nursery-grown *Saintpaulia* in northern Italy. In 1988, moreover, some specimens of *F. occidentalis* were also found in Sicily, Sardinia, Calabria, Apulia, Latium and Campania on several nursery and field-grown vegetable crops as well as on protected ornamental crops (Ciampolini et al., 1990). Reports have also come in from Tuscany, Liguria and South Italy where the pest has been detected on nursery and open field chrysanthemum, carnation and strawberry crops (Arzone et al., 1989; Del Bene and Gargani, 1989; Marullo, 1991), and from Sardinia (Luciano and Piga, 1988-92). *F. occidentalis* can currently be found in the Venetia and Emilia-

Figure 4: Distribution *Frankliniella occidentalis* in Europe.

Romagna regions as well, so that it can be considered to be present Italy-wide. Although it preferentially attacks protected crops, the pest can also be found on open field vegetable and ornamental crops.

2.1.3 Morphology and biology

F. occidentalis identification can be made by applying the following morphological keys developed by Moulton (1948), Mound and Walker (1982), Zur Strassen (1986), Bournier and Bournier (1987) and Palmer et al. (1989).

Lengthwise, the macropterous adult of *F. occidentalis* is characterized by the following measurements: 0.9-1.1 mm from the tip of the antennae to the tip of the abdomen in the male and 1.3-1.4 mm in the female. Keys useful for its identification are given in Figure 5 (Brødsgaard, 1989a). Both the young instars and the adult possess piercing and sucking mouthparts. The thrips feed by piercing leaf cells with the mandible and ingesting cell contents through the feeding tube formed by the maxillary stylets.

As in all Terebrantia thrips, the female of *F. occidentalis* features a saw-like ovipositor with which it drills holes into the parenchymal tissues of leaves, flowers and fruits, where it deposits a kidney-shaped opaque egg of 0.25 x 0.50 mm in size (Brødsgaard, 1989a). Three different colour forms of the polymorphic species *F. occidentalis* can be found in California (Bryan and Smith, 1956; Sakimura, 1962), one being black, one being pale and the other featuring an intermediate colour. The first two forms have a homozygous genotype while the third form has a heterozygous genotype. Only the females, which are diploid, feature all three of the possible chromatic phenotypes while the males, which are haploid, feature only the pale colour. Bryan and Smith (1956) have demonstrated that this colour diversification is independent of host-plant variety but it is rather related to seasonal factors. Most of the darker varieties were found in California in spring, while the paler ones were found in summer and autumn. The third type, featuring an intermediate colour, was found throughout the whole year. The authors concluded that perhaps the darker variety was more resistant to low temperatures while the paler one to high temperatures. In northern Europe (Germany and The Netherlands) and in Italy, only the pale and intermediate colour types have been found except for a single case of the darker variety discovered in Denmark (Brødsgaard, 1989a).

F. occidentalis post-embryonic development involves two larval instars, as well as prepupa and pupa stages before the adult stage. The newly moulted larva is characterized by a glassy white colour and starts feeding immediately, becoming yellowish. As with all exopterigotes, the young instar is similar to the adult one in appearance except for the fact that it is wingless and that it exhibits reddish eyes and antennae which present fewer segments. Second instar larvae are more active than first instar larvae and feed more abundantly, up to three times more than during the first instar. The young second instar larvae is smaller than first instar but develop into adult size upon reaching maturity. During this stage, they take on a yellowish-waxy colour.

Upon maturity, the larvae display positive geotaxis together with negative phototaxis, moving away from the flower or the plant towards the soil (Arzone et al.,

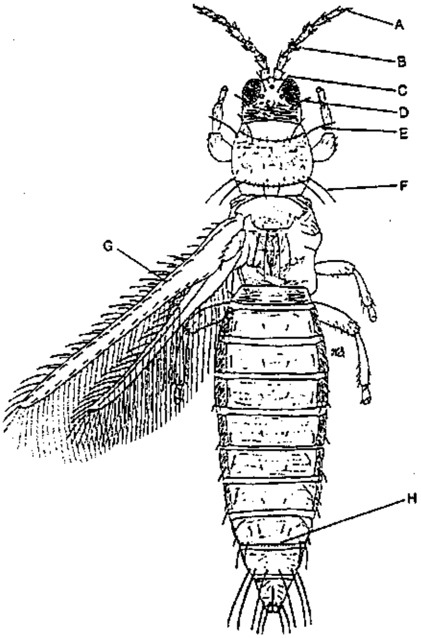


Figure 5: *Frankliniella occidentalis* female. Dorsal aspect, right wing pair not drawn, some key characters (from Brødsgaard, 1989a):

A. Antennae 8-segmented
B. Forked trichomes on antennal segments III and IV
C. Interocellar setae III long and at the margin of the ocellar triangle
D. Postocular setae long
E. Anteroangular and one pair of anteromarginal setae long
F. Posteroangular and one pair of posteromarginal setae long
G. Forewing with complete row of setae (16-20) on first vein
H. Tergite VIII with complete comb on posterior margin (only females).

1989). At a depth of between 1.5-2.0 cm, the larvae then develop into the prepupal stage (Arzone et al., 1989). The prepupa already features wing buds and antennae which, however, are shorter than in adult and unsegmented. Prepupae have a whitish colour and are immobile unless disturbed. Upon developing into a pupa, the insect still remains under the soil surface, and features longer antennae which face backwards towards the abdomen. Initial segmentation of the antennae is already evident at this stage and the wing buds have also developed further. Pupae continue to remain immobile and do not feed. Adult dimensions are achieved by the end of the pupal stage. The adult emerges upon the last moult and features a whitish colour which becomes progressively darker within 48 hours of moulting (Brødsgaard, 1989a; Del Bene and Gargani, 1989). Shortly after having emerged, the insect begins feeding voraciously. Adults can fly only 24 hours after emergence (Del Bene and Gargani, 1989).

The duration of development from egg to adult is closely related to environmental conditions, especially temperature. Table 2a presents the data concerning this relationship collected by several authors under different conditions. In particular, the table shows findings as to insect development time as well as female fertility, which also seems to differ depending on climatic conditions and host-plant variety. The development time of WFT on cucumber, at 25°C is longer (13.4 days, from egg to adult) (Mollema et al., 1990) than on Chrysantemum at the same temperature (12.2 day) (Del Bene and Gargani, 1989). Photoperiod influence was investigated by Brødsgaard (1991), little differences in the development time, in longevity and fertility of WFT were detected at constant temperature of 25°C and high air humidity (near 100%), as showed in Table 2b. According to Lublinkhof and Foster

Table 2a: Biological traits of *F. occidentalis* at different temperatures and hostplants

Temperature (°C)	Host plant	Eggs (days)	1st larval stage (days)	2nd larval stage (days)	Prepupa (days)	Pupal stage (days)	Youth stages . total no (days)	Imago (days)	Preoviposition (days)	Oviposition (days)	Fecundity no. eggs offspring	Source
12	Pepper	2-14	1-4	4-8	1-5	1-4	20	-	–	–	– –	Lacasa, 1990
15	Radish	13	7	12	4.2	8	44	90	3	30	40	Bryan and Smith, 1956
15	Bean	11.18	4.9	9.08	2.9	5.6	33.7	70.8	10.4	60	24.2	Lublinkhof and Foster, 1977
15	Chrysanthemum	10	5.6	11.5	3.6	8.6	39.1	46	6.4	–	50	Robb, 1989
16.7	Chrysanthemum	3	2	4	2	3	14	45	–	–	300	Robb and Parella, 1987
20	Radish	6	3.3	5.7	2	4.8	21.8	40	3	0	65	Bryan and Smith, 1956
20	Bean	6.37	2.33	5.22	2.2	2.9	19	56.8	2.4	54	95.5	Lublinkhof and Foster, 1977
20	Chrysanthemum	6.6	2.9	9.5	2.2	5.1	26.1	75	2.1	–	26	Robb, 1989
25	Chrysanthemum	3.2	1.7	4.8	1.1	2.7	12.9	31.	1.7	–	136	Robb, 1989
25	Chrysanthemum	5	3	2-3	1-2	3-4	14-17	15	3	12	100	Arzone et al., 1989
25	Chrysanthemum	2	2.1	4.4	1.7	2	12.2	30	3	25	30-40	Del Bene and Gargani, 1989
25	Pepper	3.2	2.4	4.9	1.8	4.1	16.4	32	2.5	28	33	Lacasa, 1990
26.7	Radish	4	2.3	3.8	1.1	2.7	13.9	40	3	–	- -	Bryan and Smith, 1956
27.2	Chrysanthemum	3	I------4.2------I		0.9	2.3	10.2	34	1.7	–	229	Robb, 1989
30	Chrysanthemum	2.5	1.3	2.6	0.9	2	9.3	13	1.6	–	42	Robb, 1989
30	Bean	4.26	1.11	4.32	1.4	1.6	12.6	27.5	2.4	25	43.8	Lublinkhof and Foster, 1977
35	Chrysanthemum	2.4	1.4	3.3	1	1.9	10.7	9.5	1.4	–	5	Robb, 1989
36.7	Chrysanthemum	3	1	2	1	1	8	30	–	0	150	Robb and Parella, 1987
18.5-36	Chrysanthemum	2.8	I------4.5------I		1.1	2.6.	11.2	26.8	1.4	–	129	Robb, 1989

(1977), fertility is especially affected by temperature, more than by host-plant variety and life-span is seen to diminish with increase in temperature; no highest fertility seems to be recorded at medium temperatures. Although in 1936 Watts had found no difference in fecundity between mated and unmated *Frankliniella tritici* (Fitch) females, according to Robb and Parrella (1987) mated females seem to be more fecund than unmated ones. Pollen is so important from a nutritional and reproduction point of view that females fed on pollen have a net reproductive rate (R_0) four times as high as that of females fed solely on cotton leaves (Trichilo and Leigh, 1988). Life-span, however, does not seem to be affected by feeding behaviour (Brødsgaard, 1989a). Reproduction of *F. occidentalis* occurs by facultative parthenogenesis, i.e. partly bisexual and partly parthenogenetic. Parthenogenetic reproduction is always arrhenotokous, unfertilized females laying eggs all of which develop into males, while most of the eggs laid by fertilized females develop into females (Brødsgaard, 1989a).

Both the adults and the young instars are thigmotactic and therefore particularly attracted to buds and complex flowers such as those of chrysanthemum, which offer perfect protection and allow the insect to go deep into the plant. In Italy, adults overwinter in a state of quiescence protected under dry vegetable remains or immediately under the upper surface of the soil, even in open fields (Del Bene and Gargani, 1989). In South Italy and probably in other Mediterranean area of infestation WFT can have continuous generations in the greenhouse and outdoors, in field with a temperature not below 5-6 °C, it can overwinter on wild plants as *Amaranthus* L., *Chenopodium* L., *Solanum nigrum* L. and *Heliotropium europeum* L. (Marullo, 1991). Unlike *T. tabaci*, at the end of winter *F. occidentalis* females have already mature eggs.

2.1.4 Behaviour

The species feeds on foliage and is anthophilous, even though it can also prey on *Tetranychus* spp. (Trichilo and Leigh, 1986; Pickett et al., 1988). As Pickett et al.

Table 2b: Development time and preoviposition period, longevity and fertility of unmated *F. occidentalis*, reared on bean leaves at three photoperiods, high air humidity and at constant temperature of 25 °C. (from Brødsgaard, 1991).

Parameter		Photoperiod (L-D hours)		
		4-20	8-16	16-8
Stage	egg	3.55	3.59	3.50
	1st instar	1.12	1.05	1.06
	2nd instar	6.02	5.52	4.94
	prepupa	1.18	1.15	1.05
	pupa	2.88	2.61	2.59
	egg to imago	14.75	13.92	13.15
	egg to egg	16.65	15.45	14.80
Adult	preoviposition period	1.90	1.53	1.65
	longevity	13.32	9.63	10.80
	fertility (offspring)	22.00	24.95	10.80

(1988) and Yudin et al. (1988) have observed, *F. occidentalis* prefers plants with flowers. In fact, when the photoperiod is unfavourable, thus preventing blooming, WFT populations diminish even to the point of not developing further (Arzone et al., 1989). Most of the population colonizes the upper parts of the plant, where it settles until the crop is harvested (Lacasa, 1990). Being an extremely polyphagous species, the insect feeds and reproduces on a wide range of wild plants, which are the vehicle through which crops are subsequently infested. In several crops, the edges of the cultivated fields are the first to be infested, while in orchards initial infestation of the flowers occurs from the weeds and nut. Peak population is encountered in the hottest months of the year, while in temperate regions the insect tends to go into diapause during the winter months. Along the coastal regions of southern Spain, however, climatic conditions are such that *F. occidentalis* is to be found active even during winter months (Lacasa, 1990).

Data as to population patterns and trends can be obtained, using (see also chapter 5, sampling) a number of methods, including:

1. Direct methods, by collecting the plant and subsequently counting the number of individuals, which allows to determine the exact distribution of the various types of thrips on the plant, or indirectly, by settling the soil (the so-called Berlese method).

2. Indirect methods, using special traps which exploit the insect's behaviour and reactions to specific chromatic stimuli, or with other traps such as transparent sheets.

A wide number of studies using chromotropic traps have yielded contrasting results. Lewis (1973), for example, is of the opinion that, as *F. occidentalis* belongs to the Thripidae family, it is attracted to white, an assumption also endorsed by Yudin et al. (1986 and 1987) and Moffit (1964), who showed that for adults of *F. occidentalis*, the colour white is a much stronger attractant than yellow. Other authors, however, such as Fougeroux (1988), Del Bene and Gargani (1989), Robb and Parrella (1989) and Torres del Castillo et al. (1989), are of the opinion that yellow is the most attractive colour to this insect, whereas Brødsgaard (1989b) found special shades of blue to be most effective. Brødsgaard (1989b), too, observed that in a mixed culture of white, rose pink, dark blue and light blue *S.ionantha*, *F. occidentalis* always preferred the light blue flowers. Another study was done by Vernon and Gillespie (1990b) about the response of WFT at sticky traps coloured with different reflective intensity. These studies showed that WFT was attracted in relation to the same reflective intensity. This fact could be explained considering *F. occidentalis* polyphagy and that adults should be attracted by the colours of flowers to a wide range of cross-fertilization hosts. Also the difference between fluorescent and non-fluorescent coloured sticky traps was tested by Vernon and Gillespie (1990a) and no significant differences in attractiveness between the two kind of traps was detected.

Anyway in several crops yellow sticky traps are usually employed for capturing WFT as they also capture other pests such as *Liriomyza* Mik spp., *Trialeurodes vaporariorum* (Westw.) and *Bemisia tabaci* (Genn.).

2.1.5 Host plants

Two hundred and forty four species of plants belonging to sixty two different fami-

Table 3: List of crops, ornamentals and fruit crops which are more commonly infested by *F.occidentalis* in the United States.

group	host plant species	reference
crop	*Gossypium* L. spp., cotton	Hightower and Martin, 1956
	Allium cepa L., onion	Elmore, 1949
	Carthamus tinctorius L., safflower	Carlson, 1962; Anonymous, 1989
	Fragaria vesca L., strawberry	Allen and Gaede, 1963
	Brassica oleracea L., cabbage	Oatman and Platner, 1969
	Lactuca sativa L., lettuce	Yudin et al., 1988
	Capsicum annuum L. , pepper	
	Lycopersicon esculentum Miller, tomato	
	Cucurbitaceae	
	Beta vulgaris L., beet	
	Daucus carota L., carrot	
ornamentals	*Gladiolus* L. spp.	Weigel and Smith, 1933
	bitterbrush	Ferguson et al., 1963
	Leucaena glauca Benth.	Yudin et al., 1986
	Rosa L. spp., rose	
	Dianthus L. spp., carnation	
	Lathyrus odoratus L., sweet-pea	Anonymous, 1989
fruit trees	*Ficus carica* L., fig	Baker, 1939
	Vitis L. spp. , grapevine	McNally et al., 1985
	Malus domestica Borkh., apple	Venables, 1925
	Prunus L. spp., plum	
	Armeniaca vulgaris Lam., apricot	
	Persica vulgaris Miller., peach	
	Prunus persica nucipersica Scheid., nectarine	Anonymous, 1989

lies, and which include open-field ornamental, fruit, garden and agricultural crops, have been found to host *F. occidentalis* in the United States (Anonymous, 1989), a selection of which is listed in table 3.

Amongst non-European Mediterranean countries, data of crop infestation by *F. occidentalis* is available for Israel, where the insect has been reported on the following crops: *Rosa* L. spp. (rose), *Dianthus* L. spp. (carnation), *Gypsophila* L. spp.. *Limonium* Miller spp., *Aster* L. spp., *Chrysanthemum* L. spp., *Ruscus* L. spp., Solidaster spp., *Impatiens* L. spp. (waxflower) (Gokkes, 1991).

In Europe, *F. occidentalis* has till now been found mostly on protected crops as indicated in table 4.

In Italy, *F. occidentalis* can be found on weeds and indigenous wild plants too, like *Anagallis arvense* L., *Senecio vulgaris* L., *Papaver rhoeas* L. (Del Bene & Gargani, 1989) and *Amaranthus*, *Chenopodium*, *Solanum nigrum*, *Heliotropium europeum* (Marullo, 1991). In glasshouse areas in The Netherlands adults have been found during the summer period on garden plants like *Liathris* L. cultivars, *Aconitum napellus* L., *Aster novi-belgii* L. Larvae were recorded from *Rosa* sp. (Mantel and Van de Vrie, 1988).

Table 4: European countries and their crops most commonly infested by F. occidentalis.

Country	Ornamental	Vegetable	Fruit trees	Reference
Netherlands	Saintpaulia, Chrysanthemum, Gerbera, Kalanchoe, Rademarchera			Van de Vrie, 1987
Sweden	Poinsettia, Chrysanthemum, Cyclamen, *Saintpaulia*, Kalanchoe, Fuchsia, Gerbera, Impatiens			Nedstam, 1991
Finland	Saintpaulia, Rose	Cucumber and other (a)		Tiitanen & Markkula, 1989 Brax & Lindqvist, 1989 Kurppa, 1989
Hungary	Gerbera, Carnation	Cucumber, Tomato, Sweet Pepper		Jensen & Tusnadi, 1989; Szabo & Ceglarska-Hodi, 1991
Poland	Gerbera, Rose, Chrysanthemum, Carnation, Pot Plant Crops	Cucumber		Labanoswki, 1991; Piatkowski, 1991
Germany	Saintpaulia, Geranium, Rose (b)			Zur Strassen, 1986; Gundel, 1988
Denmark	Saintpaulia			Brødsgaard, 1989a; Pilgaard, 1990
Great Britain	Chrysanthemum			Buxton & Wardlow, 1991
France	Saintpaulia, Chrysanthemum (c)			Bournier & Bournier, 1987
	Cyclamen, Rose, Azalea, Gerbera,	Egg-plant		
	Begonia, Hibiscus,Geranium,	Cucumber		
	Hibiscus, Geranium,Carnation,	Lettuce		Fougeroux, 1988;
	Lisianthus, Dahlia, Fuchsia,	Tomato, Melon		
	Impatiens, Zinnia, Orchid,	Bean, Strawberry		
	Gloxinia	Vegetable narrow (c)		
			Nectarines	Nicolas & Kouta, 1991
Belgium	Chrysanthemum (d)	Strawberry		Sterk, 1990; De Clercq, 1991
Spain		Pepper, Tomato		
		Egg-plant, Bean		
		Cucumber		Rodriquez & Belda Suarez, 1990
		Melon		
		Water-melon		
		Strawberry		Ribes, 1990
Portugal	Chrysanthemum	Melon	Apple	Leite, 1990
	Rose, Carnation,	Tomato, Bean	Plus-tree	
	Gerbera, Saintpaulia,	Strawberry	Peach	
Italy	Saintpaulia, Geranium			Rampinini, 1987 & 1989
	Chrysanthemum, Cirsium,	Parsley		
	Sonchus			Arzone et al, 1989
	Gipsophila, Gladiolus, Azalea, Statice,	Pumpkin		Del Bene & Gargani, 1989
	Poinsettia, Gillyflower,			
	Carnation, Rose, Cyclamen,	Pepper, Egg-plant,		Ciampolini et al., 1990;
	Gerbera, Lisianthus	Cucumber, Bean,		Bellardi & Vicchi, 1990;
		Green Bean,		Lisa et al., 1990;
	(e)	Vegetable narrow,		De Sena & Asero, 1991;
	Gloxinia	Strawberry	Table grapes	Ciampolini et al., 191 Marullo, 1991

a) *F. occidentalis* has also been found in open-field crops during the summer months;
b) WFT is currently one of the main nursery ornamental crop pests in Germany;
c) Open-field crops infested by WFT besides Gladiolus, Pansy and *Reine-Marguerite*;
d) The thrips has been found on 20 different families of 50 species of nursery-grown vegetable and ornamental crops;
e) Some ornamental plants are known to have been infested in open-field during the summer months

2.2 Other thrips species

Morphological, biological and epidemiological characteristics of the main thrips species found in protected crops will be described.

2.2.1 *Thrips tabaci* Lindeman (Terebrantia, Thripidae, Thripinae)

T. tabaci (onion thrips) is one of the species which features greatest intraspecific variability with regards to wing and body colour, ranging from light yellow to dark brown. The number of antenna segments is always equal to seven, of which the first is paler than the others. The main vein of the front wings features from 4 to 5 distal bristles, while no bristles are found on the abdominal sternites (Bournier, 1983). Insects born in winter are darker than their summer counterparts. Many biological studies have been conducted on this pest (Sakimura, 1932, 1937; Harris et al., 1936; Dimitrov, 1976; Zawirska, 1976).

T. tabaci reproduction is by constant thelitokous parthenogenesis (Table 4). Males have never been found on protected crops in British and French populations (Morison, 1957; Bournier, 1983) and probably neither in the rest of Europe. Morison (1957) found some males in open fields in the U.K., but not in greenhouse climates, concluding that this thrips was incapable of bisexual reproduction in protected environments. Bournier (1983) has even gone so far as to hypothesize the existence of two strains, one of which made up only of females and the other of bisexual individuals with a sex ratio of 1:1. O'Neil (1960) suggests that parthenogenesis is the most common reproductive strategy employed by imported species as it is the easiest and most direct method of reproduction. A possible confirmation to O'Neil's contention comes from the Middle East, for example Iran, where the sex ratio has found to be 1:1 (Bournier, 1983), while in other parts of the world males are decidedly rare, for example in Hawaii, where 1 male has been found for every 1000 females (Sakimura, 1932), and in Sudan where out of 3000 females not one male was found (MacGill, 1927). According to O'Neil, then, this species would seem to have originated from Central Asia, and, in fact, it was already known to be present in Egypt at the time of the Pharaohs (Chittenden, 1951). As with all thrips, the female lays eggs within plant tissues.

T. tabaci emerges from plant tissue through the tunnel drilled by the ovipositor. The first instars feature fewer antenna segments than the adults, while the integument, initially almost transparent, quickly develops pigmented spots depending on feeding patterns. Both first and second instars are extremely voracious. Pupal moulting normally takes place in the soil or humus around the host- plant within cells or on the plant itself. Duration of pre-imaginal stages is obviously a function of temperature (see Table 5).

The species features a number of ecotypes, each of which is polyphagous and can be hosted by a wide range of plants. In France, the insect has been found to reproduce parthenogenetically, and while it has never been found on tobacco, it has been reported on a variety of vegetable plants, mainly those belonging to the Liliaceae family, and in particular on onions, but also on cucumbers and roses. Zawirska (1976) has observed two strains to be present in Poland, one autochtho-

Table 5: Examples of the mean egg production and approximate rate of oviposition (Lewis, 1973) (B= normal bisexual, T= thelitokous).

Species	Type of Reproduction	Temp. (°C)	Total eggs	Rate (eggs/day)	Source
Heliothrips haemorrhoidalis	T	15.5-20	25	0.6	Rivnay, 1935
Heliothrips haemorrhoidalis	T	25.5-28	47	1.4	Rivnay, 1935
Taeniothrips dianthi	B	23	55	3.0	Pelikan, 1951
Thrips tabaci	T	18	80	1.8	Sakimura 1937

nous, which reproduces parthenogenetically and which was not found on tobacco, and the other which was found to spread gradually across the territory beginning from the Ukrainian border. The latter ecotype reproduces bisexually and is capable of transmitting virus-induced diseases, such as Tomato Spotted Wilt (see chapter 4 for further details).

T. tabaci is an extremely polyphagous species, it is known to infest about 300 plant species including, amongst others, leek, tobacco, vegetables of the Liliaceae family, cabbage, pea, melon, lettuce, potato, tomato and carnation. It is particularly harmful to cotton crops, especially in the Balkans, Asia Minor and Egypt. It has been studied in many countries with special reference to factors affecting the growth of the insect, extent of damage and control methods (Ghabn, 1938, 1950; Gawaad and Shazli, 1969, 1970, 1971; Gawaad and Soliman, 1972; Gawaad et al., 1973).

2.2.2 Thrips palmi (Thysanoptera, Thripidae, Thripinae)

T. palmi is similar to *Thrips flavus* Schrank (Palmer et al., 1989) which is an economically unimportant and cosmopolitan flower thrips. The morphological differences between the two species are reported by Anonymous (1989a). *T. palmi* called 'palm thrips' or 'melon thrips', is about 1.3 mm long and has a pale yellow body with blackish setae (II urotergite with four lateral setae, VIII with complete comb in both sexes).

The life cycle of *T. palmi* is slightly different in respect to other thrips species, in fact the second instar larvae move into the ground where they develop and pupate. In Japan this species can overwinter on outdoor vegetation only in a limited area of the South (Anonymous, 1989a). The insect was collected in 1921 from tobacco in Sumatra, Indonesia (Karny, 1925) and it was introduced in Japan in 1978 (Sakimura et al., 1986). Many studies, regarding integrated and biological control, were carried out in this country (Kawai and Katimura, 1990). *T. palmi* was found in Hawaii in 1982, in Puerto Rico in 1986 and in Florida in 1991 (Anonymous, 1991; Childers and Beshear, 1992). The crops attacked by *T. palmi* in these countries are mainly cucumber, watermelon, cantaloupe, Chinese spinach. lettuce, sweet pepper, eggplant, bean species, ornamental plants and citrus (Johnston, 1986; Childers and Beshear, 1992). Now the melon thrips is a key pest of cucurbits and solanaceous plants in several temperate and tropical regions. It was accidentally introduced in Central Europe probably by imported ornamentals and potted plants (Schliephake, 1990) and was intercepted and destroyed on *Ficus benjamina* in The Netherlands late 1992 and early 1993 (Loomans, pers. comm.).

The damage caused by this thrips are those typical of the order. *T. palmi* is polyphagous and is a vector of TSWV on watermelons in Japan and is therefore an important quarantaine pest. Integrated control is recommended in greenhouses in Japan since it was demonstrated that none of the repeatedly used insecticide applications caused a mortality higher than 80 % (Anonymous, 1989a).

2.2.3 Thrips fuscipennis Haliday (Terebrantia, Thripidae, Thripinae)

T. fuscipennis can be easily confused with *T. tabaci*, from which it differs, however, in a number of morphological features including darker wings. Moreover, while the antennae are also divided into seven segments as *T. tabaci*, the first is darker than the others; around the edge of the pronotum, three small hairs can also be seen, while on the back edge of the eighth tergite the hair comb breaks off at the center.

The insect reproduces by thelitokous parthenogenesis. The females overwinter on dry stems or in the bark but never in the soil. In rose nurseries, they continue living on the foliage, feeding and moving without, however, laying eggs (Speyer, 1932, 1936). This tends to demonstrate that the insect goes into a winter diapause which lasts until the end of March. Egg-laying begins in early April, when the eggs are deposited in sprouts or in the bracts and sepals of buds. The number of generations which can develop during the reproductive period is unknown. Albeit polyphagous, this species is known to prefer roses but carnations are also frequently infested. It has been found in all palearctic regions (Bournier, 1983).

2.2.4 Thrips simplex Morison and *Thrips meridionalis* Pr. (Terebrantia, Thripidae, Thripinae)

Both are similar in appearance, in particular the adult of *T. meridionalis* is brown or black, only at the base of the fore wings the colour is paler. Antennae present 8 segments and the final two are smaller. Two hairs are in the posterior corner of the prothorax. On the eighth tergite a comb of hairs is present. *T. meridionalis* is commonly found on fruit orchard plants. Morphological differences between *T. simplex* and *T. meridionalis* include 5 to 6 distal hairs instead of 3, located on the main vein of the front wing as well as three antenna segments shorter by 20 to 21 μm and only a single row of accessory hairs on the seventh sternite instead of the two featured by *T. meridionalis* (Bournier, 1954). *T. simplex* is amongst the species which reproduce by arrhenotokous parthenogenesis (Bournier, 1956a). Females can lay their eggs in any part of the plant, including the bulb, the leaves and the flowers. Discovered before 1930, and originating in Australia, it spread worldwide following the trade of gladiolus bulbs, which is the plant it most commonly infests and upon which it overwinters. It begins to reproduce itself at temperatures above 12°C (Bournier, 1983). During development, the insect does not appear to go into diapause and at 30°C the growth cycle is completed within 11 days (see Table 5). Pupation takes place either on the plant itself, into the soil or among bulb scales. This species is almost exclusively encountered on gladiolus, although it may occasionally be found also on carnation, iris, narcissus, freesia and tritoma.

2.2.5 Taeniothrips dianthi Priesner (= *Pesothrips dianthi* (Priesner)) (Terebrantia, Thripidae, Thripinae)

T. dianthi is also similar in appearance to *T. meridionalis* from which it differs morphologically in the fact that it features a crown of thick and dark hairs around the tip of the third segment of the antennae. After winter, mated females emerge from the litter or from the soil around April and settle on carnation seedlings. Moving towards the heart of the seedling, they lay an average of three eggs a day (see Table 4). Development times at 23°C are shown in Table 5. The second instars move down the plant and go deep down into the litter or the soil. During the reproductive period, three complete generations and a fourth partial one have been observed to develop in Central European countries (Pelikan, 1951). *T. dianthi* is related only with other species belonging to the *Dianthus* genus, which originate from south and south-eastern Europe. It is a particularly thermophilic species, and was introduced from the colder regions, such as the south-west of Poland, into the rest of Europe, where it found an ideal environment for its development, through the trade of carnation cuttings.

The species is practically monophagous and found only on carnations, where it causes considerable damage, morphologically altering the flowers and conferring on them a particular appearance called 'bird's head' (Pelikan, 1951; Bournier, 1983).

2.2.6 Heliothrips haemorrhoidalis (Bouché) (Terebrantia, Thripidae: Panchaetothripinae)

Heliothrips haemorrhoidalis takes its name from the colour, featuring a black body (although the immature stages are paler), and a red abdomen tip. The surface of the body is covered throughout by a clearly distinguishable reticular pattern. The legs are glassy in appearance and the wings, when at rest, form a white contrast against the black body. Antennae are divided into eight segments, the first two being light brown, the other three yellow, the sixth brown in the distal portion and the last two pale and filiform. *H. haemorrhoidalis* reproduces itself by obligatory thelitokous parthenogenesis and males are extremely rare (Bournier, 1956a) (table 4).

Some females deposit a drop of excrement on the egg, probably in order to seal the hole drilled by the ovipositor, while others lay their eggs deeper into the plant tissues, which then close themselves over the eggs. Larval instars of this species are known to secrete a rectal liquid which frightens away potential predators. This peculiar characteristic has probably been developed as larvae move very slowly especially when feeding.

Five to seven generations are found in Mid-Mediterranean countries between June and October, and up to 15 are known to develop in nursery environments as, under these conditions, the insect does not go into diapause. The adults overwinter on fallen dead leaves and bark.

Cosmopolitan and polyphagous, this species is found in all countries with

Table 6: Duration (in days) of stages of the life-cycle of some thrips at different temperatures (°C) (modified after Lewis, 1973).

Species	Tempe-rature	Eggs	1st larval stage	2nd larval stage	Prepupa	Pupal stage	Youth stages total no.	Preovi-position	Imago	Source
At constant temperatures										
Taeniothrips dianthi	23	7.0	5.5	8.0	1.0	5.0	26.5	–	–	Pelikan, 1951
Thrips simplex	15	12.8	(--- 18.6 ---)		(--- 11.7---)		23.4	–	–	Herr, 1934
Thrips simplex	30	2.9	(--- 3.9 ---)		(--- 3.5---)		10.3	–	–	Herr, 1934
Thrips tabaci	17.5	15.1	(------------------ 15.3 ------------------)				30.4	5.7	–	Edelson & Magaro, 1988
Thrips tabaci	20	8.4	(------------------ 11.9 ------------------)				20.4	3.2	–	Edelson & Magaro, 1988
Thrips tabaci	25	6.0	(------------------ 7.3 ------------------)				13.3	1.1	–	Edelson & Magaro, 1988
Thrips tabaci	25	6.0	(---- 6.1 ---)		1.2	2.8	16.1	–	–	Harris et al, 1936
Thrips tabaci	27.5	4.3	(------------------ 6.8 ------------------)				11.1	1.0	–	Edelson & Magaro, 1988
Thrips tabaci	30	4.0	(---- 4.2 ---)		1.0	2.0	11.2	–	19.9	Harris et al, 1936
Haplothrips cottei	30		(------------------ 23 ------------------)				23.0	–	13.0	Bournier, 1983
Haplothrips cottei	23		(------------------ 43 ------------------)				43.0	–	–	Bournier, 1983
Haplothrips cottei	18		(------------------ 67 ------------------)				67.0	–	–	Bournier, 1983
At fluctuating-temperatures (*mean*)										
Thrips tabaci	30.8	4.8	(---5.9 ---)		1.4	2.4	13.9	–	20.2	Lall & Singh, 1968
Thrips tabaci	26.7	4.6	(------------------ 8.6 ------------------)				14.4	1.0	–	Edelson & Magaro, 1988

favourable climatic conditions as well as on a wide variety of plants, such as, *Viburnum* L. spp., *Photinia* spp., azalea, *Ficus* L. spp., *Dracaenae* spp., orchids, roses, *Croton* L. spp., avocado, citrus fruit, grapevine, tobacco, *Eucalyptus* spp. L'Hér., etc. In Mid-Mediterranean countries, it is most frequently found on *Viburnum tinus* L. High infestation may cause complete defoliation of the plant.

2.2.7 Parthenothrips dracaenae (Heeger) (Terebrantia, Thripidae, Panchaetothripinae)

Parthenothrips dracaenae is light brown in colour with a reticular pattern over the body similar to that of *H. haemorrhoidalis*. The legs feature dark femurs and pale tibias, while the wings are characterized by two black transversal spots which are clearly visible when the wings are folded, the antennae has 8 segments. The initial five segments being light brownish yellow, the sixth and seventh dark brown and the last filiform. *P. dracaenae* is the first species which has been observed to reproduce by parthenogenesis, a fact which accounts for its name. Populations encountered in glasshouses with temperatures ranging between 25 to 28°C are made up almost exclusively of females, while some males have been found in populations at lower temperatures, namely between 18 and 20°C (Lewis, 1973). An interaction, therefore, between photoperiod and feeding seems to induce deuterotokous parthenogenesis.

Immediately after moulting, second instar larvae are smaller than first instars but develop into adult size upon reaching maturity. This characteristic is similar to that of *F. occidentalis*. If temperature remains within 18 to 20°C, approximately one generation a month can develop. Females lay their eggs on leaves, while the larvae live gregarious (Bournier, 1983).

Although cosmopolitan, this species can only survive in milder winters than *H. haemorrhoidalis*. Not surprisingly, therefore, in Europe it is only found in greenhouse environments.

The polyphagous insect infests a number of plants, including *Dracaenae* spp. vand. *Aralia* L., *Begonia* spp. L., Canna, *Croton* spp. L., *Ficus* spp. L., *Kentia* spp. Moore et Mueller, *Pandanus* spp. Parkinson, *Phoenix* spp. L., etc.

2.2.8 Haplothrips cottei (Vuillet) and *Haplothrips tritici* (Kurdjumov) (Tubulifera, Phlaeothripidae, Phlaeothripinae)

These species belong to the sub-order Tubulifera and are similar in appearance. *H. tritici* is found particularly on Gramineae. The female of *H. tritici* is black and 1.5 mm long, the end of the front tibia and tarsus are pale. The antennae present 8 segments, but the end of the second, the third and the first part of the fourth segment are paler than the other. The wings are hyaline, without veins, fringed along the margin. The front wings have a double line of 5-8 hairs posteriorly. The tenth abdominal segment is shaped as a long tube. *H. cottei* differs from *H. tritici*, however, in that it has a longer head; moreover, the tenth abdominal segment (or tube) is shorter and the insect does not exhibit the double fringe around the back portion of the front wings. This species can be found in a number of different forms, namely brachypterous at temperatures below 17°C, macropterous at 30°C and 87 to 100% relative humidity, and brachypterous at 30°C and 17% relative humidity, with the entirely macropterous generation being found only in winter (Ghabn, 1932). The development times are showed in Table 5.

Similarly to *T. dianthi*, this species only infests carnation and it is thermophilic. It has been found in Egypt, Spain and all Mediterranean coastal regions.

2.2.9 Liothrips vaneeckei Pr. and *Liothrips oleae* Costa (Tubulifera, Phlaeothripidae, Phlaeothripinae)

Both are similar in appearance. The adult of *L. vaneeckei* is black and it differs from the latter, however, in the colour of its front tibiae which are completely yellow instead of black; moreover, the middle and back tibiae are both yellow in their distal portions while the abdominal segment or tube is longer, i.e. 285 instead of 210μm. The third antenna segment is shorter (84 μm) than that of *L. oleae* (105 μm). Wings are without veins, with a double line of 15-18 hairs. It reproduces by arrhenotokous parthenogenesis (Bournier, 1956b). In Europe, it is known to develop at least four generations a year (Hodson, 1935; Bailey, 1939; Titschack, 1960). It can be found worldwide, where it has spread following on the flower bulb trade. Bulb-induced contamination seems to take place via wind- borne intermediaries which have moved up from the soil onto the stems of the lilies (Titschack, 1960). First being limited to wild *Lilium martagon* L., *L. vaneeckei* has subsequently colonized lily crops. *L. oleae* infests olive trees.

3. Direct damage

3.1 Damage caused by Thysanoptera in general

All phytophagous Thysanoptera cause direct damage to plants due to the mechanical action of the mouthparts during feeding and within Terebrantia to oviposition too. More precisely, feeding and egg-laying behaviour entail:

- perforation of plant tissues as a consequence of the introduction of mouth stylets;
- injection of saliva into plant tissues and consequent cell lysis;
- sucking up of cellular contents;
- ovipositor penetration and egg-laying into plant tissues.

Each puncture into the plant tissues causes the destruction on average of 1 epidermal cell and of between 1-2 underlying parenchymal cells. Moreover, cells are often injected with a phytotoxic substance which can determine specific tissue reactions as observed by Kloft and Ehrhardt (1959) using radioactive isotopes. These attacks bring about cell dehydration and discoloration, resulting in superficial necrosis.

Amongst the various thrips examined above, some species are monophagous, including *T. dianthi,* which only infests carnation, and *T. simplex,* which is only to be found on gladiolus. Typically polyphagous species, on the other hand, include *T. tabaci* and *F. occidentalis.*

Another peculiar characteristic of thrips is that, while some species can be extremely harmful to a certain crop in a certain region, they are completely harmless in other regions. An example is given by *T. tabaci,* which is widespread in all temperate and sub-tropical regions of the northern hemisphere. In fact, while attacking several varieties of tobacco in Turkey and Greece, it does not seem to infest tobacco crops in France (Bournier, 1983).

The type of damage which thrips can cause to crops depends on a number of factors including:

- the organ of the plant actually infested;
- the growth stage of the plant itself;
- the degree of toxicity of the saliva of the species considered in relation to host-plant characteristics.

3.1.1 Damage caused to highly cutinized and fully developed leaves

The surface of the leaf exhibits emptied and discoloured cell, initially taking on a mother-of-pearl appearance and subsequently turning brown. In the case of massive infestation, the leaves wither and fall. It sometimes appears to be similar to that caused by mites but, in addition to larval exuviae, the presence of brownish transparent faecal drops is a clear indication of thrips infestation. This type of damage to leaves is often encountered in protected crops (Moulton, 1928), caused especially by the action of *H. haemorrhoidalis* and *P. dracaenae*, which are known to infest in particular ornamental crops such as *Ficus* spp., *Philodendron* spp., *Croton* spp., *Dracaenae* spp., *Phlox* spp., etc.

3.1.2 Damage to developing leaves

This damage is more frequently encountered than the previous one. The reaction of the leaves to the toxic saliva of the thrips normally differs according to plant species, and often also to plant variety. If the saliva does not penetrate below the surface layer, then the leaf continues to grow, exhibiting only necrotic spots in the immediate vicinity of the puncture. On the other hand, if the saliva penetrates further, both sides of the leaf limb are deformed. In fact, as the leaf grows it takes on the form of a half-open umbrella. *T. tabaci*, for example, can destroy all the epidermal cells of an onion, thus causing the leaf to completely wither (Ghabn, 1948). In other cases, the leaf can continue to develop, taking on an undulated form resulting from the impossibility of growing normally along the damaged parts. *T. tabaci* on leek always causes silvering, mottling or blotching on the affected surfaces of leaves, through feeding punctures, sometimes in longitudinal stripes along the growing leaf the major part of damages of *T. tabaci* are during warm summers (Theunissen and Legutowska, 1991). On cabbage, the visible injury, caused by *T. tabaci*, consists of papillary callus proliferation on the lower and upper surfaces of the leaves, and reducing the quality of the crop (Giessmann, 1988). Another example of this kind of damage is found on carnation plants infested by *T. dianthi* (Bournier, 1983).

3.1.3 Damage to stems and to terminal buds

Damage to the stem, caused by punctures at its vegetative apex, only occurs when this part of the plant is still young and tissues, therefore, soft. Suberization of the tissue is similar to that caused to the leaves. In France, attacks of this kind have been reported on grapevines beginning after mid-August (Bournier, 1957). Given their size, thrips are capable of penetrating into the heart of buds. In this case, their punctures may destroy small leaves and meristems. *T. tabaci*, for example, is known to attack cotton crops when these are still at the cotyledon stage of development (Bournier, 1983).

3.1.4 Damage to flowers

Damage to flowers may include damage to petals, stamens, pistils and peduncles.

Petals: Thrips may attack a wide variety of flower species. When infested, petals exhibit white spots which subsequently turn brown, after which the petals become deformed. Not infrequently, the insects penetrate into the flower buds before blooming, completely destroying them. A typical example of this kind of damage is to be found in carnations, where infestation causes deformation of the bud into the shape of a 'bird's head' (Pelikan, 1951; Bournier, 1983).

Stamens: A single puncture in the stem may cause total destruction of the stamen. Moreover, as anthers have been found to be a source of food for various species of thrips, another dehiscence may ensue, as is the case, for example, with *F. occidentalis* infested plants.

Pistils: *Kakothrips robustus* (Uzel) is known to also puncture the pistil and the ovary, thus causing destruction of certain parts of the young fruit which, upon subsequent development, appears deformed with only a few seeds (Bühl, 1936).

Peduncles: Damage to the peduncles of flowers is less frequently caused by the thrips considered in this paper, it is mainly induced by tree-infesting thrips.

3.1.5 Damage to fruit

Damage to fruit may include that to the fruit proper as well as to the pericarp.

Developing fruit: Developing fruit is the most frequently damaged as at this stage the fruit still features a very soft epidermis. Epidermal suberization ensues which, in turn, causes deformation of developing fruit. This kind of damage is usually encountered in peaches, which are thus made unmarketable, as well as in grapes, plums and cherries (Bournier, 1983).

Pericarp: Damage of this kind is known to cause a change in colour of the wheat pericarp. Even if controversial, it has also been reported in mushroom following on punctures by *H. tritici*.

3.1.6 Damage to bulbs and rhizomes

A bulb can be described as a bud consisting of fleshy leafy scales or layers, while a rhizome is a scaly underground stem. It is these scales which are subject to thrips attack. In lilies, for example, *L. vaneeckei* punctures the superficial scales, thus permitting microorganisms in the soil to penetrate into the bulb, infesting it and causing its decay (Schopp, 1936; Titschak, 1960). Wounds inflicted by *T. simplex* to gladiolus cause, instead, dehydration and subsequent darkening (Bournier, 1954).

3.1.7 Intoxication and growth of galls

When punctures are inflicted on young stems and especially at growth apex, saliva induced intoxication may result. In addition to leaf deformation caused by *T. dianthi*, Bournier (1983) also observed a considerable shortening of internodes and most of deformed whorls of the plant. In most cases, the effects of intoxication diminish or disappear with subsequent plant growth. Saliva toxicity can induce abnormal cell multiplication in the plant, in particular in the parenchymal tissues. Vessel bundles are destroyed due to circulating cell proliferation and the collenchyma and sclerenchyma develop irregularly throughout the plant. The leaf mesophyll hardens due to tannin and anthocyanin build-up. The leaves may still fold in on themselves, thus forming mantle or overcoat galls, as has been observed in *Ficus microcarpa* Vahl growing in the Mediterranean basin, punctured by *Gynaikothrips ficorum* Marchal (Bournier, 1983).

3.2 Damage caused by *F. occidentalis*

3.2.1 General damage symptoms

Damage to crops caused by *F. occidentalis*, as with that caused by other thrips, features different characteristics according to extent and period of attack, as well as to plant parts involved. Generally, the major symptoms of *F. occidentalis* infestation include a discoloration of the upper leaf surface where attack occurs. The pattern of damage is more coarse than damage by *T. tabaci*. Silvering, deformity, growth malfunction and brown-coloured bumps may also be present on the foliage of ornamental plants. Halo spotting is another symptom of thrips damage consisting of small dark scars surrounded by whitish tissue. On some host plants (sweet pepper), oviposition causes a reaction of the surrounding plant tissue. Thrips' feeding causes discoloration and scarring of open blooms and petals. It also results in deformation of buds if the feeding occurs before they start opening. Kloft and Ehrhardt (1959) have shown that the action of the saliva injected into plant cells is the real cause of damages for its toxic effects on plant tissues. This was demonstrated by the use of radioactive tracers (P32), which show how saliva spreads abundantly through the cell walls, thus invading and destroying the entire region around the puncture. The cytoplasm of the dead cells dehydrates and the cells lose their pigmentation, turning to a mother of pearl whitish colour before becoming brown. The damage caused by WFT, as with other thrips, (already described in section III) is often hard to distinguish from spider mite damage but a good indication of thrips attack is the appearance of liquid faecal deposits which cause dark- green speckling, while spider mites produce black granules. Female WFT can lay their eggs in petal tissue which causes a 'pimpling' effect in flower such as orchids (Anonymous, 1989).

3.2.2 Damage symptoms on specific host plants

Chrysanthemum- Chrysanthemum flowers attacked by *F. occidentalis* exhibit, for example, distorted petals, discolouration, and extensive streaking, especially on dark flowers. Unlike *Saintpaulia* and *Gloxinia* spp. flowers, which wither as a consequence of pollen dispersion, attacks to *Chrysanthemum* pollen granules do not seem to affect the flower. Two types of alterations have been observed in the foliage depending on the age of affected tissues. As regards buds, for example, attacks by *F. occidentalis* cause irregular growth of small leaves as well as distortion and failure to open of the parenchymal foliage. Attacks to open leaves, on the other hand, only cause necrotic scars and silvering, as is also the case on rose and gerbera sepals (Fougeroux, 1988; Ciampolini et al., 1990).

Geranium - Damage caused by *F. occidentalis* to geranium (Rampinini, 1989) can already be detected on the young leaves, which grow deformed, curling upwards and exhibiting whitish and suberose bumps on the upper leaf surface which are even more marked on the lower leaf surface, on the peduncles, petioles and stems. Flowers can abort and, if they bloom, display deformed petals with long or marginal discoloration. These symptoms tend to worsen at higher temperatures such as those found in glasshouses. Humidity is also an important factor in aggravating these symptoms, which do not diminish, however, even when the plant is transferred outside. *F. occidentalis* causes typical corky spots on the lower surface of the leaves, and lateral necrotic spots were also found (Gundel, 1988).

Grapevine – In 1990, *F. occidentalis* was reported to infest this crop in southern

Italy (Ciampolini et al., 1991; Laccone, 1992), causing in particular considerable damage to table grapes. The extent of the damage from one region to another varies according to a number of ecological factors such as climate, humidity, type of soil and the presence of grass covers which are the source of inoculation of the infesting organism. The pest attacks almost exclusively the grape bunch at the growth stage between flower bud separation and post-setting, and in particular during full blossom. This causes peduncle and grape withering as well as a slight deformation of the rachis. The most serious damage, however, is caused to the grape by wounds due to oviposition. This leads to tissue necrosis which, as the grape grows, becomes more and more marked until a dark spot appears as a consequence of suberization of the epicarp and of the underlying layers. The thrips can lay more than one egg in each single grape, so that the damage can be even more extensive. Apart from damage to the grape, other parts of the plant do not show significant damage.

Strawberry – Infestation of this crop mainly affects the flowers, while damage to the leaves is negligible. Damage to flowers is typically caused by punctures due to feeding. Initial symptoms are rusty spots at the base of the flowers above the sepals, which can also be observed in the unripe fruit. The major damage, however, is represented by the flowers going into necrosis and withering (Ribes, 1990).

Rodriguez and Belda Suarez (1989), who examined the damage caused by thrips to a number of vegetable crops in Spain, describe the symptoms as follows:

Bean – The population is mainly localized on the lower leaves of the plant where punctures of both adults and the larvae can be seen. Albeit only occasionally, damage to fruit can be considerable, appearing as a markedly white halo around the punctures. The population on the flowers is mainly adult, but this does not seem to adversely affect the fruit-bearing capacity of the plant or to cause pod deformation.

Egg-plant – Thrips infestation peaks when the plant is in full bloom. Other parts of the plant are less subject to infestation, a fact accounted for by the presence of tomentous layers with which the plant is endowed, especially on the leaves. The damage on the leaves is given by silvery spots close to the veins, which become necrotic. This damage is particularly evident in the upper foliage, where the adults are localized. The larvae are uniformly distributed throughout the plant. Upon blossoming, adults attack the flower and especially the ovary. Whitish punctures can be seen at the tip of the fruit. The peduncle may exhibit damage from feeding punctures, with spots becoming necrotic and then rusty.

Cucumber – Thrips population increases progressively as the plant grows, being localized on the leaves and fruits but above all on the flowers, where adults are especially found, particularly on the petals. The typical symptoms of damage caused by feeding punctures are observed on the leaves, the spots becoming larger and larger and forming extensive necrosis, thus hampering the regular physiological processes of the plant. The flower and the fruit are known to host all thrips species. However, no apparent relationship seems to exist between the damage caused by the thrips and the eventual bending observed on the fruit. The fruit's marketability is compromised by the necrotic spots located around the peduncle or in areas directly in contact with the leaves.

Melon – Thrips are found mainly on the leaves. In the extensive areas in which this crop is grown during the summer months, the instar population is greater than the adult one. Damage caused by feeding punctures increases as the leaf surface area grows larger, eventually causing the leaf to wither. The older leaves are infested first, after which infestation spreads to the rest of the plant, which becomes damaged in all its parts to the point of damaging the whole crop. The fruit is the least susceptible to thrips attack and its marketability is not affected.

Pepper – Infestation is initially restricted to the leaves. As the plant grows, the adults progressively move towards the younger parts of the plant, finally settling on the blooming flowers. Silvering and subsequent necrosis are the most evident damage displayed by the leaves, of which the older are the most affected. Punctures only occasionally occur on the fruit; these are localized at the point of intersection between the calyx and the fruit itself, where the larvae shelter. Feeding punctures initially cause silvering, followed by necrosis and rusty spotting especially in the peduncle and much more marked on red than on green fruits. This damage is extremely serious as it can depreciate the fruit's market value, especially in cases where it is extensive.

Tomato – Most of the population is to be found on the lower leaves of the plant, with larvae settling in particular under folded leaf edges. Damage to leaves caused by feeding punctures is characterized by silvery spots which subsequently become necrotic. In case of massive attacks, withering may result. When punctured, both green and ripe fruits display a whitish halo all around the punctures. In addition to feeding punctures, fruits also display punctures caused by oviposition.

Zucchini – The greatest damage is caused to leaves in the early stages of plant growth. The thrips subsequently move into the flower in order to feed on the pollen, and it is at this stage that infestation reaches its peak. The typical spots due to thrips feeding appear on the leaves, localized around the limb and petiole. Damage to the fruit is negligible except for a few silvery spots on the peduncle.

Watermelon – Thrips distribution is more or less uniform over the leaves, even if the adults prefer the younger parts of the plant and the flowers. The typical spots caused by feeding punctures can easily be detected on the leaves but are less evident on the fruit and almost invisible on the ripe fruit.

4. Indirect thrips-induced damage

4.1 Viruses

Thysanoptera feed by first injecting saliva into plant cells and then sucking the contents of the destroyed cells resulting from the action of the lysins. This feeding pattern means that the insects can acquire and consequently transmit viruses. Many authors have therefore assumed that thrips are carriers of plant virus-induced diseases. For example, Bondar (1924) studied the mosaic disease of the manihot, Kreutzberg (1940, 1955) the rosette disease of the pistachio, and Messieha (1969) the ring spot of tobacco. Heinze (1959) has made a list of 19 species of thrips considered to be common carriers of plant infesting viruses. It should be noted, however, that in most cases virus transmission is not as evident as may be thought. It seems that Tobacco Streak Virus (TSV) can be transmitted by *F. occidentalis* and *T. tabaci* (Kaiser et al., 1982). The authors reports that additional studies will be needed to determine whether *F. occidentalis* or *T. tabaci* is the primary vector of TSV and to clarify other aspects of the virus-vector relationship.

A clearly established case of transmission of virus-induced disease with thrips as carriers concerns the disease caused by the tomato spotted wilt virus (TSWV) (Pittman, 1927; Samuel et al., 1930; Bonnemaison, 1939; Sakimura, 1962a; Reddy and Wightman, 1988; Marchoux et al., 1991), in this case, the carriers were found to include: *T. tabaci*, *Frankliniella schultzei* (Trybom), *F. occidentalis*, *Frankliniella fusca* (Hinds). Recently, ELISA testing has permitted to establish that over 50% of adult *F. occidentalis* are infected by TSWV (Marchoux, 1990). Studies about virus transmission by WFT are in progress. Wykamp and Peters (unpublished) have recently shown that less than one-day-old first instar of *F. occidentalis* can acquire the virus and that 80% of larvae could transmit the virus before pupation.

This particular viral disease was first observed in Australia in 1915, spreading afterwards to America and Asia (De Sena and Asero, 1991), Smith observed TSWV in the United Kingdom in 1932. Diffusion of this virus in several regions of North America was also reported, for example, by Paliwal (1974, 1976), Allen and Broadbent (1986), and Miller (1989). One of the main channels of transmission of this virus is, in fact, via thrips. In India, TSWV has been found to be transmitted by another two species of thrips, namely *Scirtothrips dorsalis* Hood and *Thrips palmi* Karny (Amin et al., 1981; Marchoux, 1990). TSWV can affect a wide variety of plants: 299 species of 48 botanic different families (Edwardson and Christie, 1986; Berling et al., 1990) and in particular vegetable, flower and ornamental crops (Allen et al., 1990). After having reached Europe, the virus went through a period of relative dormancy, but in recent years a number of European countries, including The Netherlands (Van der Hoeven, 1988), France (Gebre-Selassie et al., 1989), Italy (Bellardi and Bertaccini, 1989; Lisa et al., 1990), Spain (Estevez, 1990), Great Britain (Fletcher, 1990), as well as Greece (Tsakiridis and Gooding, 1972; Podikakis, 1991 pers. comm.), have been particularly hard-hit by this disease (De Sena and Asero, 1991), a fact probably as a result of the diffusion of *F. occidentalis*. Allen and Matteoni (1991) suggests the use of Petunia as an indicator plant to monitor TSWV carried by thrips in greenhouses. It is important to underline that it is difficult to make a right diagnosis of the infection from TSWV only by observing the plants: the necrosis and the concentric chlorotic rings, like on Gloxinia and Begonia (hosts of the virus too), are easily confused with symptomatology due to fungi infections (like for example *Phytophtora parasitica* Dast. on Gloxinia) and bacterial infections (for example *Xanthomonas campestris* (Pammel) Dowson on Begonia). Besides, on Saintpaulia and Gloxinia the concentric chlorotic rings, used for the diagnosis, can be seen only sometimes because they are correlated with the kind of TSWV isolated and with the environmental condition in which the plant is at that moment of the infection (Vicchi et al., 1992).

Not all forms of *T. tabaci* are capable of transmitting the virus (Zawirska, 1976). In France, for example, TSWV is not found at all in the southern regions where research conducted on indigenous strains of *T. tabaci* has shown that these are incapable of transmitting the virus (Nkouka, 1977). TSWV is transmitted, in a persistent way (Sakimura, 1962b) even though it is more correct to say that viral transmission patterns are typically circulatory. In fact, larvae puncture the virus-infected plant, thus absorbing viruses which go into the haemocoelic cavity through the digestive tube and finally into the salivary glands, from which they are then reinjected into healthy plants. Fifteen minutes are necessary for the larvae to acquire the virus. The time necessary for the virus to reach the salivary glands usually coincides with the time taken for the insect to develop into an adult, at which stage the virus has become highly virulent, the maximum period of transmission of virus being 3-4 weeks after when it was acquired (Bellardi and Vicchi, 1990). The period between acquisition and transmission, i.e. in which the thrips is not infectious, is ranging from 4 to 18 days for *T. tabaci* and 4 to 12 days for *F. fusca* (Sakimura, 1963). In cases where development of first instar larvae into second instar larvae is slowed down by temperature factors, the second instar larvae are already themselves infesting agents (Bournier, 1983). If the infection by the insect has not occurred at the larval stage, adults do not contract the virus. Both females and males are capable of inoculating the virus (Sakimura, 1962a). Thrips take from 5 to 15 minutes to inoculate the virus but once infested the insect can remain virulent throughout its life-span without however transmitting the viral cells to its offspring (Ie, 1970; De Sena and Asero, 1991). *T. tabaci* is also a carrier of 'Pineapple Yellow Spot'. The larva is the stage during which the virus is picked up. Then 10 days of incubation are required for transmission in respect to 5 days circa for TSWV. The transmission of TSWV is easier than Pineapple Yellow Spot (Bailey, 1935).

4.2 Bacteria

It can be safely assumed that thrips are vectors of conveying a large number of bacteria from one plant to another, in which case the bacteria can probably penetrate into the plant through the punctures made by thrips. Infection due to thrips has definitely been reported for non-European countries. As far as Europe is concerned, at least three cases of plant infection which have been reported as possibly due to thrips-borne bacteria. These include infections induced by *Erwinia amylovora* (Burr.) Winslow et al., which causes pear bacterial fire (Bournier, 1983), two bacteria which predispose plants to attack by *Fusarium moniliforme* Sheld *fici* and which seem to be borne by *T. tabaci*, reported in Provence (Caldis, 1927) as well as a bacterium affecting bean crops and carried by *Hercinothrips femoralis* Reuter (Buchanan, 1932).

4.3 Fungi

Thrips have often also been reported to be fungi-vectors. In fact, spores can easily be trapped in the bristles of several thrips species and consequently deposited on healthy plants. Bournier (1983) cites a number of examples including Yarwood (1943) who observed a number of thrips- associated mildews such as: *Uncinula necator* (Schw.) Burr. in grapevine, *Sphaerotheca pannosa* (Wall.) Lév. in roses, *Sphaerotheca humuli* (De Candolle) Burr. in strawberries, *Erisyphe cichoracearum* D.C. in melon, etc. Ghabn (1932) found that carnations were inoculated by a *Haplothrips cottei* borne *Alternaria* Nees, while Ondrej (1973) made the same observation with regards *Botrytis fabae* Sard. Many other such reports have come in from the United States, and it can be safely assumed that the list is far from being complete.

5. Sampling

Sampling techniques mainly useful for collectors are reported by Lewis (1973). However in applied entomology sampling is directed towards survey and monitoring of harmful insects and Lewis reports also sampling and extraction methods that give qualitative and quantitative estimates of the size and distribution of living thrips populations. So, to detect thrips it is possible to employ different methods. One of the easiest techniques to collect the thrips is by shaking the flower on a sheet of paper or by extracting them from leaf-litter and soil. More recently Lacasa (1990) suggests several kinds of sampling and collecting techniques divided in direct and indirect methods. The latter are for example: Berlese funnels or Berlese modified dry funnels and chromothropic traps. Several studies were carried out with chromothropic traps (see at biology). Recently Brødsgaard (1989b) reported references and new data regarding the most attractive colours for *F. occidentalis*. Now, for example, blue sticky traps are sold to growers because this is the most effective technique for collecting *F. occidentalis* in protected crops.

Other studies involve semiochemicals. It is known that insects are attracted by odour plants for feeding and oviposition. Several synomones such as floral scents are important mainly for pollinators and some of these allelochemicals have been studied also for thrips. Kirk (1985) reports about components which attract several species of thrips. The potential use of synthetic odours to collect thrips in greenhouses, either for monitoring or for control purposes is reviewed by Teulon and Ramakers (1990). References concerning the influence of scent on flying thrips have been carried out for benzaldehyde, anisaldehyde, salicaldehyde or cinnamaldehyde and other not clearly defined chemicals. *T. tabaci* and some species of *Frankliniella* genus were attracted and collected in traps in great number when anisaldehyde was added compared to unbaited traps. Brødsgaard (1990) demonstrated that just for *F. occidentalis*, anisaldehyde increases the number of thrips caught on scented window traps compared to unscented window traps. The capture of thrips could be enhanced by using semiochemicals. Presently, sampling techniques for flying thrips consist of counting the adults caught in sticky traps of different colours. Many authors are working now on sampling techniques to obtain more information about thrips population dynamics.

6. Conclusions

Based on the references cited in this paper we can conclude that direct damages due to thrips attack can be less important in respect to indirect damages, especially the diffusion of diseases. *F. occidentalis* (Western Flower Thrips) is able to acquire viruses, the most important being Tomato Spotted Wilt Virus, and to transmit it in a persistent way. Also other thrips species are able to transmit viruses, but not in all infested geographical areas where they occur, i.e. as is the case with *T. tabaci*. Nowadays problems induced by viruses in several protected crops are particularly severe, forcing growers to lower the economic threshold of pest control.

The knowledge of bionomics, life-cycles and biological traits is fundamental to control the several species of harmful thrips. In Europe the most common species considered as a pest of several crops is *F. occidentalis*. In many cases this pest is becoming more and more dangerous, occupying new habitats and substituting other thrips pest species. Undoubtedly WFT has spread throughout Europe because of the market distribution of plants or plant parts, but resistance developed to most pesticides applied frequently in protected and open field crops has been of great importance too. It must be noted that possible new strains of other species of thrips may evolve and become pesticide resistant and we must bear in mind that the introduction of exotic thrips species is still possible and must be avoided. Recently, for example, *Thrips palmi* Karny, already resistant to many pesticides, is spreading around the Pacific Basin of the USA, coming from Australia (Mau et al., 1989) and it is recently introduced in continental U.S.A. and in Europe (Anonymous, 1991; Childers and Beschear, 1992; Schliephake, 1990). When introduced accidentally into the USA continent and into Europe, it could produce another case of danger for the growers.

Furthermore, mismanagement like applying broad spectrum insecticides at high dosages and using repeatedly the same active ingredients, etc., can lead to the development of resistance in thrips species in very few years. Pesticide selective pressure therefore must be reduced and it is necessary to find alternative ways to control thrips in general and WFT in particular. On a research level, biological control and host plant resistance breeding can offer important tools in the development of new control strategies. The possibility for advisory staff and growers to know and identify the species of thrips that infest the crop is very important as is their epidemiological awareness which can be obtained by monitoring the crop during the growing season on a regularly basis.

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Predators of *Frankliniella occidentalis* (Perg.) and *Thrips tabaci* Lind.: a review

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Contents

Abstract

Frankliniella occidentalis and *Thrips tabaci*, vectors of the tomato spotted wilt virus, have become increasingly important agriculture pests, both in the open field and in greenhouses. These thrips are difficult to control chemically and treatments have to be repeated frequently, causing residue problems and disrupting Integrated Pest Management programs that have been adopted. Use of biological control systems may help to reduce both pest populations and virus incidence. In this article the present state of biological control research using predators is reviewed as a first step towards selecting suitable candidates. The most studied families of predators are Phytoseiidae and Anthocoridae. For each predator, the information published in the literature up to November 1993 and the characteristics of each species as a good natural enemy are discussed.

1. Introduction

The thrips species *Frankliniella occidentalis* (Perg.) (Western Flower Thrips) and *Thrips tabaci* Lind. cause serious damage to vegetable and ornamental crops both in the open field and in greenhouses. Their short generation time and the excessive pesticide treatments to which they are subjected contribute to rapid development of resistance to insecticides (Robb, Parrella and Newman, 1988). Their pest status has been particularly aggravated by the incidence of tomato spotted wilt virus (TSWV). Both *F. occidentalis* and *T. tabaci* are capable of vectoring of this virus and the potential of them of transmitting TSWV lower their economic thresholds. Attempts to control TSWV by means of chemical treatments against the vectors have not been successful and insecticides cause residue problems when intensively applied (Marchoux, 1990). Biological methods may offer a more suitable solution for both controlling the thrips population and virus incidence, but the lack of efficient biological control systems for these insects at present also makes it difficult to apply Integrated Pest Management (IPM) programmes in vegetable crops.

Most IPM programs are based on the utilization of insect parasitoids. Less attention has been paid to predators, and this group of natural enemies can be very effective in warmer areas where they are spontaneous. In these areas such biocontrol agents are a major factor in preventing outbreaks in populations of many pest species. At low prey densities, general predators are extremely effective, not being completely dependent on populations of the target pest (Pimentel, 1981). This effectiveness is necessary in the case of insects that are vectors of virus such as *F. occidentalis* and *T. tabaci*. The objective of this article is to review the literature on the present state of biological control research using predators, and is intended to provide a basis for later research to determine a good candidate for the control of *F. occidentalis* and *T. tabaci*. Several reviews and annotated bibliographies give us information on natural enemies, in particular on predators, that are related with Thysanoptera (Ananthakrishnan, 1973, 1979, 1984; Ananthakrishnan and Sureshkumar, 1985; Herting and Simmonds, 1971; Fry, 1987; Lewis, 1973; Thompson and Simmonds, 1965). This review focuses on *F. occidentalis*, and *T. tabaci*. *Thrips tabaci* was, until the arrival of *F. occidentalis*, by far the primary Thysanoptera pest of European vegetable crops.

2. Methodology

We have used a computerized bibliographical search to find what has been published on predators of Thysanoptera, using the key words: Thysanoptera, *F. occidentalis* and *T. tabaci* combined with predator, biological control and natural enemies. Additional references not directly related to these key words are not expected to be exhaustive.

The computerized information was obtained from the databases: CAB abstracts (on line) 1972-1983; CAB abstracts CD ROM, 1984-90; BIOSIS 1969-91/may; PASCAL 1983-91/june; SCI 1980-90; AGRIS 1975-90; LIFE-SCI 1982-90; AGRICOLA 1970-91/april; CRIS/ICAR 1991/March; Review of Applied Entomology, Series A, Vol. 67-77 (1979-89); Review of Agricultural Entomology, Vol. 78-79(7) (1990-91).

The main attributes which we summarized for each predator are:

(1) geographic distribution, prey insects upon which they fed, and plant species on which they have been found.

(2) Life history which includes:

- field studies on natural control,
- their biology and behaviour,
- results of practical application of biological control programs where those species were applied,
- natural enemies of the predators,
- possibilities for rearing these that are not available.

3. Predators of Thysanoptera

Many arthropods are known to be predators of thrips including Anthocoridae and Miridae, Syrphidae, Cecidomyiidae, Chrysopidae, Sphecidae, Araneida and Pseudoscorpiones (Ananthakrishnan, 1979). Most species mentioned in the bibliography as predators of *F. occidentalis* and *T. tabaci* belong to Acari, Gryllidae, Chrysopidae, Anthocoridae, Nabidae, Lygaeidae, Thysanoptera, Coleoptera and Diptera.

3.1 Heteroptera: Anthocoridae

The Anthocoridae, including the genera *Orius* Wolff, *Anthocoris* Fallen, *Montandoniola* Poppius, *Xylocoris* Dufour and *Scoloposcelis* Fieber, etc., are known as active general insect predators, and are effectively used in biological control programs (Sohm, 1981; Schmitt and Goyer, 1983; Ananthakrishnan and Sureshkumar, 1985).

3.1.1 Orius albidipennis (Reuter 1884)

3.1.1.1 Distribution, prey and host plants

O. albidipennis is a palaearctic species. It is mainly found in the southern Mediterranean from North Africa, where it is common in the Magreb and Egypt, to the Near East, Iran and Russian Asia Minor. It is also found in Spain, the Canary Islands and Cape Verde (Péricart, 1972).

It is mentioned as a predator of *Frankliniella occidentalis* (Carnero et al., 1993) (Ref. in Table 1), *Thrips tabaci* (Puchkov, 1961; Saxena, 1977; Ananthakrishnan and Sureshkumar, 1985) (Ref. in Table 1) *Gynaikothrips ficorum* Marchal (Ananthakrishnan and Sureshkumar, 1985) and *Aeolothrips fasciatus* L. (El-Serwiy et al., 1985). Salim, Masud and Khan (1987) and Peña (1990) cite it as predator of unspecified *Thrips* spp. It has also been mentioned as a predator of: Acari, *Eryophyes tlaiae* Trabut (Bergevin, 1934), *Tetranychus* spp. (Salim el al., 1987); Homoptera, *Aphis gossypii* Glover (Puchkov, 1961; Afifi et al., 1976; Salim et al. 1987), *Zaphis graminum* Rond. (Puchkov, 1961), *Rhopalosiphum maidis* Fitch (Carayon and Steffan, 1959), *Amrasca devastatus* (Dist.), *Bemisia tabaci* Gem (Salim et al., 1987); Lepidoptera, *Heliothis armigera* Hb., *Spodoptera litura* (F.), *Earias* spp., *Pectinophora gossypiella* (Saund.) (Salim et al., 1987), *Phtorimaea operculella* Zell., *Anagasta kuehniella* Zell. (Zaki, 1989); and Coleoptera, *Tribolium confusum* Duv. (Zaki, 1989).

It can be found on several vegetable plants including onion (Saxena, 1977; El-Serwiy et al., 1985), pepper (Peña, 1990), clover (Afifi et al., 1976), cotton (Al-Faisal and Kardou, 1986; Salim, 1987), *Zea mays*, *Sorghum vulgare*, *Althaea*

Table 1. Anthocoridae predators of *F. occidentalis* and *T. tabaci* found in several crops ([a]Fo= *F. occidentalis*. Tt= *T. tabaci*, [b]Lab= Laboratory studies).

Predator	Prey[a]	Cucumber	Pepper	Other Vegetables	Cotton	Ornamentals	Other Crops	Field Crop	Greenhouse	Lab[b]
A. nemorum	Fo					8			8	
Orius spp.	Fo		5,21	14,31		14		14,31	5,14,21	
	Tt	1	5		19,24			1,19	5,24	
O. albidipennis	Fo	9	9,27	9			9	9	9,27	
	Tt			11	4		2	2	4,11	
O. insidiosus	Fo	44	25,30			7,10,13 26,34			7,10,13,25 26,30,34	42
O. laevigatus	Fo		38	45					38,45	32,42
	Tt				39		2,39	2,39		
O. limbatus	Fo			9			9	9		
O. majusculus	Fo	12,20,41	12,20	20,29					12,20,29,41	12,32
O. minutus	Tt	3	28	3					3,28	
O. niger	Fo		43						43	42
	Tt	3		3					3	
O. sauteri	Tt									47
O. tristicolor	Fo	15,16,40	15,16,40	22,23,33	18,18,35,36 37,46		6,22,23,33 35	6,17,18,22, 23,33,35, 36,37,46	15,16,40	6,15,16,33
	Tt	15,16	15,16						15,16	15,16
O. vicinus (Ribaut)	Tt	3		3					3	

1. Abbas, et al., 1988; **2**. Afifi, et al., 1976; **3**. Akramovskaya, 1978; 4. Al-Faisal and Kardou, 1986; **5**. Altena and Ravensberg, 1990; **6**. Benedict and Cothran, 1980; 7. Brfdsgaard, 1991; **8**. Buxton and Wardlow, 1991; 9. Carnero et al., 1993; **10**. Claudio, 1991; **11**. El-Serwiy et al., 1985; **12**. Fischer et al., 1992; **13**. Fransen, et al., 1993; **14**. Fenton and Howell, 1957; **15**. Gilkeson, 1990; **16**. Gilkeson et al., 1990; 17. Gonzalez et al., 1982; **18**. Gonzalez and Wilson, 1972; **19**. Habib et al., 1980; **20**. Jacobson et al., 1993; **21**. Lacasa et al., 1989; **22**. Letourneau, 1990; **23**. Letourneau and Altieri, 1983; **24**. Mallah and Lohar, 1987; **25**. Van den Meiraker and Ramakers, 1991; **26**. Nedstam, 1991; **27**. Peña, 1987; **28**. Ramakers, 1978; **29**. Ramakers, 1990; **30**. Ramakers, 1993; **31**. Ribes, 1990; **32**. Riudavets et al., 1993; **33**. Salas-Aguilar and Ehler, 1977; **34**. Sörenson and Nedstam, 1993; **35**. Stoltz and McNeal, 1982; **36**. Stoltz and Stern, 1978a; **37**. Stoltz and Stern, 1978b; **38**. Tavella, Arzone and Alma, 1991; **39**. Tawfik and Ata, 1973; **40**. Tellier and Steiner, 1990; **41**. Trottin-Caudal et al., 1991; **42**. Tommasini and Nicoli, 1993; **43**. Van de Veire and Degheele, 1992; **44**. Van de Veire and Degheele, 1993; **45**. Villevieille and Millot, 1991; **46**. Yano, 1990; **47**. Zhou and Wang, 1989.

rosea, *Trifolium alexandrium*, *Nicotiana tabacum*, *Abelmoschus esculentus*, *Abutilon* spp., *Hibiscus rosa-sinensis* (Salim et al., 1987), *Tamarix* sp. (Péricart, 1972), *Bitumaria bituminosa*, *Ploclama pendula*, *Nerium oleander*, *Heliotropum erosum*, *Tagetes* sp., *Irschfeldia incana*, *Tamarix*. *canariensis*, *Echium auberianum* (Carnero et al., 1993) and steppic Compositae (Lindberg and Hak, 1953).

3.1.1.2 Life history

It is found on clover in Egypt as one of a group of associated predators made up of *Coccinella unidecimpunctata* Reiche, *Scymnus interruptus* Goeza, *Paederus alfierii* Koch and *Chrysopa carnea* Steph and *Orius laevigatus* (Fieb.), which control the populations of *T. tabaci* (Afifi et al., 1976). Together with *A. fasciatus* it controls *T. tabaci* on onions in Iraq (El-Serwiy et al., 1985). It also reduces *T. tabaci* populations on cotton in Iraq (Al-Faisal and Kardou, 1976).

According to Carnero et al. (1993) the total preimaginal development takes 22.9 days at 20°C, 20.7 at 23°C and 14.5 at 27°C with *E. kuehniella* as prey. At 24-28°C, Zaki (1989) found similar preimaginal development on *T. confusum* and *A. kuehniella* (10.0±0.28 and 11.1±0.30 days, respectively). The development is longer on *Ph. operculella* (16.3±0.47 days). No differences are found in the longevity of the females fed with these three species (20-23 days), whereas the longevity of the males feeding on *Ph. operculella* is shorter than those fed an other prey species. According to Carnero et al., (1993) female longevity is 29.5, 25.1 and 21.1 at 20°C, 23°C, and 27°C, repectively. Fecundity ranges from 125 to 160 eggs per female during its lifespan of 20-23 days (Zaki, 1989).

We can find it during the whole year throughout its range of distribution with several generations per year (Péricart, 1972). It overwinters in shed plant material, cotton flowers and in *A. rosea* (Salim et al., 1987). Adult hibernation has been mentioned in the literature by Puchkov (1961). On the Canary Islands, it is detected with mites and aphids in greenhouse peppers where IPM is performed and the pressure of treatments is low (Peña, 1990).

O. albidipennis might prove to be a promising biocontrol agent due to its wide distribution, continuous presence in cotton agroecosystems in fairly high abundance, wide range of prey, high predation capacity and ability to survive even in the absence of prey (Salim et al., 1987).

3.1.2 Orius insidiosus (Say, 1832)

3.1.2.1 Distribution, prey and host plants

O. insidiosus is nearctic. Prey of this predator include: Thysanoptera, *Frankliniella occidentalis* (Ref. in Table 1), *Sericothrips variabilis* (Beach) (Ramakers, 1978; Isenhour and Yeargan, 1981b; Isenhour and Yeargan, 1981c; Isenhour and Yeargan, 1982; Ananthakrishnan and Sureshkumar, 1985; Kiman and Yeargan; 1985), *Frankliniella tritici* (Fitch) (Ramakers, 1978; Isenhour and Yeargan, 1982; Ananthakrishnan and Sureshkumar, 1985), *Caliothrips phaseoli* (Hood) (Saucedo-González and Reyes-Villanueva, 1987), *Anaphothrips obscurus* (Muller) (Ananthakrishnan and Sureshkumar, 1985), *Leptothrips mali* (Fitch), *Haplothrips subtilis-*

simus Haliday (McCaffrey and Horsburgh, 1986b). Other prey are: Acari, *Panonychus ulmi* (Kock) (Parrella et al., 1980; McCaffrey and Horsburgh, 1982; McCaffrey and Horsburgh, 1986b), *Tetranychus urticae* (Kock) (Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986b), *Aculus schlechtendali* (Nalepa), *Neoseiulus fallacis* (Garman), *Zetzellia mali* (Ewing) (McCaffrey and Horsburgh, 1986b); Homoptera, *Aphis* sp., *Dysaphis plantaginea* (Passerine), *Quadraspidiotus perniciosus* (Cosmtoceca), *Typhlocyba pomaria* McAtee (McCaffrey and Horsburgh, 1986b); Lepidoptera, *Helicoverpa zea* (Boddie) (Barber, 1936), *H. virescens* (Fabr.) (Isenhour and Yeargan, 1981a; Kiman and Yeargan, 1985), *Spodoptera frugiperda* (Smith) (Isenhour et al., 1990), *Cydia pomonella* (L.), *Plataynota flavedana* Clemens (McCaffrey and Horsburgh, 1986b); Coleoptera, *Trogoderma glabrum* (Herbst) (Kingsley and Harrington, 1981). *O. insidiosus* is also reported to feed upon the cecidomyiid aphid predator *Aphidoletes aphidimyza* (Rondani) (McCaffrey and Horsburgh, 1986b).

According to Barber (1936), *O. insidiosus* has been found on trees, shrubs, field crops, vegetables, and many wild plants. It has been reported on the following host plants: soybean (Blickenstaff and Huggans, 1962; Ramakers, 1978; Bechinski and Pedigo, 1981; Isenhour and Yeargan, 1981a; Isenhour and Yeargan, 1981b; Isenhour and Yeargan, 1981c; Isenhour and Yeargan, 1982; Kiman and Yeargan, 1985); maize (Dicke and Jarvis, 1962; Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986b; Saucedo-González and Reyes-Villanueva, 1987; Isenhour et al., 1990); cotton (Whitcomb and Bell, 1964); alfalfa (Fenton and Howell, 1957; Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986b), chrysanthemum (Brfdsgaard 1991; Claudio, 1991; Nedstam, 1991); apple trees (Parrella et al., 1978; McCaffrey and Horsburgh, 1986b); *Cardus acarthoides* and *Verbascum thapsus* (McCaffrey and Horsburgh, 1986b). *O. insidiosus* also develops on *Phaseolus limensis* (Askari and Stern, 1972) and *P. vulgaris* (Isenhour and Yeargan, 1981a; Kiman and Yeargan, 1985; Saucedo-González and Reyes-Villanueva, 1987) under laboratory conditions.

3.1.2.2 Life history

It represents 55% of the total predator population on soybeans in the U.S.A. (Barry, 1973), and in conjunction with *Aeolothrips fasciatus* (L.) (Robinson et al., 1972) or *Nabis* spp. (Bechinski and Pedigo, 1981) it is one of the most abundant predatory insects. Its main prey is *S. variabilis* (Isenhour and Yeargan, 1981b; Isenhour and Yeargan, 1981c). In conjunction with *L. mali* and *Stethorus punctum* Le Conte, it is the most important predator in apple orchards (Parrella et al., 1978). It is an important predator of mites, and is able to rapidly colonize other habitats and to prey on other pests (McCaffrey and Horsburgh, 1986a). In the field *O. insidiosus* exists as groups of individuals that are slightly aggregated, and the crowding is greater for nymphs than for adults (Bechinski and Pedigo, 1981).

The females of *O. insidiosus* eat more *S. variabilis* than the males, and the larvae eat less than the adults. There are no significant differences in the number of larvae of *S. variabilis* consumed between the different developmental stages of *O. insidiosus* (Isenhour and Yeargan, 1981b). Evaluation of the quality of different arthropod prey, including *T. urticae* and eggs of *H. virescens* shows little difference in the development of *O. insidiosus* (Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986b).

O. insidiosus exhibited a type-II functional response with *S. variabilis* adults, *C. phaseoli* adults, and *S. frugiperda* eggs and neonates (Isenhour and Yeargan, 1981b; Saucedo-González and Reyes-Villanueva, 1987; Isenhour et al., 1990). The type-II or the type-III models provided the best fit to the data on *P. ulmi*, depending on temperatures (McCaffrey and Horsburg, 1986a).

The developmental time between 28 and 32 °C is 12 days, at 24°C 20 days and at 20°C 34 days when it feeds on *H. virescens* eggs (Isenhour and Yeargan, 1981a). The lower thermal temperature for *O. insidiosus* preimaginal development is 10 °C with *P. ulmi* as prey, and the degree-day requirements are 201.7±13.7 (13.9 days at 23 °C, 9.5 days at 29°C) (McCaffrey and Horsburgh, 1986b). Smaller differences are seen with eggs of *H. virescens* (13.7°C lower thermal temperature, 147.9±7.9 degree-days) (Isenhour and Yeargan, 1981a), and with *T. glabrum* (10.2 °C lower thermal temperature, 249.5 degree-days) (Kingsley and Harrington, 1981) as prey. Adult longevity and female fecundity at 26°C varied with the diet. They are 42.3±1.8 days and 144.3±9.5 eggs on *E. kuehniella* eggs and 17.1±1.3 days and 65.7± eggs on *F. occidentalis* adults (Tommasini and Nicoli, 1993). Female longevity is significantly higher in diets with only pollen or those which contain eggs of *H. virescens* than in diets which contain *S. variabilis*. Fecundity is significantly higher in diets which contain eggs of *H. virescens* than with pollen or *S. variabilis* (Kiman and Yeargan, 1985). Field observations suggest that *O. insidiosus* feeds on soybean pollen (Dicke and Jarvis, 1962; Kiman and Yeargan, 1985). In the laboratory they can survive on an artificial diet consisting of pollen plus water (91.2 % survival to the adult stage). However, the nymphs cannot fully develop with only beans as food (Kiman and Yeargan, 1985). On sweet pepper plants the predator population persistence at very low prey densities, may be explained by the use of alternative food sources such as pollen (van den Meiracker and Ramakers, 1991). Ruberson et al. (1991) found that nymphs of *O. insidiosus* developed faster at 10:14 (L:D) (♀19.7 days and ♂18.7 days at 20°C) than at lower photoperiods. Females entered diapause when reared under short photoperiods and 20°C, with a critical photoperiod between 12 and 13h. of day length. The oviposition behaviour of *O. insidiosus* causes any damage to a pepper crop. Females lay eggs in or adjacent to the growing tips and very few eggs in flowers and fruits (van den Meiracker and Ramakers, 1991).

Although studies of interactions between the predatory Thysanoptera *L. mali* and *O. insidiosus* indicate that they are not fully compatible and in 75% of cases *Orius* kills or eats *L. mali*, they kill more mites together than separately. In a field situation *L. mali* could move to other leaves and escape attack by *O. insidiosus* (Parrella et al., 1980). McCaffrey and Horsburg (1982) reported that *O. insidiosus* appears to coexist with *L. mali* and prey at the same time, at least during the periods when there are moderate or high prey densities (McCaffrey and Horsburgh, 1982). After releases of *O. insidiosus* and *N. cucumeris* on greenhouse sweet peppers for the control of *F. occidentalis*, *O. insidiosus* influence the abundance of *N. cucumeris* more via prey competition than by direct predation (Ramakers, 1993).

O. insidiosus is succesfully applied for the control of *F. occidentalis* on pepper in Holland and Belgium (van de Veire and Degheele, 1993; van Schelt, pers. comm.). Experimental releases of *O. insidiosus* resulted in successful control of *F. occidentalis* in chrysanthemum and saintpaulia but not in roses (Fransen et al., 1993). In combination with *N. cucumeris* resulted in fairly good control of *F. occidentalis* in saintpaulia, impatiens, brachyscome and gerbera (Sörenson and Nedstam, 1993).

Many general predators that prey on *O. insidiosus* have been identified. The most important are the arachnids *Philodromus* spp, *Misumenops oblongus* (Keyserling), *M. asperatus* (Hentz), *Misumenoides formospides* (Walckenaer), *Xysticus spp.*, *Metaphippus galathea* (Walckenaer), *Theridion albidum* Banks, and other *Theridion spp.* Other predators include the mirid bug *Deraeocoris nebulosus* (Uhler) and larvae of *Chrysopa* spp. Cannibalism has also been reported (McCaffrey and Horsburgh, 1986b).

O. insidiosus can be reared in the laboratory in closed pots with snap beans as a vegetable surface for oviposition, with a diet of *H. virescens* eggs (Isenhour and Yeargan, 1981a).

3.1.3 Orius laevigatus (Fieber 1860)

3.1.3.1 Distribution, prey and host plants

O. laevigatus is west palaearctic and found in areas with a marine influence. It has been found throughout the Mediterranean area, especially in the Iberian Peninsula, the Atlantic area of western Europe, and on the Canary, the Madeira and the Azores Islands (Péricart, 1972).

Three species of thrips have been mentioned as prey of *O. laevigatus*: *Frankliniella occidentalis* (Ref. in Table 1.), *Thrips tabaci* (Péricart, 1972, Ananthakrishnan and Sureshkumar, 1985) (Ref. in Table 1), and *Hercothrips fasciatus* Perg. (Tawfik and Ata, 1973; Ananthakrishnan and Sureshkumar, 1985). It is also a predator of many other arthropods including Acari, *Metatetranychus ulmi* Kock, *Eatetranychus cucurbitaceorum* Say (Péricart, 1972; Ananthakrishnan and Sureshkumar, 1985), *Tetranychus telarius* L. (Tawfik and Ata, 1973); Homoptera, Aleurodidae (Péricart, 1972), *Rhopalosiphum maidis* (Péricart, 1972), *Aphis gossypii* (Tawfik and Ata, 1973; Afifi et al., 1976); Lepidoptera, *Anagasta kuehniella*, *Chilo agamemnon* Bletz, *Earias insulana* (Boisd.), *Pectinophora gossypiella*, *Phtorimaea operculella*, *Pyrausta nubilalis* Hbn., *Spodoptera litura* (Tawfik and Ata, 1973; Péricart, 1972; Zaki 1989); and Coleoptera *Tribolium confusum* (Zaki, 1989).

It is associated with in a great number of plant species, especially on herbaceous plants and shrubs (*Ulex*, *Erica*, *Tamarix*, *Achillea*). Crop plants include strawberry (Villevieille and Millot, 1991), pepper (Tavella et al., 1991), broad bean, cotton and maize (Tawfik and Ata, 1973), and clover (Tawfik and Ata, 1973; Afifi et al., 1976).

Table 2. Biological studies of several *Orius* spp. fed with different prey. (^{*a}) Prey: Thrips.

	Development time. N°days (T°C)		Fecundity No.eggs/♀ (T°C)	Overwintering	Reference
	Nymph	egg+nymph			
O. albidipennis	22.9-(20°C) 20.7-(23°C) 14.5-(27°C) 11.1-(24-28°C)		143.4-(24-28°C)	yes	Zaki 1989. Carnero et al., 1993.
O. insidiosus		34.0-(17°C) 33.6-(20°C) 13.9-(23°C) 20.0-(24°C) 12.6-(28°C) 9.5-(29°C) 12.1-(32°C) 8.3-(35°C)	106.4-(24°C) 144.3-(26°C) 17.1-(26°C)^{*a}	yes	Isenhour & Yeargan 1981. Kiman & Yeargan 1985; McCaffrey & Horsburgh 1986a-b. Tommasini & Nicoli 1993.
O. laevigatus	13.2-(24-28°C) 13.9-(26°C)		160.6-(24-28°C) 112.4-(25°C) 118.8-(26°C) 55.6-(26°C)^{*a}	yes	Tawfik & Ata 1973. Zaki 1989. Tommasini & Nicoli 1993.
O. majusculus	45.2-(12°C) 13.9-(25°C) 15.2-(25°C)^{*a} 10.4-(30°C)	44.0-(15°C) 25.7-(20°C) 16.6-(25°C)	195.3-(15°C) 158.2-(20°C) 236.9-(25°C)	yes	Alouzet et al., 1990. Husseini et al., 1993.
O. niger			54.1-(26°C) 18.4-(26°C)^{*a}		Tommasini & Nicoli 1993.
O. tristicolor	26.4-(21°C) 13.9-(24°C) 14.4-(25°C) 9.3-(26°C)^{*a} 8.4-(33°C)		129.0-(25°C) 59.6-(26°C)^{*a}	yes	Askari & Stern 1972. Salas-Aguilar & Ehler 1977. Hollingsworth & Bishop 1982.

3.1.3.2 Life history

It can be associated with other predators such as *Coccinella unidecimpunctata*, *Scymnus interruptus*, *Paederus alfierii*, *Chrysopa carnea* and *O. albidipennis* and controls populations of *T. tabaci* in clover (Afifi et al., 1976).

In the laboratory at 20°C and with *F. occidentalis* as prey, *O. laevigatus* nymphs consume 1.95±0.75 larvae or 2.10±0.03 adults thrips per day. At the same temperature *O. laevigatus* females consume 1.73±0.11 larvae or 2.37±0.43 adults per day (Vacante and Tropea Garzia, 1993). At 27°C the incubation period of the egg ranged between 3 and 4 days (Tawfik and Ata, 1973). The duration of the nymph stage varies between 13.2±0.50 days with *T. confusum*, 14.8±0.42 days with *A. kuehniella*, 15.9±0.69 days with *Ph. operculella* (Zaki, 1989), 14.67 days with *S. litura* and 13.91 days with *T. telarius* (Tawfik and Ata, 1973). The duration of the first generation in IPM strawberry tunnels at 13°C is ca. 2 month (Villevieille and Millot, 1991). The males do not live as long as the females, and both live longer when fed with *A. kuehniella* (♂29.5±2.27; ♀34.5±2.63 days) and *T. confusum* (♂29.6±1.78; ♀39.2±0.08) than with *Ph. operculella* (♂21.6±1.66; ♀29.5±1.99) (Zaki, 1989). The total amount of eggs laid by a single female fed on *A. gossypii* (at 25.5°C and 48.0% R.H.) averages 112.7 eggs, with a range 54 to 167. Oviposition period ranges between 18 and 33 days. No significant differences are found in fecundity of females when fed upon the three prey studied, and number of eggs ranges from 149 to 165 (Zaki, 1989). Tommasini and Nicoli (1993) found a fecundity of 118.6±9.4 eggs with *E. kuehniella* eggs as prey and 55.6±7.8 eggs with *F. occidentalis* adults as prey (26°C, 80% RH, 16:8 L:D).

O. laevigatus adapts very well to a protected environment, and it can survive even without thrips prey (Tavella et al., 1991). *O. laevigatus* hibernate as adults in European climates, with two generations occurring in southern England (Péricart, 1972). This predator is successfully released for the control of *F. occidentalis* on strawberry tunnels in Italy (Benuzzi, pers. comm.).

3.1.4 Orius majusculus (Reuter 1879)

3.1.4.1 Distribution, prey and host plants

O. majusculus is palaearctic. It is very common throughout all Central Europe from Poland to France, part of the British Islands and southern Scandinavia. It is also found in southern Europe. In Russia, it occurs between the Volga and the Caucasus, and also in Asia Minor. It is not found in North Africa (Péricart, 1972).

Ramakers (1990) and Trottin-Caudal et al. (1991) describe it as a predator of larvae and adults of *F. occidentalis*, both in the open field and in greenhouses (Table 1). It also feeds on Acari, *Metatetranychus ulmi* (Péricart, 1972); Homoptera, *Rhopalosiphum pyri* and *Psylla pyri* (L.) (Carayon and Steffan, 1959; Alauzet et al., 1990); and eggs of Lepidoptera (Péricart, 1972), *Ephestia kuehniella* (Alauzet et al., 1990)

It is associated with a great number of herbaceous plants and trees (Péricart, 1972). On cucumber plants, adults of *O. majusculus* are found on both upper and lower leaf surfaces, while nymphs are found primarily on the underside of the leaf (Trottin-Caudal et al., 1991).

3.1.4.2 Life history

The winter population is mainly composed of females which become active in March-April in the United Kingdom. Oviposition begins in May (Péricart, 1972). With eggs of *E. kuehniella* as prey, the average number of eggs laid per female was 195.3, 158.2, and 236.9 at 15°, 20° and 25°C respectively. The average duration of the egg stage at the same temperatures was 9.43, 6.02, and 3.95 days (Alauzet et al., 1990; Fischer et al., 1992). Preimaginal development time and mortality rate are strongly influenced by temperature, and to a lesser extent by food. When fed with *E. kuehniella* eggs, development lasted 34.6, 19.7 and 12.7 days at 15°, 20° and 25°C, respectively. When fed with *R. padi* developmental time was 35.8, 20.7 and 16 days, and with *P. pyri*, 46.4, 22, and 15.8 days (Alauzet et al., 1990). Duration of nymphal stages at 25°C is 13.9±1.1 reared on *T. putriscentiae* and 15.2±1.2 reared on *F. occidentalis* (Husseini et al., 1993). According to Fischer et al. (1992) the total degree-day requirement for development is 182 and the lower developmental threshold range from 7.8°C for the first nymphal stage to 11.7°C the third nymphal stage. Adult longevity at 26°C varied with the diet. It is 47.0±2.8 days on *E. kuehniella* eggs and 19.7±1.3 days on *F. occidentalis* adults (Tommasini and Nicoli, 1993). The total consumption of inmature stadia of *O. majusculus* is 122.0±8.1 *F. occidentalis* larvae at 25°C (Husseini et al., 1993). Péricart (1972) observed that *O. majusculus* was occasionally phytophagous on chrysanthemums in Holland.

Good control of *F. occidentalis* was obtained in cucumber greenhouses in France. Treatments included different densities of *F. occidentalis* and *O. majusculus*. The best results were obtained at ratios of 1 predator per 100 thrips when starting with infestations of 10 thrips per leaf (Trottin-Caudal et al., 1991). In Switzerland, *O. majusculus* showed a good efficacy in reducing *F. occidentalis* infestations and established breeding populations on cucumber and pepper, but not on tomato. However, *O. majusculus* releases in early crops do not establish. Females enter diapause at short photoperiod conditions (Fischer et al., 1992). Jacobson (1993) formulate release methods and number of *O. majusculus* to be released in greenhouses to supplement the use of *N. cucumeris* in the 1993 season. On pepper indicates that it is necessary to make in the early season release of 3-5 *O. majusculus* per m^2 followed by a general introduction of 1.5 per m^2. From early May onwards, at the first sign of *F. occidentalis* release of 0.5 *O. majusculus* per m^2. On cucumber and eggplant in the early season release of 5-10 *O. majusculus* per m^2 followed by a general introduction of 1-2 per m^2. During mid season, at the first sign of *F. occidentalis* release of 2-3 *O. majusculus* per m^2.

O. majusculus can be easily reared in the laboratory on a diet of *E. kuehniella* eggs with *Pelargonium peltatum* used as an oviposition substrate (Alauzet et al., 1990).

3.1.5 Orius minutus (L. 1758)

3.1.5.1 Distribution, prey and host plants

O. minutus is palaearctic. According to Péricart (1972) its distribution is across Europe and western Russia, east of Turkestan, China and Siberia. Although rare in the

Mediterranean region, it is also identified from North Africa. It has been introduced into western North America. Precise information is often lacking because of taxonomic confusion with other species of *Orius* in its extensive range (Lattin, Asquith and Booth, 1989).

It is a predator of thrips including *Thrips tabaci* (Ref. in Table 1), *Frankliniella dampfi* Priesner (=*F. sulphurea Schmutz)* (Ramakers, 1978), *Megalurothrips distalis* (Karny), *Haplothrips ganglbaueri* Schmutz (Viswanathan and Ananthakrishnan, 1974), Sorghum thrips (Miao and Sun, 1987). Other prey are the Acari, *Tetranychus urticae* (Ramakers, 1978), *T. telarius* (Anderson, 1962), and *Metatetranychus ulmi* (Askari and Stern, 1972); Homoptera, *Aphis gossypii*, *Melanaphis sacchari* (Zehntner) (Miao and Sun, 1987), *A. pomi* De beer (Askari and Stern, 1972); Lepidoptera, *Ostrinia* spp., *Pseudaletia separata* Walker (Miao and Sun, 1987). Péricart (1972) mentions as prey of *O. minutus*: Aphidae, Psyllidae, Jassioidea, Thysanoptera, Acari, and eggs of Pentatomidae and Lepidoptera.

It has been found on many vegetables (e.g. peppers) (Ramakers, 1978), trees and herbaceous plants (e.g. *Glyricidia maculata)* (Viswanathan and Ananthakrishnan, 1974).

1.3.5.1 Life history

In the presence of *T. urticae* and thrips, *O. minutus* shows a preference for thrips. It consumes all stages unless they are on the ground (Ramakers, 1978). Observations of fluctuations of *O. minutus* field populations on *G. maculata* showed an increase in thrips populations (*M. distalis*, *F. dampfi*, *H. ganglbaueri*) was followed by an increase in the predator population. This leads to a fall in the thrips population (Askari and Stern, 1972).

O. minutus females lay eggs on different vegetable hosts such as *Eryngium*, *Achillea*, *Urtica*, *Verbascum* and *Rubus* (Fulmek, 1930). Eggs are laid individually or in small groups at the base of developing flower buds (Fulmek, 1930), and on the underside of leaves (Collyer, 1953). In Austria, it has 2 to 4 generations per year (Fulmek, 1930), and hibernation occurs in the adult stage (Fulmek, 1930; Puchkov, 1961). In Holland, the females leave overwintering sites at the end of March, and the first generation of adults appears in June. These adults then enter the greenhouses (Ramakers, 1978).

Fulmek (1930) states that *O. minutus* can feed on plant juices and in fact can complete its development when fed only with plant material. It is distributed on all parts of pepper plants, but especially on the flowers where the adults of *T. tabaci* feed on pollen. First instar larvae are similar in size to adult *T. tabaci*, and may reach the same places (Ramakers, 1978).

Artificial introduction of specimens collected in an apple orchard were successfully established in a greenhouse in Holland (Ramakers, 1972).

3.1.6 Orius niger (Wolff, 1811)

3.1.6.1 Distribution, prey and host plants

O. niger occupies the whole east of the palaearctic. It is very common in middle

Europe, from France to Russia. It is also found in North Africa, the Canary Islands, the Near East and the Middle East. It was mentioned in the U.S.A. by Van Duzeet in 1917, but was not confirmed in Herving's 1966 revision (Péricart, 1972).

Its prey includes the Thysanoptera (Péricart, 1972; Greathead, 1976; Ramakers, 1990), *Thrips tabaci* (Ref. in Table 1); Acari (Péricart, 1972; Akramovskaya, 1978), *Tetranychus urticae* (Puchkov, 1961; Péricart, 1972); Homoptera, *Aphis gossypii* (Akramovskaya, 1978); and Lepidoptera, *Heliothis armigera*, *Mamestra brassicae* (L.), *Spodoptera exigua* (Hübner), *Ostrinia nubilialis* (Hübner) (Puchkov, 1961), and eggs of Pentatomidae and Lepidoptera (Péricart, 1972).

It is found on the vegetable families Cucurbitaceae and Solanaceae (Akramovskaya, 1978), but it is most common on Compositae (Péricart, 1972).

3.1.6.2 Life history

It has at least two generations per year in U.K., and may have three to five in more favourable conditions (Sands, 1957). In Armenia the adults begin hibernation in late October, and become active again in early April, appearing in weeds before migrating to crops (Akramovskaya, 1978). Eggs are inserted vertically in the tender regions of the stem apex, inside the flowers, and in small groups around the base of the style, with only the operculum protruding (Sands, 1957). Adult longevity and female fecundity with *E. kuehniella* eggs as prey is 50.0±3.4 days and 54.1±11.1 eggs, respectively. With *F. occidentalis* adults as prey is 18.4±1.9 days and 16.8±4.3 eggs, respectively (26°C, 80% RH, 16:8 L:D) (Tommasini and Nicoli, 1993). Adults live from 20 to 25 days under laboratory conditions (Akramovskaya, 1978).

O. niger is important in the biological control of *A. gossypii* and *T. tabaci* on eggplants and on several Cucurbitaceae (Akramovskaya, 1978). Greathead (1976) states that this species may be interesting for controlling thrips in greenhouses.

3.1.7 Orius tristicolor (White, 1879)

3.1.7.1 Distribution, prey and host plants

O. tristicolor is nearctic and neotropical. It has a wide distribution in North America (Kelton, 1963).

It is a polyphagous predator. Its prey include Thysanoptera: *Frankliniella occidentalis* (Thomson and Simmonds, 1965; Lewis, 1973;, Ananthakrishnan and Sureshkumar, 1985) (Ref. in Table 1); *F. tritici* (Hollingsworth and Bishop, 1982; Ananthakrishnan and Sureshkumar, 1985), *F. minuta* Moulton, *F. moultoni* Hood, *Caliothrips fasciatus* (Perg.), *Haplothrips verbasci* (Osborne), *Micocephalothrips abdominalis* (Crawford), *Odentothrips loti* (Haliday) (Lewis, 1973), *Hercothrips fasciatus* Perg, *Thrips abdominalis* Crwf. (Thomson and Simmonds, 1965), *Taeniothrips inconsequens* Uzel, *Taeniothrips simplex* Morison, *Thrips tabaci* (Thomson and Simmonds, 1965; Lewis, 1973). Other prey which have been mentioned are: Acari, *Tetranychus pacificus* McGregor (Salas-Aguilar and Ehler, 1977), *Tetranychus telarius* (Thomson and Simmonds, 1965), Homoptera, *Therioaphids* *maculata* (Monell) (Gooddarzy and Davis, 1958), *Myzus persicae* (Sulzer) (Hollingsworth and Bishop, 1982), *Anuraphis bakeri* Corwen (Thomson and Simmonds, 1965), whiteflies (Salas-Aguilar and Ehler, 1977), *Paratrioza cokerelli* Sulc. (Thomson and Simmonds, 1965); Lepidoptera, *Helicoverpa zea* (Vandenbosch and Hagen, 1966).

O. tristicolor has been mentioned on these different host plants: cucumber (Gilkeson, 1990; Gilkeson et al., 1990; Tellier and Steiner, 1990); potato (Hollingsworth and Bishop, 1982); alfalfa (Gooddarzy and Davis, 1958); cotton (Vandenbosch and Hagen, 1966; Stoltz and Stern, 1978ab; Yokoyama, 1978; Stoltz and McNeal, 1982); courgette, maize and cowpea (Letourneau and Altieri, 1983; Letourneau, 1990).

3.1.7.2 Life history

O. tristicolor population dynamics followed that of thrips more closely than did other polyphagous predators (Stoltz and Stern, 1978a), and when thrips were abundant in cotton fields *O. tristicolor* could increase and provide a continuous population for suppression of mid- and late-season cotton pests (González and Wilson, 1982; Ananthakrishnan and Sureshkumar, 1985). *O. tristicolor* prefer thrips to any other prey (Vandenbosch and Hagen, 1966; Hollingsworth and Bishop, 1982). According to Salas-Aguilar and Ehler (1977), *O. tristicolor* has been found associated with *F. occidentalis* in almost 90% of their sampling, and in almost 1/3 of their samples with other non-Thysanoptera prey (spiders mites, aphids).

O. tristicolor females mated soon after emerging from the 5th. instar. Oviposition began 2-3 days after mating, and each female laid approx. 130 eggs (Askari and Stern, 1972). *O. tristicolor* sometimes lay eggs in clusters, but they are usually laid singly, inside the plant tissue. When fed on *Tetranychus pacificus* McGregor at 25.5±1.1°C and 46±4% RH the duration of the egg stage was 3-5 days (Salas-Aguilar and Ehler, 1977). Adult longevity, nymphal survival and fecundity increases as the food supply of thrips increases (Stoltz and Stern, 1978b). Mean nymphal developmental time at 26.6°C varied with the diet. It was 15.71 days on green bean and 9.33 days on pollen + *F. occidentalis*. The best diet for increasing adult longevity (15.36 days) and total egg production (59.6 eggs/♀) was bean + pollen + *F. occidentalis*, bean + thrips was intermediate, and bean + pollen the worst (at 26.6° C., 14:10 L:D) (Salas-Aguilar and Ehler, 1977). With 10, 5 or 1 *M. persicae* per day, the time required from egg to adult (13.9 days) was not significantly affected by the number of prey (at 24±2.9°C 45±5% HR 12:12 L:D) (Hollingsworth and Bishop, 1982). Both nymphs and adults are able to prey on all the developmental stages of thrips, and on adults (Gilkeson, 1990). Feeding times are variable depending on the prey stage. *O. tristicolor* adults spent 3-15 minutes feeding on thrips larvae, and 16-25 minutes feeding on adults (Salas-Aguilar and Ehler, 1977).

Adults and nymphs are frequently found in flowers. These observations suggest that their presence on floral structures corresponds to their feeding on thrips or pollen, or both (Kelton, 1963; Salas-Aguilar and Ehler, 1977). Occasionally nymphs and adults probed plant tissue, perhaps to take in moisture. An occasional probing with the rostrum is probably not harmful to the plant. However, it is not able to live only on plant tissue (Askari and Stern, 1972; Salas-Aguilar and Ehler, 1977). Early colonization was observed in polycultures versus slower colonization in monocultures (Letourneau and Altieri, 1983; Letourneau, 1990). Omnivorous feeding behaviour may explain the absence of a strong numerical response to an increasing population of suitable preferred prey species (Yokoyama, 1978; Stoltz and McNeal, 1982). Cannibalism occurs under certain conditions making mass rearin difficult. Cannibalism will be limited in nature because high concentrations of nymphs do not frequently occur (Askari and Stern, 1972).

In Canada, most late-season field-collected adults were males which did not survive, suggesting that females are the overwintering stage and they seek hibernation sites earlier (Tellier and Steiner, 1990).

Thrips control with *O. tristicolor* in a Canadian cucumber greenhouse (0.4 ha., 3000 plants) was successful with releases of one bug per plant. One advantage of using this predator on ornamental or bedding plants is that they are easily shaken from plants ready to be sold, so they can be kept in the greenhouse and need not be reintroduced when the crop is replaced (Gilkeson et al., 1990). *O. tristicolor* seems to be compatible with *Amblyseius cucumeris* (Oudemans), and both together are able to reduced thrips populations (Tellier and Steiner, 1990).

Laboratory rearing is described with bean pods for oviposition sites and with *T. pacificus* (Askari and Stern, 1972) or *F. occidentalis* as food (Stoltz and Stern, 1978b).

3.2 Other Heteroptera

Although many Heteroptera families are known as predators, only some species of the Lygaeidae, Nabidae and Miridae have been mentioned as predators of *F. occidentalis* and *T. tabaci.*

3.2.1 Geocoris spp. (Fallen).

There are some predatory species in the family Lygaeidae, though the majority are phytophagous. Three species which have been described as predators of Thysanoptera: *Geocoris ochropterus* Fabr., *Geocaris pallens* (Stal), and *Geocoris atricolor* Montandon.

3.2.1.1 Geocoris ochropterus

G. ochropterus is found in India and China. It has been mentioned as predator of 11 species of thrips (Daniel, Bakthavatsalam and Kumar, 1984; Kumar and Ananthakrishnan, 1985).

G. ochropterus is abundant on groundnuts, on *Achyranthes aspera* and on *Arachis hypogaea* (Daniel et al., 1984; Kumar and Ananthakrishnan, 1985). They prefer to eat thrips in the second stage. The females are more efficient preying on thrips than males or nymphs. In laboratory studies it has been found that the order of prey preference is: thrips, mites, aphids, tingids, whiteflies (Kumar and Ananthakrishnan, 1985).

3.2.1.2 *G. pallens* and *G. atricolor*

3.2.1.2.1 Distribution and prey

G. pallens and *G. atricolor* are nearctic. *G. pallens* is distributed in Hawaii, Central America, Mexico, the USA and Canada. *G. atricolor* is found on the whole American continent.

The described prey of *G. pallens* are: Thysanoptera, *Frankliniella occidentalis* (Ref. in Table 3); Acari, *Tetranychus urticae*, *T.turkestanea* Ugarof and Nikolski (González and Wilson, 1982; González, 1982), *T. pacificus* (González and Wilson, 1982); Homoptera, *Acyrtosiphon pisum* (Harris) (Tamaki and Weeks, 1972; Benedict and Cothran, 1980), *Aphis gossypii* (González and Wilson, 1982), *Therioaphis maculata* (Monell), *Circulifer tenellus* (Baker) (Tamaki and Weeks, 1972), *Trialeurodes vaporariorum* (Westwood) (González and Wilson, 1982); Hemiptera, *Lygus hesperus* Knight (Benedict and Cothran, 1980; González and Wilson, 1982); Lepidoptera, *Colias eurythem* Boisd., *Spodoptera praefica* (Grote) (Benedict and Cothran, 1980).

G. atricolor feeds on: Thysanoptera, *Frankliniella occidentalis* (Ref. in Table 3); Homoptera, *Acyrthosiphon pisum* (Tamaki and Weeks, 1972; Benedict and Cothran, 1980) *Therioaphids maculata* (Monell) (Tamaki and Weeks, 1972); Hemiptera, *Lygus hesperus* (Benedict and Cothran, 1980), *Nysius ericae* (Schill)

Table 3. Non-anthocorid Heteroptera predators of *F. occidentalis* and *T. tabaci* ([a] Fo = *F. occidentalis* Tt = *T. tabaci*, [b]Lab = Laboratory studies).

Predator	Prey[a]	Cucumber	Bean	Cotton	Alfalfa	Tobacco	Field Crop	Lab[b]
Nabidae								
Nabis alternatus	Fo				2		2	
N. americofernus	Fo		10		2,10		2,10	
N. ferus	Tt					3	3	
N. pseudoferus	Tt					3	3	
Lygaeidae								
Geocoris atricolor	Fo				2		2	
G. pallens	Fo			8,11 12	2		2,8 11,12	
Miridae								
Deraecoris pallens	Tt	1					1	
Dicyphus eckerleini	Tt						3,6 7	3,6 7
D. tamaninii	Fo	13						9
Macrolophus caliginosus	Fo							9
M. rubi (=*M.costalis*)	Tt					3,4 5,6 7	3,4 5,6 7	

1. Abbas et al., 1988; **2.** Benadict and Cothran, 1980; **3.** Dimitrov, 1975a; **4.** Dimitrov, 1975b; **5.** Dimitrov, 1976; **6.** Dimitrov, 1977; 7. Dirimarov and Dimitrov, 1975; **8.** González and Wilson, 1982; **9.** Riudavets et al., 1993; **10.** Stoltz and McNeal, 1982; **11.** Stoltz and Stern, 1978b; **12.** Yano, 1990; **13.** Gabarra et al., in press.

(Tamaki and Weeks, 1972); Lepidoptera, *Colias eurythem*, *Spodoptera praefica* (Benedict and Cothran, 1980).

3.2.1.2.2 Life history

G. pallens and *G. atricolor* form part of the complex of predators in cotton and alfalfa (Stoltz and Stern, 1978; Yokoyama, 1978; Benedict and Cothran, 1980; González and Wilson, 1982). Of the Hemiptera sampled in California alfalfa fields, 6% were *G. pallens* and 16% *G. atricolor* (Benedict and Cothran, 1980). They are the most abundant predators in cotton together with *O. tristicolor* (González and Wilson, 1982). Where *G. pallens* is abundant, populations of *F. occidentalis* decrease and vice-versa, helping to maintain the thrips populations of thrips at low levels (Stoltz and Stern, 1978).

The maximum number of eggs laid per female *G. atricolor* is 234 at 30°C and for *G. pallens* 89.1 at 30°C and 93.4 at 32.2°C. Developmental time of *G. atricolor* eggs ranges from 14 days at 23.9°C to 4.5 days at 35°C. For *G. pallens* it ranges from 12.3 days at 23.9°C. to 4.1 days at 35°C (Dunbar and Bacon, 1972). According to Tamaki and Weeks (1972), the developmental time of *G. pallens* eggs is 13.62±2.52 days at 22.8°C.

The developmental time of *G. atricolor* nymphs fed on *Phthorimaea operculella* (Zeller) ranges from 48.3 days at 23.9°C to 14.1 days at 35°C. For *G. pallens* it ranges from 42.2 days at 23.9°C to 12.1 days at 35°C. (Dunbar and Bacon, 1972). Acoording to González and Wilson (1982) nymphal development is 26, 16 and 14 days at 26.6°C, 32.2°C and 37.7, respectively. The temperature range at which *G. pallens* moves is 18.3°C to 40.5°C (González and Wilson, 1982).

Geocoris spp. is omnivorous and it frequently consumes plant juices (Yokoyama, 1978; Benedict and Cothran, 1980; González and Wilson, 1982). An arthropod diet increases its fecundity and survival (González and Wilson, 1982). The absence of a numerical response to the increases in *F. occidentalis* may be due to this omnivorous behaviour (Yokoyama, 1978).

A method for rearing laboratory colonies of *G. pallens* on a sunflower seed and *Oncopeltus fasciatus* (Dallas) diet is described by Yokoyama (1980). Dunbar and Bacon (1972) indicates that the optimum temperature for rearing *G. atricolor* is 30-35°C, and for *G. pallens* it is 23.9-32.2°C.

3.2.2 Nabis sp. (Latreille) (Nabidae)

This family is made up mainly of predatory species. Four species have been described as predators of Thysanoptera. Two of these have nearctic distribution (*Nabis alternatus* (Parshley) and *Nabis americoferus* (Carayon) (Canada, USA, and Mexico)), and two are of palaearctic distribution (*Nabis ferus* (L.) (Euro-Siberia, rare in the Mediterranean region) and *Nabis pseudoferus* Remane (Central and southern Europe, southern England and southern Scandinavia, the Magreb, the Middle East and the southern Caspian Sea).

3.2.2.1 Prey and host plants

The prey of *Nabis alternatus* and *N. americoferus* are: Thysanoptera, *Frankliniella* *occidentalis* (Ref. in Table 3); Heteroptera, *Lygus hesperus* (Benedict and Cothran, 1980; Stoltz and McNeal, 1982); Lepidoptera, *Colias eurytheme*, *Spodoptera praefica* (Benedict and Cothran, 1980), *Estigmene acraea* (Drury) (Perkins and Watson, 1972), *Plathypena scabra* (F.) (Sloderbeck and Yeargan, 1983); Homoptera, *Acyrthosiphon pisum* (Harris) (Richards and Harper, 1978; Benedict and Cothran, 1980; Stoltz and McNeal, 1982); and Diptera, *Agrymoza frontella* (Rondani) (Guppy 1986).

They are found in alfalfa (Benedict and Cothran, 1980), bean (Stoltz and McNeal, 1982) and soybean (Bechinski and Pedigo, 1981).

3.2.2.2 Life history

N. americoferus and *N. alternatus* are the most abundant predatory Hemiptera on alfalfa in California, the former being most abundant. Together with *Orius* spp. and *Geocoris* spp. they represent 72% of all predators (Benedict and Cothran, 1980). *N. americoferus* and *O. tristicolor* are the most abundant predators on US beans, and in 1980 they represented 80% of the total population of predators on this crop (Stoltz and McNeal, 1982). According to Ellington et al. (1984), on US cotton *Nabis* spp. represents 43% of the predators.

There is a rapid increase in *N. alternatus* and *N. americoferus* on alfalfa during April and May, and the first population peak occurs in July. The second and highest peak is found between July and August, and the third and lowest in September/October (Benedict and Cothran, 1980). *N. americoferus* does not increase in abundance on beans until the end of the crop (Stoltz and McNeal, 1982). Guppy (1986) reports that it has two generations per year in Ontario (Canada). The adults in the field occur singly with a random distribution, but the nymphs are aggregated (Bechinski and Pedigo, 1981).

No studies of their biology and feeding on Thysanoptera have been made. At 28°C and fed on *E. acraea* the longevity of the males is 35.2 days and that of females 37.3 days, with the same pattern of survival. The females lay a total of 281 eggs during a period of 31 days. The duration of the egg stage is 6.5 days. The developmental time is 3, 2.5, 2.6, 2.8 and 4.7 days for stages 1 to 5 respectively (Perkins and Watson, 1972). At 23°C with a diet of *A. pisum* females lay a total of 157 eggs in 18.6 days. The duration of the egg stage is 7.3 days. Developmental time is 2.9, 3, 3.6, 4.5 or 6.7 days for stages 1-5, respectively. The lower developmental threshold is 10.6°C, and the total degree-day requirement for development is 370.4 (Guppy, 1986).

Both adults and nymphs are predatory (Benedict and Cothran, 1980). Phytophagous behaviour has been reported for *Nabis* spp., although only to obtain water (Ridgway and Jones, 1968). Perkins and Watson (1972) found that cannibalism occurs between nymphs under laboratory conditions.

Lattin (1989) reviewed parasites and predators of the Nabidae, and found these to include some species of the Sphecidae, Pentatomidae, Reduviidae and Acari.

3.2.3 Miridae

Table 3 summarizes the information about the Miridae species which have been described as preying upon *T. tabaci* and *F. occidentalis*. All are palaearctic species:

Deraecoris pallens Reuter, *Dicyphus eckerleini* Wagner, *D. tamaninii* Wagner, *Macrolophus rubi* Woodroffe (= *M. costalis* Fieber), and *M. caliginosus* Wagner.

M. rubi and *D. eckerleine* which feed on *T. tabaci* were the most numerous beneficial insects of the predator complex on Bulgarian tobacco (*M. rubi* being 88.7% of the predaceous Heteroptera captured). This complex of predators was able to keep pest populations at such low levels that no chemical treatment was required for 3 years. Supplementary early releases of *M. rubi* adults and nymphs at a rate of 1 predator to 30-35 *T. tabaci* showed that predators kept the thrips population at low density throughout the season (Dimitrov A., 1975a, 1975b, 1976, 1977; Dirimarov and Dimitrov, 1975).

D. tamaninii and *M. caliginosus* are able to complete preimaginal development and they lay eggs only after feeding on *F. occidentalis* (Riudavets et al., 1993). On cucumber, *D. tamaninii* is able to control *F. occidentalis* populations in cage trials (Gabarra et al., in press).

3.3 Thysanoptera

Only a small proportion of Thysanoptera are thrips predators. They are mainly in the genera: *Haplothrips* Amyot and Serville, *Scolothrips* Hinds, *Franklinothrips* Back and *Aeolothrips* Haliday.

Species of the genus *Aeolothrips* mentioned as predators of Thysanoptera are: *A. collaris* Priesn. (Saxena, 1977); *A. fasciatus* L.; *A. intermedius* Bagnall; *A. kuwanii* (Moulton) (Herting and Simmonds, 1971; Lewis, 1973); *A. melisi* Priesn. (Lacasa, 1988); *A. tenuicornis* Bagnall (Lacasa, 1988; Lacasa et al., 1989) and *A. vittatus* (Haliday) (Lewis, 1973).

3.3.1 Aeolothrips fasciatus L

A. fasciatus was introduced to America from Europe. It is described as a predator of *Frankliniella occidentalis* (Baker, 1988), *Thrips tabaci* (Ferrari 1980; El Serwiy et al., 1985) and *Sericothrips variabilis* (Robinson et al., 1972).

In Iraq it first appears in fields by the third week of April, but populations were observed to decrease in May as a result of attack by *O. albidipennis* (El Serwiy et al., 1985). It is insufficient to control severe outbreaks of *T. tabaci* on onion (Ferrari, 1980). In California it has two generations per year. It can live temporarily on plants, but it needs an arthropod diet to complete its preimaginal development (Robinson et al., 1972).

3.3.2 Aeolothrips intermedius Bagnall

3.3.2.1 Distribution, prey and host plants.

Lacasa (1980) indicates that *A. intermedius* is found throughout western and eastern Europe, the Middle East and India.

The most frequent prey of *A. intermedius* are Thysanoptera: 44 species which include *Thrips tabaci* (Bournier et al., 1978, 1979; Lacasa, 1980; Lacasa et al., 1982; Grill, 1988), *Frankliniella* spp. (Lacasa, 1980), *Thrips* spp. (Lacasa, 1988; Lacasa et al., 1989), *Heliothrips hemorroidales* Bouché, and *Odontothrips confusus* Pr. (Bournier et al., 1979). Other prey are spider mites, larvae and eggs of psyllids, and microlepidoptera (Lacasa, 1988). In laboratory tests it has been found that they can complete their development on several mites including *Tetranychus cinnabarinus* Boid., *T. atlanticus* McGregor, *T. urticae*, *Panonychus ulmi* and *Cenopalpus pulcher* Oud. They could not complete their development on *Psylla melanoneura* Forst, *Trioza* spp., *Trialeurodes vaporariorum*, *Aphis fabae* Scop., *Aphis cracivora* Kock, *Acyrthosiphon pisum*, or *Myzus persicae* (Bournier et al., 1979).

This species may be considered cosmopolitan. It is common in many biocenoses of cultivated and wild plants such as strawberries (Ribes, 1990), onions (Lacasa et al., 1989), *Onobrychis sativa*, *Medicago sativa*, *Sysimbrium irio*, *Crataegus oxyacantha* (Bournier et al., 1978). A list of fifty host plants and genera is found in Lacasa (1980).

3.3.2.2 Life history

The first adults in the south of France appear in April and may have 3 or 4 generations per year (Bournier et al., 1978). Females start laying eggs one to three days after emergence. The average laying period is 14 days (29 eggs), with a maximum of 30 days (73 eggs) (Bournier et al., 1978; Lacasa, 1980; Lacasa et al., 1982). Egg incubation lasts 21 days at 14 °C, 6 days at 26 °C, and 4 days at 38 °C. The prey that permits the greatest fecundity is *T. tabaci* (Bournier et al., 1978; Bournier et al., 1979; Lacasa, 1980). Developmental time also varies with diet (Bournier et al., 1978; Bournier et al., 1979; Lacasa, 1980). The developmental time of the first, second, prepupal and pupal stages last 2, 6, 1.6, 3.4 days, respectively. After becoming an adult, it remains in the cocoon for 1.4 days (studies made at 26°C, 80% RH, 16:8 L:D) (Bournier et al., 1978; Bournier et al., 1979; Lacasa, 1980; Lacasa et al., 1982). The first-stage larva is already a predator. On average it consumes 25 *T. tabaci* larvae in order to complete its preimaginal development. It may kill but does not consume additional *T. tabaci* larvae. Its peak consumption occurs after each moult (Bournier et al., 1979; Grill, 1988). In southeast Spain, predation by *A. intermedius* is fairly limited and not quantitatively important (Lacasa et al., 1989).

It is omnivorous, and can complete its development by feeding only on flowers. It is found to eat pollen. It does not extract nutritional food from leaves and stems, but pierces them to extract water (Bournier et al., 1979; Lacasa, 1980).

Several natural enemies attack *A. intermedius* including other species of the genus *Aeolothrips*, *O. niger*, *Orius* sp., *Chrysopa* sp., *Coccinella septempunctata* L. and mites of the genus *Typhlodromus* (Lacasa, 1980).

Cannibalism occurs among the larvae in laboratory conditions, but this has not been observed in the field. Laboratory rearing must be performed individually or on a small scale because of the high percentage of cannibalism (Bournier et al., 1978; Bournier et al., 1979; Lacasa, 1980; Lacasa et al., 1982).

3.4 Acari: Phytoseiidae

The Phytoseiidae have several predatory genera, among which are *Amblyseius*

(Berlese), *Neoseiulus* (Hughes), *Euseius* (Wainstein), *Typhlodromus* (Scheuten) and *Phytoseiulus* (Evans). They are mainly polyphagous and feed on microarthropods such as Tetranychidae, Tenuipalpidae, Eriophyidae, Tideidae, Coccidae, Psocoptera, Thysanoptera and eggs of different insects. The genus *Amblyseius* containing the most species of this family. The species of this genus are morphologically very close and difficult to distinguish, and their taxonomic status has not been fully defined. The species of Phytoseiidae which have been described as predators of *F. occidentalis* or *T. tabaci* are: *A. addoensis* van der Merwe and Ryke, *A. barkeri* (Hughes) (=*A. mckenziei*) (Schuster and Pritchard, 1963), *A. potentillae* (Garman), *A. sessor* Delon, *A. urescens* A. and H., *N. cucumeris* (Oudemans) and *A. degenerans* Berlese.

3.4.1 Neoseiulus cucumeris (Oudemans, 1930)

3.4.1.1 Distribution, prey and host plants

N. cucumeris is a cosmopolitan species, and it is found in Europe, North Africa, California, Australia, etc.

The following species have been mentioned as prey of this predator: Thysanoptera, *Frankliniella occidentalis*, *Thrips tabaci* (MacGill, 1939) (Ref. in Table 4), *Thrips fuscipennis* Haliday (Ramakers, 1987; Ravensberg and Altena, 1987; Altena and Ravensberg, 1990), *Thrips* spp. (Lieburg and Staaij, 1985; Lacasa et al., 1989); Acari, *Tetranychus cinnabarinus*, *Acarus farris* (L.), *Acarus siro* (L.), *Tyrophagus* spp (Ramakers, 1982; Gillespie and Ramey, 1988), *Polyphagotarsonemus latus* (Banks) (Robinson et al., 1972).

N. cucumeris has been studied on many crops including peppers (Robinson et al., 1972; Beglyarov and Suchalkin, 1983; Klerk and Ramakers, 1986; Ramakers, 1987; Ravensberg and Altena, 1987; Altena and Ravensberg, 1990; Gilkeson et al., 1990; Peña, 1990; Tellier and Steiner, 1990), cucumbers (Beglyarov and Suchalkin, 1983; Ramakers, 1983; Ravensberg and Altena, 1987; Bennison, 1988; Duyn, 1988; Lindhagen and Nedstam, 1988; Gillespie, 1989; Gilkeson et al., 1990; Gilkeson, 1990; Steiner, 1990; Tellier and Steiner, 1990), strawberries (Ribes, 1990), cotton (MacGill, 1939), chrysanthemum (Stoltz and Stern, 1978a; Gilkeson et al., 1990), and streptocarpus (Sell and Kua-Sell, 1989b).

3.4.1.2 Life history

In autumn, different species of the family Phytoseiidae are found in Dutch greenhouses which are thought to have spontaneously immigrated, including *N. cucumeris* preying on *T. tabaci* (Woets, 1973).

According to Gillespie and Ramey (1988), the developmental time of *N. cucumeris* feeding on *F. occidentalis* is 11.1, 8.7 and 6.3 days at 20°C, 25°C and 30°C, respectively. Its fecundity is 1.5 eggs per day for 10 days at 20°C. The lower threshold temperature of larval development is 7.7°C. Castagnoli et al. (1990) found similar larval developmental time and fecundity. A pair of *N. cucumeris* consumes on average 4.92 first instar *F. occidentalis* and 3.8 of *T. tabaci* per day at 25°C. It cannot survive below 0°C, but it can be stored at 9°C with low mortality

Table 4. Known phytoseiidae predators of *F. occidentalis* and *T. tabaci* ([a]Fo= *F. occidentalis* Tt= *T. tabaci*, [b]LAB= Laboratory studies).

Predator	Prey[a]	Cucumber	Pepper	Other Vegetables	Orna-mentals	Other Crops	Field Crop	Greenhouse	Lab[b]
Amblyseius addoensis	Tt					36	36		
A. barkeri (=*A.mckenziei*)	Fo	14			8,19			8,14,19	
	Tt	2,3,4 15,16,17,18 24,25,33,35	21,27,28 29,30,32,33					4,15,16,17,18 21,24,25,27,28 29,30,32,33,35	2,3,6
A. degenerans	Fo		20					20	
A. potentillae	Tt		27					27	
A. sessor	Tt	4				37	37	4	
A. urescens	Tt		27					27	
Neoseiulus cucumeris	Fo	9,10,12 14,23,31,41,42	1,10,12 26,31,42	22,23,34	8,11 19,38			1,8,9,10,11,12 14,19,22,23,26 31,34,38,41,42	7,10,12 13,39,40,42
	Tt	4,5,9,10 12,13,14,31,33 41,42	1,10,12 27,28,30,31 33,42					1,4,5,9,10,12 13,14,27,28,30 31,33,41,42	7,10,12 42

1. Altena & Ravensberg, 1990; **2**. Bakker & Sabelis, 1986; **3**. Bakker & Sabelis, 1987; 4. Beglyarov & Suchalkin, 1983; **5**. Beglyarov & Ushchekov, 1974; **6**.-Bonde, 1989; 7. Castagnoli et al. 1990; **8**. Claudio, 1991; **9**. Duyn, van, 1988; **10**. Elliot et al., 1987; **11**. Fougeroux, 1988; **12**. Gilkeson et al., 1990; **13**. Gillespie & Ramey, 1988; **14**. Grimstad, 1988; **15**. Hansen, 1985; **16**. Hansen, 1988; **17**. Hansen, 1989; **18**. Hansen & Geyti, 1987; **19**. Hessein & Parrella, 1990; **20**. Van Houten & Van Stratum, 1993; **21**. Klerk, de & Ramakers, 1986; **22**. Lacasa et al., 1989; **23**. Lindhagen & Nedstam, 1988; **24**. Lindqvist & Tiitanen, 1989; **25**. Mikkelsen & Paulsen, 1988; **26**. Peña, 1990; **27**. Ramakers, 1978; **28**. Ramakers, 1983; **29**. Ramakers, 1987; **30**. Ramakers, 1988; **31**. Ramakers, 1990; **32**. Ramakers & Lieburg, van, 1982; **33**. Ravensberg & Altena, 1987; **34**. Ribes, 1990; **35**. Saion, 1987; **36**. Schwartz, 1988; **37**. Sciarappa et al., 1977; **38**. Sell & Kuo-Sell, 1989a; **39**. Sengonca & Bendiek, 1983; **40**. Shipp & Whitfield, 1991; **41**. Steiner, 1990; **42**. Tellier & Steiner, 1990.

(87% and 63% after 2 and 10 weeks, respectively) (Gillespie and Ramey, 1988). Sengonca and Bendiek (1983) state that when *N. cucumeris* feeds on *F. occidentalis,* its fecundity is lower than when it feeds on *T. cinnabarinus.* The critical thermo-photoperiod at which 50% of the females start diapause is 12.5 hours of light at 22 °C during the day and 17 °C at night. The percentage of females in diapause decreases when the conditions inducing diapause occur in a more advanced stage of development. Diet has not been observed to affect diapause induction (Gilkeson et al., 1990; Morewood and Gilkenson, 1991). According to Claudio (1991), *N. cucumeris* seems more sensitive to the onset of diapause when compared to *A. barkeri.*

N. cucumeris moves to high density patches of prey (Gillespie, 1989) and preys only on first instar of thrips (Gillespie and Ramey, 1988; Gilkeson, 1990; Claudio, 1991). Eggs are laid close to recently born thrips larvae (Robinson et al., 1972). Beginning with second instar thrips larvae defend themselves with more energy, moving the last segment of the abdomen and emitting a drop of excrement. Due to its specificity to first instar thrips, it may take a few months for *N. cucumeris* to control *T. tabaci* (Gilkeson, 1990).

There have been successes and failures in introductions in greenhouses in different countries. The success rate has been lower on cucumbers than on peppers, and it has been lower for the control of *F. occidentalis* than for *T. tabaci.*

In Holland *N. cucumeris* has been used for the control of *T. tabaci* and *F. occidentalis* on peppers and on cucumber. According to different authors, *N. cucumeris* successfully controls *T. tabaci* on peppers (Ramakers, 1978; de Klerk and Ramakers, 1986; Ravensberg and Altena, 1987). On cucumbers it has not given good results due to the limited availability of pollen in the crop. The effectiveness of *N. cucumeris* depends on its reproduction which is dependent upon availability of pollen (Altena and Ravensberg, 1990). *N. cucumeris* is able to establish itself on the crop even before the pest appears (Ramakers, 1983; Ramakers, 1990). A more selective method of control is needed against *F. occidentalis* besides *N. cucumeris* (Ramakers, 1987; Altena and Ravensberg, 1990). This predator fails to control *F. occidentalis,* because the females enter reproductive diapause during winter and the egg hatching success drops at low humidity conditions (van Houten et al., 1993). According to Ramakers (1983), an inundative release for the control of *T. tabaci* would be easier in spring, after the appearance of the pest (1200/pl.), but control of the pest is less predictable than with inoculative introductions. The populations of *N. cucumeris* remain active until August, when growers begin to use insecticides against aphids and noctuids. Most farmers make two introductions on pepper (Ravensberg and Altena, 1987; Ramakers, 1990). The first commercial application (60 ha) for control of *T. tabaci* was made in 1985, at a release rate of 24,000 predators per ha. The number of hectares to which *N. cucumeris* is being applied has gradually increased, reaching ca. 530 in 1990. Commercial insectaries advise release of 150,000,000 predators/ha./season (de Klerk and Ramakers, 1986; Ramakers, 1990).

In Canada introductions for control of *T. tabaci* and *F. occidentalis* have been made on greenhouse cucumbers, peppers and chrysanthemums (Elliott et al., 1987; Gillespie, 1989; Gilkeson et al., 1990; Gilkeson, 1990; Morewood and Gilkeson, 1991). Gillespie (1989) stated that on greenhouse cucumber *N. cucumeris* manages to keep *T. tabaci* and *F. occidentalis* populations low, showing a numerical response to increases in the pest. There have been positive results in chrysanthemum crops (Gilkeson, 1990). After successful experimental introductions on cucumbers in 1985, the first commercial introductions were made in 1986 with 200,000 predators/ha./week on 4 ha. This increased to 25 ha. in 1989 (Elliott et al., 1987; Gillespie, 1989; Gilkeson et al., 1990). Inundative releases of 100-200 predators per plant would be sufficient according to Gillespie (1989), and the cost is similar to that of pesticides (Gilkeson, 1990). They do not recommend the use of *N. cucumeris* if the night-time temperature is below 21 °C in order to avoid diapause (Morewood and Gilkenson, 1991). With other release with *O. tristicolor* control is more effective (Gilkeson et al., 1990, Tellier and Steiner, 1990). Selection of pesticide resistent strains (Elliott et al., 1987) and selection of non-diapausing races (Morewood and Gilkenson, 1991) are being considered.

In the United Kingdom successful introductions have been made to control *T. tabaci* on cucumbers. They are introduced when the first symptoms of thrips damage are seen by inundation with 250 predators per plant, and then three consecutive introductions of 50 per plant every 15 days (Bennison, 1988). *N. cucumeris* is used against *T. tabaci* in greenhouse cucumbers in Rusland, and they control the pest when released at predator-prey ratios of 1:1, 1:2 and 1:5 (Beglyarov and Suchalkin, 1983). *N. cucumeris* is also successfully used to control *T. tabaci* in cucumbers in France (Grill, 1988).

Tests have been made for *F. occidentalis* control in several countries with hopeful results (on greenhouse cucumbers in Norway (Grimstad, 1988), and on *Streprocarpus* in Germany (Sell and Kuo-Sell, 1989b). On greenhouse cucumbers in Sweden, *N. cucumeris* maintained the *F. occidentalis* populations low, although there was some reduction in fruit quality. Despite repeated introductions in melon, *N. cucumeris* has not been successfully established (Lindhagen and Nedstam, 1988). In Spain good control of *F. occidentalis* with *N. cucumeris* has not been achieved in protected crops (Lacasa et al., 1989). Field releases of *N. cucumeris* in strawberries has not resulted in establishment (Ribes, 1990).

Cannibalism has been observed both in the field and in the laboratory (Ramakers, 1983). If mixed populations of *N. cucumeris* and *A. barkeri* are introduced in peppers, *N. cucumeris* may displace *A. barkeri* (Ramakers, 1983). However, on greenhouse cucumbers *N. cucumeris* is displaced by *A. barkeri* in situation of interspecific competition (Brfdsgaard and Hansen, 1992). *N. cucumeris* is more aggressive than *A. barkeri* and is better adapted to other hosts (Claudio, 1991).

Massive rearing is performed with *A. farris* on wheat bran and 100,000 Phytoseiidae/litre can be produced (Ramakers and Lieburg, 1982; Ravensberg and Altena, 1987; Gillespie and Ramey, 1988; Hessein and Parrella, 1990). According to Hessein and Parrella (1990) the approximate production cost (in 1990) is $1/2 every 1,000 predators.

3.4.2 Amblyseius barkeri (Hughes, 1948) (=*Amblyseius mckenziei* (Schuster and Pritchard, 1963)

Table 5. Biological studies of the predatory mites *N. cucumeris* and *A. barkeri* ([a]Fo = *F. occidentalis*, Tt = *T. tabaci*).

	prey[a]	Preimaginal time developmental (days)			N° eggs/♀/day		consumption of thrips larvae/day	reference
		20°C	25°C	30°C	20°C	25°C		
N. cucumeris	Fo	11.1	8.7	6.3	1.5			Gillespie & Ramey (1988)
	Fo		9.0			1.8	6.6	Castagnoli et al., (1990)
	Tt		8.2			2.0	3.6	Castagnoli et al., (1990)
A. barkeri	Tt		6.2			2.3	3.0	Bonde (1989)
	Tt		6.0			2.0		Beglyarov & Suchalkin (1983)

3.4.2.1 Distribution, prey and host plants

A. barkeri is cosmopolitan, and can be found in Europe, northern and equatorial Africa, California and Israel. According to Ferragut, Domínguez-Gento and García-Marí (1990) it is the most abundant Phytoseiidae on wild plants in Spain comprising 44% of the total.

Its prey includes *Frankliniella occidentalis, Thrips tabaci* (Ref. in Table 4), *Thrips palmi* Karny (Kajita, 1986; Guyot, 988), *Tetranychus urticae* (Karg, Mack and Baier, 1987; Petrova and Khrameeva, 1989), *Tyrophagus putrescentriae* (Schrank) (Kajita, 1986), and *Acarus farris* (Oudemans) (Beglyarov and Suchalkin, 1983; Ramakers, 1983; Hansen and Geyti, 1987; Hessein and Parrella, 1990).

Crops on which it is found or has been introduced are cucumbers (Beglyarov and Suchalkin, 1983; Ramakers, 1983; Bakker and Sabelis, 1986; Grasselly et al., 1987; Hansen and Geyti, 1987; Ravensberg and Altena, 1987; Saion 1987; Hansen, 1988; Mikkelsen and Paulsen, 1988; Grimstad, 1988; Hansen, 1989; Linqvist and Tiitanen, 1989), peppers (Robinson et al., 1972; Ramakers, 1983; de Klerk and Ramakers, 1986; Ravensberg and Altena, 1987; Ramakers, 1988; Ramakers, 1990), horticultural crops (Hansen, 1985), chrysanthemums (Hessein and Parrella, 1990), and other ornamental plants (Ferragut et al., 1990).

3.4.2.2 Life history

It is found with other species of *Amblyseius* preying on *T. tabaci* in greenhouse peppers in Holland at the end of the crop (Woets, 1973). The distribution of *A. barkeri* coincides with where thrips lay their eggs, a few centimetres from the top of the shoot (Robinson et al., 1972). They lay their eggs individually on the underside of the leaves (Bonde, 1989).

A. barkeri lays an average of 2.3 eggs/day according to Bonde (1989), and 2 eggs/day according to Beglyarov and Suchalkin (1983). The developmental time is 6.2 days at 25 °C when it feeds on *T. tabaci*, divided into 2.2 days for egg development and 4 days for immature development according to Bonde (1989). Beglyarov and Suchalkin (1983) determined developmental time to be 6 days at the same temperature. The preovoposition period is 2.1 days. Female longevity is 29.6 days, and male longevity is 27.4 days (Bonde, 1989). Females and males consume an average of 89 and 82 first larvae stages of *T. tabaci*, respectively, during their lifespan (Bonde, 1989). In 24 hours, they are capable of consuming 2.0 *T. palmi* larvae (Kajita, 1986). *A. barkeri* shows a preference for the first larval stage of thrips over the second (Kajita, 1986; Bakker and Sabelis, 1987; Hansen and Geyti, 1987; Guyot, 1988; Bakker and Sabelis, 1989). They do not prey on adults (Kajita, 1986; Gillespie, 1989). According to Sengonca and Bendiek (1983), the immature stages cannot completely develop only on *F. occidentalis*.

Different authors have studied release methods and the number of *A. barkeri* to be released in greenhouses to control *T. tabaci* and *F. occidentalis*.

In Denmark, successful introductions for *T. tabaci* control have been made on greenhouse cucumbers (Hansen, 1985; Hansen and Geyti, 1987; Mikkelsen and Paulsen, 1988). Hansen (1988, 1989) conducted several field trials to determine the number of predators to be released per square meter to control *T. tabaci* on cucumber. According to the same author, up to a minimum of 300-400 predators per sq m. it is not able to control the populations of thrips. In Holland *A. barkeri* has been released for *T. tabaci* control (Ramakers, 1983; Klerk and Ramakers, 1986; Ravensberg and Altena, 1987; Ramakers, 1988). According to Ramakers (1983) it is necessary to introduce 1200 predators per plant when the first symptoms of the presence of thrips are detected in order to control *T. tabaci* in greenhouse cucumbers. A second introduction may be necessary even if the pest disappears. Ramakers (1990) advises using *A. barkeri* as a biological insecticide, recommending the release of 500,00 mites/ha every fortnight. In Finland Lindqvist and Tiitanen (1989) indicate that it is necessary to make 4 to 6 introductions of *A. barkeri* at a rate of 15 to 20 predators per square meter to control *T. tabaci* on greenhouse cucumbers. Successful introductions for control of *T. tabaci* have also been made on greenhouse cucumbers in Czechoslovakia (Taborsky et al., 1988), and in Rusland (Saion, 1987; Beglyarov and Suchalkin, 1983).

Little information is available on the potential for control of *F. occidentalis* with *A. barkeri* (Hessein and Parrella, 1990). *A. barkeri* manage to keep *F. occidentalis* under control on chrysanthemums where adult thrips presure is intense with regular introductions of 3 mites per leaf. If the thrips population is low, they recommend the addition of pollen.

Cannibalism has been observed both in the field and in the laboratory (Ramakers, 1983). In greenhouses, *A. barkeri* can coexist with *N. cucumeris* over several generations, but in the end *N. cucumeris* displaces *A. barkeri* (Ramakers, 1983, 1988).

A. barkeri is more effective than *N. cucumeris* against *T. tabaci* in cucumbers (Beglyarov and Suchalkin, 1983; Saion, 1987; Mikkelsen and Paulsen, 1988). Mass rearing of *A. barkeri* is easier, and it is less sensitive to pesticides (Hansen and Geyti, 1987; Hansen, 1989). According to Ravensberg and Altena (1987), it is not satisfactory for large-scale use since it requires a lot of attention and sporadic use of insecticides.

Table 6. Other known predators of *F.occidentalis* and *T.tabaci*.

	Predators	Reference
F. occidentalis	Anystidae:Prostigmata	15
	Anystis agilis Banks	
	Laelapidae:Mesostigmata	
	Hypoaspis aculifer (Canestrini)	5,6,7
	H. miles Berlese	7
	Coccinellidae:Coleoptera	
	Cryptomorpha desjardinsi (Guér.)	11
T. tabaci	Grillidae:Orthoptera	
	Oecanthus longicauda Mats	10,15
	O. turanicusa Uv.	9,10
	Chrysopidae:Neuroptera	
	Chrysopa Leach *sp.*	15
	Chrysopa carnea Stephens	1,2,3,4,12
	Coccinellidae:Coleoptera	
	Hippodamia convergens (Guér.)	10,15
	Coccinella novemnotata Hbst.	10,15
	C. repanda Thunberg	10,15
	C. undecimpunctata Hbst.	1
	Coleomegilla maculata (Deg.)	15
	Scymnus interruptus (Goeze)	1,8
	S. nubilus Muls	12
	Malachiidae:Coleoptera	
	Laius externotatus Pic	12
	Staphylinidae:Coleoptera	
	Paederus alfierii Koch	13
	Syrphidae:Diptera	
	Mesograpta marginata Say	9,10
	Sphaerophoria ruepelli (Wiedemann)	14
	Syrphus corollae Fabricius	9,10
	Syrphus sp. Honeybess	15

1. Afifi et al., 1978; **2**. Awadallah et al., 1976; **3**. Beglyarov & Ushchekov, 1974; **4**. Dimitrov, 1975a; **5**. Gilkeson, 1990; **6**. Gillespie and Quiring, 1990; **7**. Glockemann, 1991; **8**. Habib et al., 1980; **9**. Herting & Simmonds, 1971; **10**. Lewis, 1973; **11**. Peña, 1990; **12**. Saxena, 1977; **13**. Tawfik & Abouzeid, 1977; **14**. Tawfik et al., 1974; **15**. Thompson & Simmonds, 1965.

Mass rearing of *A. farris* is made on wheat bran (Beglyarov and Suchalkin, 1983; Ramakers, 1983; Hansen and Geyti, 1987; Hessein and Parrella, 1990). Kajita (1986) reared it on *T. putrescentriae*. It is possible to produce 100,000 mites per litre can be achieved (Ramakers, 1983),and the financial cost is $1-2 per 1,000 mites (Hessein and Parrella, 1990).

3.5 Other predators of Thysanoptera

Miscellaneous predators of *F. occidentalis* and *T. tabaci* are mentioned in the literature (Table 6), but there is no information about their biology when exposed to these pest species.

4. Conclusions

Predators are recently receiving more interest as regulators of pest populations, but we do not have enough information on the predators of thrips to successfully apply IPM programmes for control of *F. occidentalis*. Tables 1 to 5 summarize the diversity of predators which can prey on *F. occidentalis* and *T. tabaci*. The number of references to predators of *F. occidentalis* is lower than to *T. tabaci*. This is probably due to the fact that *F. occidentalis* is a more recent pest whose natural enemies have not been fully studied. Therefore it is possible that future studies will extend the number of species known to prey on *F. occidentalis*.

Many studies have been conducted with Phytoseiidae due to previous experiences with this group in controlling Tetranychidae in greenhouse. In these instances, ease of mass production played a more important role than control efficiency. Much work has been done on the problems which followed their use in greenhouse IPM programs for the control of *T. tabaci* and more recently *F. occidentalis*. For the control of *T. tabaci* on peppers and cucumbers, *N. cucumeris* and/or *A. barkeri* were found to reduce the populations of thrips, though they are not so effective in other crops or against *F. occidentalis*. They are only able to prey on first stage larvae, and they enter diapause at low temperature and short photoperiod conditions. These Phytoseiidae are released in very high numbers as a biological pesticide and they are easy and economical to rear.

Because of the failure to effectively control *F. occidentalis* with Phytoseiidae, Anthocoridae are currently receiving much attention. *O. tristicolor* and *O. insidiosus* have been studied as predators of thrips. *O. tristicolor* has been successfully tested on greenhouse cucumbers in Canada and *O. insidiosus* has been introduced into Europe.

Less attention has been paid to other groups. For example, the species of palaearctic Anthocoridae and Nabidae have been studied less that those of the nearctic region, where more attention has been paid to the natural complex of predators in general. Some families, such as Miridae, Chrysopidae or Coccinellidae have not been fully studied as predators of thrips, although they have been studied on other prey. Apart from *N. cucumeris* and *A. barkeri*, other Phytoseiidae have received little attention. The same is true for predatory Thysanoptera.

There remains a group of miscellaneous predators (Table 6) for which biological studies have not been made. These species must be studied for thrips control before judging their potential efficacy.

In order to select a suitable candidate, it is necessary to study which characteristics make a good predator. Different authors have discussed the characteristics of a good natural enemy, and the criteria for selection (Huffaker and Messenger, 1976; van Lenteren, 1986; van Lenteren and Woets, 1988; Bigler, 1989). A good predator of *F. occidentalis* could be selected on the basis of some general characteristics and some more specific characteristics of the predator: presence in natural conditions at high levels; ability to prey upon most developmental stages of the thrips; ability to search on different plant parts; survival at low prey densities, ability to use other resources as alternative food; development at low temperatures without entering in diapause; no negative effects on the plant; ease of rearing; preference for the pest; compatibility with other natural enemies.

Selection criteria should be based upon the kind of control program envisioned. For inoculative biological control, it is very important to select for specific characteristics that allow establishment of the predator population in a crop. For conservation or augmentation of native predators, a predator should be considered even if it does not have the specifically desired criteria. The importance of native polyphagous predators that act in complexes is often undervalued. These complexes may be very effective, but if the predators are taken individually they might be considered relatively ineffective leading us to erroneous conclusions (Luff, 1983). On this point Waage (1990) reminds us that we cannot make too reductionist an approximation of selection, since it could lead us to loose good candidates.

For inoculative biological control it can be important to choose a predator that is able to search on different plant parts, can develop without entering diapause, does not damage the plant, has a preference for the pest, and is easy to rear. It is not necessary to find the predator at high population levels. Could be interesting to choose a predator that it preys on most developmental stages of the thrips, unless they do it very effectively in one specific stage, and it were compatible with other natural enemies. An ability to survive on the plant at low prey densities could also be important to reduce the significance of thrips as virus vectors. Non survival can be mitigated with repeated predator releases.

For conservation or augmentation of native predators it is important to choose a predator which occurs naturally at high levels, and is able to search different plant parts. It is also important that it can develop at low temperature to avoid diapause, and that it has no negative effects on the plant. Preference for the pest could also be important, but being able to consume other food sources and switch to consume thrips if the latter appears in the crop. This will be necessary to prevent thrips as vectors of TSWV. If it acts in association with other predators, both species should be compatible one another. For conservation ease of rearing would not be necessary to consider.

Most of these criteria have not been studied for all predators we reviewed. For the Phytoseiidae, it is known that they are easy to rear and prey only on first instar larvae. The temperatures at which they enter diapause are known, as is their searching behaviour on plant parts and compatibility with other predators. Predators from the order Thysanoptera are only able to prey on first instar larvae. They are difficult to rear and occasionally cause negative effects to the plant. Some species of *Orius* occur at high levels in different crops, and are found with associated predators. They prey upon all thrips developmental stages, and can search all plant parts. They can survive at low prey densities and consume alternative food sources. Diapause has not been studied for *Orius* spp.. Damage to the plant has been reported, and they are difficult to rear. *O. insidiosus* and *O. tristicolor* prefer thrips species as prey. Relatively little is known on the biology of the Heteroptera summarized in Table 3. They are present at high levels in different crops, and it is reported that they survive at low prey densities. For the remainder of the predators summarized in Table 6 little is known of their association with thrips pests.

Future research is needed on the biological aspects of most of these natural enemies. It is necessary to know the behaviour they have in the field. We should not ignore the possibility of finding good candidates for biological control of thrips among these species or others yet unknown without more thorough research.

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Biological control of thrips pests: a review on thrips parasitoids

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Contents

Abstract

As part of a study on the biological control of thrips pests in European greenhouses, a general literature review has been carried out on thrips parasitoids. Except for data already published on this group, information has been supplemented with data of yet unpublished records obtained by checking museum material and by personal communication, until December 1993. Thrips parasitoids all belong to the superfamily Chalcidoidea. Most of them are solitary endoparasitoids of larvae (Eulophidae) or eggs (Mymaridae, Trichogrammatidae) of thrips (Thysanoptera). Except for some odd species in the genus *Thripastichus* (Eulophidae: Tetrastichinae) and *Pediobius* (Eulophidae: Entedontinae), all larval parasitoids can be found in four closely related genera: *Ceranisus*, *Goetheana*, *Thripobius* and *Entedonastichus* (Eulophidae: Entedontinae). They all are solitary, internal parasitoids of the larval stages, although sometimes the prepupae and/or pupae may be attacked. Parasitoids belonging to the genus *Megaphragma* (Hymenoptera: Trichogrammatidae) and *Pediobius indicus* (Hymenoptera: Mymaridae) are known to parasitize thrips eggs.

In this review data of genera and species are presented on the distribution, host range, host plant associations, biology and behaviour of thrips parasitoids and their effectiveness as control agent of thrips pests, including several new records. Based on this information, their effectiveness is evaluated and specified pre-introduction criteria are formulated for selection of parasitoids as potential biological control agents of thrips pests, in particular those occurring in European greenhouses. Information on parasitoids is scattered and very incomplete, both on biology and taxonomy. A taxonomic revision of thrips parasitizing genera and species is therefore strongly recommended.

1. Introduction

Thrips are often considered as key pests in many crops all over the world (Umeya et al., 1988; Palmer et al., 1989; Talekar, 1991). With a continuous expanding market, changes in production and market systems and exchange of plant products as food and ornamentals all over the world, they are a constant threat to agricultural and horticultural crop pest management (Vierbergen, 1992). Because of direct feeding damage by deformation and abortion of fruits, leaves and flowers, and indirect feeding injury by scarring and deforming marketable products and by transmission of viruses (Tomato Spotted Wilt Virus), they can cause serious yield losses in many vegetables and ornamentals, both in the field as well as in greenhouses.

With a few exceptions of thrips species belonging to the order Tubulifera (*Haplothrips, Liothrips, Gynaikothrips*), most pest species belong to the order Terebrantia. Species belonging to the family Thripidae – Panchaetothripinae (e.g. *Heliothrips haemorrhoidalis* Bouché, *Parthenothrips dracaenae* Heeger) are widespread, polyphagous leaf feeders. Those species belonging to Thripidae – Thripinae, especially a number of polyphagous, multivoltine species belonging to the genera *Frankliniella* (e.g. *occidentalis, schultzei, tritici, fusca, bispinosa*), *Thrips* (*palmi, tabaci, simplex*), *Megalurothrips* (*usitatus, sjostedti*), and *Scirtothrips* (*citri, dorsalis*), have become important pests. Occasionally univoltine species (*Kakothrips pisivorus* (Westwood) in the 1930's in Europe and *Taeniothrips inconsequens* (Uzel) in recent years in Northeastern U.S.A) can cause severe losses. Until the early eighties *Thrips tabaci* Lind. was the most important thrips pest in Europe. Since the introduction of the Western Flower Thrips, *Frankliniella occidentalis* (Pergande) into Europe, this species became the number one key pest in many greenhouse and field crops, vegetables, ornamentals, fruit trees and weeds (see Tommasini & Maini, this volume). *T. palmi* is currently one of the most threatening examples, spreading worldwide very quickly (Hawaii, Florida, Caribbean, etc.), but has not yet established in Europe. Recently *Echinothrips americanus* Morgan, noted as a pest in ornamentals in the USA, was introduced in greenhouse ornamentals in The Netherlands (Vierbergen, pers. comm.).

In most crops chemical control is the most important way of controlling thrips pest outbreaks. Due to mechanical problems, their hidden lifestyle (eggs in plant tissue, pupae in soil, larval stages hidden in buds or between leaf- and flower structures (Mantel & Van de Vrie, 1988)), their short life-cycle and a zero-tolerance for some export products, chemical treatments have to be repeated often. They not only upset regular IPM programs for greenhouse crops, they also increase development of insecticide resistance (*S. citri*: Immaruju et al., 1990; *F. occidentalis*: Race, 1961; Böhmer & Eilenbach, 1987; Immaruju et al., 1992; *T. palmi*: Rajulu & Gowri, 1988). Developing monitoring systems, treatment threshold levels and application of biological control measures can decrease the number of sprays. Introduction of predators (predatory mites, pirate bugs) to control *F. occidentalis* and *T. tabaci* has already proven to be successful in a number of crops (see Riudavets, 1994). There have been only few attempts to use hymenopterous parasitoids as biological control agents in an inoculative way (Clausen, 1978). There have been little or no attempts, however, to release them in seasonal inoculative programs for controlling thrips pests in greenhouses. *T. tabaci* is parasitized by a number of parasitoid species, but little is known from parasitoids attacking *F. occidentalis* (Loomans, 1991).

This review summarizes the current situation on knowledge presented in the literature of hymenopterous parasitoids as natural enemies of thrips in general, supplemented with data of yet unpublished records obtained by checking museum material and by personal communication, until December 1993 and evaluates their potential as biological control agents of thrips pests.

2. Material and methods

2.1 Sources

We performed an intensive computer search, scanning different databases (see Loomans & Van Lenteren, 1990), e.g. CAB-PESTCD (1973-1993), AGRICOLA (1973-1993), etc. Besides this we checked all available issues of abstract and review journals (Review of Applied Entomology, Entomological Abstracts, Zoological Records), using Mantel's bibliography on WFT (Mantel, 1989) and Boucek & Askew's Index of Palearctic Eulophidae (Boucek & Askew, 1968) as a start. This review is the first comprehensive study of thrips parasitoids. Earlier reviews (Lewis, 1973; Suchalkin, 1983; Ananthakrishnan, 1984; Takagi, 1988) have been presented before. Parasitoids and their hosts have been listed on several occasions (Sakimura, 1937a; Thomson, 1950; Ferrière, 1958; Lewis, 1973; Ananthakrishnan, 1969, 1973, 1984; Takagi, 1988; Waterhouse & Norris, 1989; Loomans & Van Lenteren, 1990), but because of being outdated, reclassification of parasitoid species, incompleteness, erroneous records of parasitoids and hosts or even mistakes, a revision was needed. Also changes in the use of names and synonyms over time (listed in appendix 1 for parasitoids and appendix 2 for thrips hosts), greatly hampered the search. In order to avoid errors by recitation, we checked all original literature records. Parasitoids of thrips, which have been identified only to the genus level as well as species closely related to (within the same genus) thrips-parasitizing species, but without any host records, are also included. Information on thrips parasitoids in the literature is very scattered however, and is as far as possible completed with unpublished material of the senior author himself, personal communications or collections of colleagues (indicated as either 'pers. comm.' or 'pers. coll.') and museum collections ('BMNH' = British Museum Natural History), situation until December 1993. A future search should include scanning the Internet/E-mail personal databases as well.

2.2 Objectives

Objectives of this review are to:

1. describe shortly their taxonomy and systematics;
2. summarize the available data for each thrips parasitoid species, based on
   a. geographical and climatic distribution (Müller, 1974), host range, host plant associations
   b. biology and foraging strategy, factors influencing population development in the field, abiotic factors, previous biological control applications and rearing methods;
3. based on data mentioned under 1 and 2, evaluate the potential of all known para-

sitoids attacking thrips as a biological control agent of thrips pests, with particular emphasis on *F. occidentalis* and *T. tabaci* in the European greenhouse industry. Selection criteria for evaluation in the laboratory prior to field release will be discussed for each type of release method used (e.g. Van Lenteren, 1986) in order to develop a biological control program.

For information on the biology, behaviour, ecology, collection, morphology and control of Thysanoptera in general we refer to e.g. Lewis (1973), Bournier (1983) and Ananthakrishnan (1984); that of Hymenoptera can be found in e.g. Gauld & Bolton (1988). For the general use of evaluation and selection criteria we refer to Mackauer et al. (1990).

3. Hymenopterous parasitoids of thrips

3.1 Systematic notes

Hymenopterous parasitoids of thrips all belong to the superfamily Chalcidoidea. Most of them are solitary endoparasitoids of larvae (Eulophidae) or eggs (Mymaridae, Trichogrammatidae). A few species in the genera *Psilogaster* and *Orasema*, belonging to the Eucharitidae are reported as ectoparasites of thrips larvae (Johnson, 1988) and some sphecid species (Hymenoptera: Sphaecoidea) in the genera *Spilomena*, *Ammoplanus* and *Xysma* (Muesebeck et al., 1951; Krombein, 1958) and *Microstigmus* (Matthews, 1970) have been reported as being predacious on thrips larvae, but they will be discussed only briefly. A classification of endoparasitoids of thrips is given in table 1. In his key Boucek (1976) includes *Ceranisus* Walker, *Goetheana* Girault, *Thripobius* Ferrière, and *Entodonastichus* (*Thripoctenoides*) to the group of entedontine genera. This group of genera differs from the other entedontines by having the funicle two-segmented, and the head and thorax smooth.

Most taxonomic studies on thrips parasitoids have been done for the palearctic region. Generic keys for eulophids are available for the palearctic (Peck et al., 1964; Graham, 1963; Trjapitzin & Kostjukov, 1978), holarctic (Schauff, 1991) and oriental region (Hayat, 1985) and for tetrastichinids for the palearctic region only (Graham, 1987). Thrips parasitoid taxonomy mostly has been limited to catalogues for other regions (nearctic; Peck, 1963; Burks, 1979), (neotropical; DeSantis, 1979) (oriental region; Hussein & Kahn, 1986). More comprehensive work has been done for eulophids by Boucek (1988) for the Australasian region and by Schauff (1991) for the holarctic region and for trichogrammatids by Doutt & Viggiani (1968), worldwide. Graham (1963) and Erdös (1971) provided keys to European species of this group and Subba Rao (1969) and Lin (1992), provided keys for a number of egg parasitoid species known at that time. However there are no keys

Table 1. Systematic classification of parasitoids attacking thrips (order Hymenoptera, superfamily Chalcidoidea).

Family	Subfamily	Genus
Eulophidae	Entodontinae	*Ceranisus*
		Thripobius
		Goetheana
		Entedonastichus
		Pediobius
	Tetrastichinae	*Thripastichus*
Trichogrammatidae	Oligositinae	*Megaphragma*
Mymaridae	Mymarinae	*Polynema*

available to species for other regions of the world. The identification of species and genera of this group is greatly hampered because of this and revision of thrips parasitizing genera is badly needed.

Changes in names and synonymies of thrips species (Thysanoptera) used over time are standardized using the works of Jacot-Guillarmod (1970, 1971, 1975, 1978, 1983) and Jacot-Guillarmod & Brothers (1986). Synonyms are listed in appendix 1 for parasitoids and appendix 2 for their thrips hosts.

3.2 Larval parasitoids

Except for some odd species in the genus *Thripastichus* (Eulophidae: Tetrastichinae) and *Pediobius* (Eulophidae: Entedontinae), all larval parasitoids can be found in four closely related genera: *Ceranisus*, *Goetheana*, *Thripobius* and *Entedonastichus* (Eulophidae: Entedontinae). They all are solitary, internal parasitoids of the larval stages, although sometimes the prepupae and/or pupae may be attacked. In Boucek (1976) a key is presented to separate the four genera mentioned.

3.2.1 Eulophidae, Entedontinae

3.2.1.1 Genus *Ceranisus* Walker

Synonymy
Ceranisus Walker 1840
Thripoctenus Crawford 1911
Epomphale Girault 1915
Entedonomphale Girault 1915
Cryptomphale Girault 1917

Taxonomy
In literature other species have been described in the genus *Ceranisus* in the past, based on Walker's description of the genus (Walker, 1838). The American species from Florida referred to this genus by Ashmead (*flavipes*, *lecanii* and *flavopictus*) and the European species *crino* (Walker, 1838), have all been transferred to the genus *Tetrastichus* (*flavipes* Ashmead, *minutus* (Howard) and *flavopictus* (Ashmead) by Burks (1943) and *crino* (Walker) by Krombein (1979). *Cycloscapus pusztensis* Erdös & Novicky 1951 and *Cycloscapus arenarius* Erdös 1951 (Erdös, 1951), referred to by Erdös (1956) as both belonging to the genus *Ceranisus*, have been transferred respectively to *Diglyphus pusztensis* (Erdös & Novicky) and *Diaulinopsis arenaria* (Erdös) (Boucek, 1959). DeSantis (1979) erroneously mentioned *Euderomphale menes* (Walker) (= *E. flavimedia* Howard 1881) and *Euderomphale clavicornis* (Thomson) (= *Ceranisus pacuvius*?) as synonyms of *Ceranisus menes* (see Graham, 1963; Erdös, 1966). Fullaway & Dobroscky (1934) erroneously cited Girault (1915) that *ancylae* from New Yersey as belonging to *Thripoctenus*, but the latter author actually described it as belonging to *Sympiesis*. The three *Ceranisus (?)* species (*nigricornis*, *semitestaceus* and *subconicus*)

(Motschulsky, 1863) collected at Nuar-Ellia and Patannas on Ceylon are so poorly described that nothing can be said about their systematic position (cit. Bakkendorf, 1957).

In a number of cases, early records of parasitoid species identified before to the species level, have been referred to as *Ceranisus* (or *Thripoctenus*) sp. (for references see below), because this was the only genus which was known. Later these specimens often could be identified as belonging to *C. menes*, or another yet undescribed *Ceranisus* species. Sometimes the correctness of identification remained unclear. Some of these records however, also refer to *Thripobius* (*hirticornis* or *semiluteus*). Some species belonging to these genera, will be discussed separately below, because specific information is available, others from which this is not will be discussed in groups. Graham (1963) and Erdös (1971) both provided a key to European *Ceranisus* species, there are no keys however for other regions of the world.

3.2.1.1.1 *Ceranisus menes* (Walker 1839)

Synonymy

Pteroptrix menes Walker 1839
Diglyphus aculeo Walker 1848
Asecodes aculeo (Walker) Dalla Torre 1898
Thripoctenus brui Vuillet 1914
Epomphale auriventris Girault 1915
Epomphale rubensteina Girault 1934
Ceranisus menes (Walker) Graham 1959
Ceranisus rosilloi De Santis 1961

Taxonomy

Females are 0.66 mm (DeSantis, 1961) till 1.06 mm (Bühl, 1937) in size, the males somewhat smaller (Ishii, 1933). *C. menes* is characterized by head and thorax black and all legs yellow; the hyaline wings can be distinguished from other *Ceranisus* species by the characteristic bare space below the subcubital vein strongly sinuately curved upwards (see figure 1). The male differs from the female in its antennae and its truncate brownish abdomen, pale towards the base (Ishii, 1933; Tachikawa, 1986). The colour of the female abdomen varies quite a bit in *C. menes* as shown in table 2, described for the original synonym types. Originally described from a yellow holotype (Walker, 1839; Vuillet, 1914), later records of this species in literature refer to the same (Van Heurn, 1923) or different types of colour of the abdomen (e.g. Sakimura, 1937a). A browntip type has been described by DeSantis (1962 as *Ceranisus rosilloi*) from Argentina and has been collected in Chili too (Rodriguez pers. comm.). In many records however colouring has not been mentioned. Differences in colour-type of the abdomen of females, yellow versus browntipped, collected at several places in Europe (Loomans, 1991) and California, USA (Loomans, 1993, unpublished data) remained consistent over 40 generations during laboratory rearing.

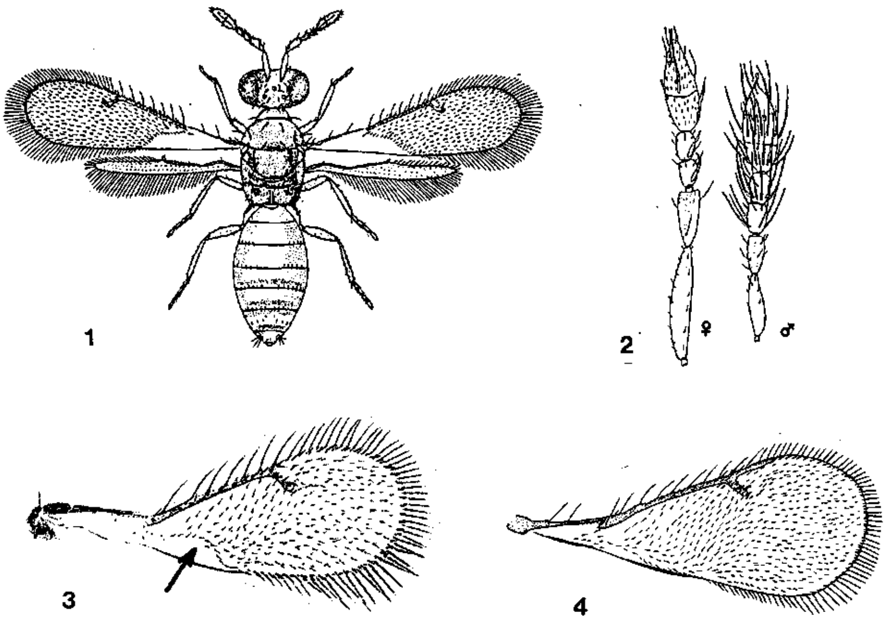

Fig. 1. *Ceranisus menes* (Walker). 1. adult ♀ (Ishii, 1933); 2. antenna ♀, antenna ♂; 3. front wing showing sinuate subcubital vein (arrow) (Tachikawa, 1986); 4. front wing *Ceranisus americensis* (Girault) (Schauff, 1991).

Distribution, hosts, host plant associations

The distribution of *C. menes* can be considered as cosmopolitan (Loomans & Van Lenteren, 1990; figure 2, table 3). It has been recorded from tropical, subtropical as well as temperate climatic regions. Most records originate from eastern Asian countries, where it is abundant: Japan, Korea (Sakimura, 1937a; Paik et al., 1981), Vladivostok-Russia (Trjaptitzin, 1983 pc), The Philippines (Ishii, 1933), Taiwan (Chang, 1990), Saipan and Palau (Yasumatsu & Watanabe, 1964), Thailand (Hirose, 1989, Napompeth, 1990), India (Narayanan, 1971; Saxena, 1971, 1981) and

Table 2. Variation in abdominal colour-pattern of *C. menes* type specimens

Type synonym	Origin	Colouration abdomen	Reference
P. menes	Britain	yellow	Walker, 1839
T. brui	France	pale yellow	Vuillet, 1914
	Japan	pale yellow	Ishii, 1933
C. menes	Britain	yellow/brownish yellow, sometimes with narrow transverse fuscous bands	Graham, 1963
E. auriventris	Australia	golden yellow with two black cross stripes third stripe vague	Girault, 1915
C. rosilloi	Argentina	base pale, tip brown	DeSantis,1961
E. rubensteina	Australia	black	Girault, 1934

Fig. 2. Worldwide distribution of *Ceranisus menes* (Walker) (Hymenoptera: Eulophidae). Indigenous occurrences: solid circle; imported and established ones: open star.

Java-Indonesia (Van Heurn, 1923; LaSalle, 1989, pers. coll.). from the Australian area it has been collected from Papua New Guinea (Boucek, 1988), Australia (West, Queensland, Victoria) (Girault 1915, 1934; Boucek, 1988; BMNH coll.) and New Zealand (Valentine, 1967; Boucek, 1988). Occasionally individuals have been reported from the neotropics: the Dominican Republic (Russo, 1928), Brazil (Loomans pers. comm.), Chile (Rodriguez pers. comm.) and Argentina (as *Ceranisus rosilloi*, DeSantis & Fidalgo). Recently it has first been found in California USA (Loomans pers. coll. 1993; Greene & Parrella, 1993: as *Ceranisus* sp.). It has been introduced into Hawaii (Sakimura, 1937c) and recovered later (Swezey, 1950; Yoshimoto, 1965). In Europe this species has been recorded on several occasions from most countries: England (Walker, 1839, 1848; Graham, 1963; BMNH, coll.), Netherlands (Loomans, 1991), Germany (Murai, coll. 1992), France (Aisne: Vuillet, 1914; mediterranean area: Loomans, 1991), Italy (Loomans, 1991; Galazzi et al., 1992), Spain (Pays Vasco, Cantabria: Loomans, pers. coll 1991; Catalonia: Riudavets, pers. coll. 1991; Murcia: Lacasa, pers. coll. 1991; Malaga: BMNH, coll. 1974), Montenegro (Boucek, 1977), Greece (Gijswijt, pers. coll.), Czechia (Boucek, 1957), Poland (Miczulski, 1968), Hungary (Erdös, 1956, 1971), Moldavia (Boucek, 1961, 1965; Trjapitzin, coll. 1960) and Russia (Trjapitzin, coll. 1986) (for additional records see table 3).

C. menes can parasitize larvae of many thrips species, many of them important pest species. It has been recorded to attack and develop on *Thrips tabaci* (Sakimura, 1937; Van Heurn, 1923; Dessart & Bournier, 1971; Carl, 1971; Murai, 1988ab; 1990), *Thrips palmi* (Hirose, 1989; 1992), *T. (= Ramaswamiahiella) subnudula* (Narayanan, 1971), *Kakothrips pisivorus* (Bühl, 1937; Antsiferova & Timraleev, 1974), *Taeniothrips alliorum* (Kurosawa, 1931), *Megalurothrips usitatus* (Chiu, 1990), *Megalurothrips sjöstedti* (Tamò, pers. comm.), *Microcephalothrips abdominalis* (Sakimura, 1937a), *Toxothrips ricinus* (Daniel et al., 1986) and (probably) *Neurisothrips fullawayi* (Yoshimoto, 1965). Murai showed that it can be reared from *Frankliniella intonsa, Thrips hawaiiensis, Thrips coloratus, Thrips setosus* (Murai, 1988ab; 1990), in high numbers. Sampling populations of *Frankliniella schultzei* and *F. occidentalis* in greenhouses in The Netherlands as well as *F. occidentalis* populations in the south of Europe during 1990, revealed that these were attacked by indigenous *C. menes* (Loomans, 1991; Riudavets, pers. coll.). In Israel it has been collected on several occasions by sampling roses and other host plants infested with *F. occidentalis* (Rubin & Kuslitzky, 1992). *C. menes* was found earlier in association with *F. intonsa* collected from rose in September 1988 in Cabrils (Spain) (Bordas, pers. comm.). *C. menes* was also collected by sampling wild vegetation inhabited by populations of species belonging to genera of the same subfamily Thripinae (Thripidae), like *Frankliniella* (*intonsa, occidentalis, pallida*), *Thrips (tabaci, major, brevicornis, hukkineni*, etc.) and *Taeniothrips* (*hispanicus*) (Loomans, 1991), but the actual host preferences were not established. Occasionally *C. menes* has been reported from thrips hosts from the subfamily Panchaetothripinae (Thripidae): *Zaniothrips vicini, Retithrips syriacus* (Daniel, 1986) and *Rhipiphorothrips cruentatus* (Chang, 1991). Murai (1988a, 1990) recorded attacks of *Haplothrips chinensis*, but no subsequent development. Its host species

Table 3. Survey of thrips parasite species belonging to *Ceranisus menes* (Walker). Distribution, host species and host plant associations.

Host species	country, region	host plant	date	reference
Frankliniella sp.	Argentina, Entre Rios	Trifolium repens	1957.xi	DeSantis, 1961
F. occidentalis	Netherlands	cactus flowers[1]	1990.xi	Loomans, 1991
	France, Hyères	rose[1]	1990.ix	
	Spain, Cabrils	carnation	1991.viii	Riudavets, 1991 pc
	USA, California	rose, alfalfa	1992.ix-xi	Greene, 1993 pc
	USA, California	mustard, alfalfa	1993.v	Loomans, 1993 pc
	Israel, Jeruzalem	rose, weeds	1990.xi	Rubin & Kuzlitski, 1992
	coastal plain	rose, weeds	1991.vi-vii	
	south	carnation[1]	1991.xii	
F. schultzei	Argentina, Entre Rios	Trifolium pratense	1957.x	DeSantis, 1961
	Netherlands	cactus flowers[1]	1990.xi	Loomans, 1991
F. intonsa	Japan, Shimane	tea	1980/4.ix-xi	Murai, 1988ab
	Spain, Cabrils	rose	1988.ix/x	Bordas, 1991pc
Thrips tabaci	Indonesia, Bogor	onion	1922.i	Van Heurn, 1923
	Java, Sindanglaoet	onion	1928.ix	Franssen & Van Heurn, 1932
	Korea, Keijo, Jinsen	onion	1934.vi-viii	Sakimura, 1937a
	Japan, Tokyo	onion	1932	Ishii, 1933
	Japan, Tokyo	onion	1932/4.vii-ix	Sakimura, 1937ab
	Japan, Okinawa, Miyako Yaeyama, Kohoku	onion	1933.iii/iv	
	Japan, Shimane	rose	v-xi	Murai, 1988ab
	Philippines	lab		Ishii, 1933
	India, Rajasthan, Kota	onion	1968.ii-v	Saxena, 1971
	India, Rajasthan, Jaipur	onion	1966.ii-v	Saxena, 1981
	India, Bangalore	onion	1969.iii-ix	Narayanan, 1971
			1970.ix	BMNH (Boucek)
	India, Hyderabad		1984.xi	BMNH
	USA, Hawaiian Isl.		1933/34	Sakimura, 1937c[1]
	Hawaii	Nasturtium	1936.iii	Swezey, 1936/37
	Argentina, Entre Rios	flax	1957.ix	DeSantis, 1961
	France, Maguio	onion	1968.ix	Carl, 1971
	France, Montpellier	onion	1970.ix	Dessart & Bournier, 1970
	Italy, South	onion		Domenichini pc
	Bulgaria	onion		Pelov, 1990 pc
T. palmi	Japan, Fukuoka	eggplant	1988.viii-x	Hirose et al., 1993
T. palmi	Thailand, Chiang Mai, Bangkok, Nakhon	eggplant	1988.i-iii	Hirose, 1989
T. coloratus	Japan, Shimane	lab. test		Murai, 1988ab
T. hawaiiensis	Japan, Shimane	lab. test		Murai, 1988ab
T. setosus	Japan, Shimane	lab. test		Murai, 1988ab
T. flavus	Germany	lab. test	1934.vi/vii	Bühl, 1937
Taeniothrips alliorum	Japan, Tokyo	onion	1931.viii	Kurosawa, 1931
		lab		Sakimura, 1937a
Microcephalothrips abdominalis	Japan, Tokyo			Sakimura, 1937a
	Korea			Paik et al., 1981
Neurisothrips fullawayi	Hawaii Islands	Nasturtium	1936.iii	Swezey, 1936
		Acacia koa	1950.iv	Swezey, 1950

Table 3. Continued.

Host species	country, region	host plant	date	reference
Kakothrips	France, Dercy (Aisne)	*Pisum sativum*	1913.vii	Vuillet, 1914
pisivorus	France, Nord Seine	*Pisum sativum*		Anon., 1967
	Germany, Kitzeberg	*Pisum sativum*	1932.vi/vii	Bühl, 1937
	Russia, Mordovin	*Pisum sativum*		Antsiferova et al., 1974
	Switzerland, Balgach	*Pisum sativum*	1992.vii	Teulon et al., 1992
Megalurothrips	Benin	*Tephrosia candida*	1991-1992	Tamò et al., 1993
sjöstedti		cowpea	xii-xii	Tamò, 1993 pc
		P. santalinoides		
M. usitatus	Taiwan, Pingtung	adzuki bean	1988.xii	Chang, 1990
	Philippines, Batangas	*Dolichos lablab*	1991.iv	Tamo, 1991 pc
	Lipa City	*Centrosema* sp.		
	Los Banos	*Cajanus cajan*	1992.iv	
Toxothrips ricinus	India, Arcot, Madras	*Ricinus communis*	1982.xii-v/	Daniel et al., 1986 1984.xii-v
Ramaswamiahiella subnudula	India, Bangalore	*Calotropis* sp	xii-i	Narayanan, 1971
Zaniothrips ricini	India, Tamil Nadu	*Ricinus communis*	1981.xi-iv/	Daniel et al., 1983 1982.xi-vi
	India, Tamil Nadu		1981.xi-vi/	Daniel, 1986 1983.vi
Retithrips syriacus	India, Tamil Nadu	*Ricinus communis*	1982.i-iv/	Daniel, 1986 1983.xii
Rhipiphorothrips cruentatus	Taiwan, Taichung Chi-Hu	wax apple		Chang, 1991

[1] : from greenhouse, [i]: introduced and established

C. menes collected from roadside vegetation and weeds, in association with a variety of native species belonging to the genera *Frankliniella*, *Thrips* and *Taeniothrips* (Thripinae) have not been included in this list (France, Italy: Loomans, 1991; Spain-Pays Vasco, Cantabria, Netherlands: Loomans unpubl.)

range can probably be extended with other species within the genera mentioned, when exposed to *C. menes*, e.g. *Frankliniella* species (Baranowski, pers. comm.) and *Thrips flavus* (Bühl, 1937).

C. menes has been found on a wide range of host plants in different biotopes. It seems that no specific biotope is preferred: it has been found along roadsides and natural ecosystems (Loomans, 1991), in agricultural ecosystems like gardens (Bühl, 1937; Hirose, 1989; Hirose et al., 1992), cultivated fields, weeds as well as fallow land and forests (table 4), up to 1341 m. elevation (Swezey, 1950). Collection results from the Mediterranean area indicate that *C. menes* is regularly occurring on wild vegetation in France, Italy (Loomans, 1991), Spain (Lacasa, pers. comm.) and Israel (Rubin & Kuslitzky, 1992) and the Atlantic region (Pays Vasco, Cantabria) of Spain (Loomans, pers. coll.). Occasionally it has been found among thrips infested cultures in greenhouses (Loomans, 1991; Rubin & Kuslitzky, 1992). Literature records of associations of parasitoids with thrips however often do not mention if the plant is actually a host plant for the thrips species found, i.e if larvae have been found of the species that were collected as adults, and if these were parasitized or not. The possible migration of thrips adults between plants (or plant parts) which are used for reproduction and feeding (e.g. Kirk, 1985), can mystify parasitoid-host relationships.

Plant structure can influence host searching efficiency and overall parasitization success to a large extent. Its physiological host range probably is much wider than its ecological host range, but quantitative checks of host preference in relation to the thrips host and host suitability for parasitism are scarce. Larvae of some species (*T. tabaci*, *T. fuscipennis*, *T. vulgatissimus*, *T. major*) collected in the field and exposed in the laboratory to *C. menes*, were readily attacked and progeny developed from it, although larvae collected outside were not parasitized, (Loomans, pers. comm.). Except from leaves of onion (Liliaceae) (Van Heurn, 1923; Sakimura, 1937ab; Saxena, 1971; Carl, 1971), eggplant (Solanaceae) (Hirose, 1989; Hirose et al., 1992), castor (Euphorbiaceae) (Daniel et al., 1983) and waxapple (Myrtaceae) (Chang, 1991), *C. menes* mostly has been collected from flowering plants, representing more than 20 different families (table 4). Searching for hosts, the female parasitoid can sneak into very narrow spaces to reach a host. Saxena (1971) observed the parasitoid entering the leaf of onion plants and ovipositing hosts feeding inside and Bühl (1937) observed *C. menes* foraging in flowers and on the pods of *Pisum sativum*. On onion, larvae congregating on open surfaces like those of *T. tabaci*, are parasitized more than those which prefer to feed under leaf sheaths or blade folds, like *T. alliorum* larvae. *T. tabaci* feeding on rough surfaced plants, hairy surfaces or flowers, like *Emilia sagittata* (Sakimura, 1937a) were less frequently parasitized. It might be however that below the species level host and host plant relationships have developed (Carl, 1971).

Except possible preferences yet unknown of this parasitoid for certain hosts or host habitats, extensive chemical spraying practices certainly will have played a role in a low frequency of its presence in protected crops. Results published by Hirose (1989), Hirose et al. (1993) and Hirose et al. (1992) also showed a very low% of parasitization by *C. menes* in sprayed crops in Thailand and Japan respectively.

Biology

C. menes is a solitary internal parasitoid of thrips larvae, which reproduces both by arrhenotokous and thelytokous parthenogenesis. During collections of *C. menes* only females have been found thus far in Europe (e.g. Vuillet (France), 1914; Bühl (Germany), 1937; Erdös (Hungary), 1956; Dessart & Bournier (France), 1970; Miczulski (Poland), 1968; Antsiferova & Timraleev (Russia), 1974; BMNH coll. (England); Loomans (Netherlands, France, Italy), 1991; Galazzi et al. (Italy), 1992), Israel (Rubin & Kuslitzky, 1992), Africa (BMNH, coll. (Nigeria); Tamò (Benin), pers. coll.), North America (Loomans, pers. coll.) and South America (Brazil; Loomans unpubl. data; Chile: Rodriguez, pers. coll.; DeSantis (Argentina), 1961: as *C. rosilloi*)). It is of interest to notice that in field collections of *C. menes* made in several Asian countries, males are present as well (Ishii, 1933; Tachikawa (Japan), 1986; Saxena (India), 1971, 1981). Museum material collected in Australia by Boucek also contained males as well as females (BMNH, coll. 1976, 1977, 1980). Females mostly are predominant (sex ratio 3:2, Sakimura (Japan), 1937; Daniel (India), 1986; Van Heurn (Indonesia), 1923) or numbers are equal (0.47:

Table 4. Host plant range of *Ceranisus menes* (cultivated host plants underlined).

Leguminosae	*Dolichos lablab*, *Centrosema pubescens*, *Cajanus cajan*, *Pedicularia phaseoloides* (Philippines[1]); *Trifolium repens* (Italy[2], Argentina[3], Spain[4]); *Trifolium pratense* (Argentina[3], Spain[4]); *Vicia faba*, *Lathyrus odoratus* (France[5]), *Pisum sativum* (France[5], Russia[6], Switzerland[7], Germany[8], Nl[9]); *Medicago sativa* (alfalfa) (France[9], California[4]); *Vigna unguiculata* (cowpea) (Nigeria[10], Benin[1]); *Thephrosia candida*, *Pterocarpus santalinoides* (Benin[1]); *Vigna angularis* (adzuki) (Taiwan[11]);
Compositae	*Matricaria recutita*, *Senecio jacobea* (Nl[4]); *Picris hieracioides*, *Dittrichia viscosa*, *Solidago virgaurea*, *Leontodon* sp. (Italy[2]); *Hieracium* sp. (France[9], Italy[9]); *Bellis perennis* (Germany[12]); *Senecio vernalis* (Israel[13]); *Sonchus* sp. (UK)[?];
Rosaceae	*Spirea* sp. (UK[10], Nl[4]); *Filipendula ulmaria* (Nl[4]); *Rosa* spp. (Nl[4], France[9], Israel[13], California[14], Spain[15], Japan[12]); *Thea sinensis* (tea) (Japan[12])
Cruciferae	*Brassica nigra* (California[4]); *Brassica napus*, *Brassica oleracea* (Poland[16]); *Lantana* sp. (France[9]); *Nasturtium* sp. (Hawaii)[17];
Solanaceae	*Solanum tuberosum* (potato) (Czechia[18], Hungary[19], Indonesia[10]), *Solanum melongena* (aubergine) (Japan[20], Thailand[21]);
Euphorbiaceae	*Euphorbia cyparissias*, *Euphorbia lucida* (Hungary[19]); *Ricinus communis* (India[22]);
Liliaceae	*Allium cepa* (onion) (Japan[23], Korea[23], Indonesia[24], India[25], France[26], Italy[27]);
Umbellifereae	*Pastinaca sativa* (Nl[4]), *Angelica graveolens* (Moldavia[28]);
Valerianaceae	*Centranthus ruber* (France, Italy)[9];
Polygonaceae	*Polygonum auberti* (Italy[2], France[9], Spain[4]);
Linaceae	*Linum usitatissimum* (flax) (Argentina[3]);
Caryophyllaceae	*Dianthus caryophyllus* (carnation) (Spain[29], Israel[13]);
Asclepiadaceae	*Calotropis* sp. (India[30]);
Convolvulaceae	*Convolvolus arvense* (Israel[13]);
Ericaceae	*Erica tetralix* (Nl[4]);
Rubiaceae	*Galium aparine* (Nl[4]);
Gramineae	*Hordeum vulgare* (barley) (Spain[31]);
Myrtaceae	*Eugenia malaccensis* (wax apple) (Taiwan[32]);
Oleaceae	*Ligustrum ovalifolium* (Nl[4]);
Mimosaceae	*Acacia koa* (Hawaii[33]);
Cactaceae	Cactus spp. (Brazil[4], Nl[9]).

[1]: Tamò, unpubl., [2]: Galazzi et al., 1992, [3]: DeSantis, 1961, [4]: Loomans, unpubl., [5]: Vuiillet, 1914, [6]: Antsiferova & Timraleev, 1974, [7]: Teulon et al., 1992, [8]: Bühl, 1937, [9]: Loomans, 1991, [10]: coll BMNH, [11]: Chang, 1990, [12]: Murai, coll., [13]: Rubin & Kuslitzky, 1992, [14]: Greene, unpubl., [15]: Bordas, coll., [16]: Miczulski, 1968, [17]: Swezey, 1936, [18]: Boucek & Askew, 1968, [19]: Erdös, 1971, [20]: Hirose, 1989, [21]: Hirose et al., 1993 [22]: Daniel, 1986, [23]: sakimura, 1937a, [24]: Van Heurn, 1923, [25]: Saxena, 1971, [26]: Carl, 1971, [27]: Domenichini, unpubl., [28]: Boucek, 1961, [29]: Riudavets, unpubl., [30]: Narayanan, 1971, [31]: Lacasa, unpubl., [32]: Chang, 1991, [33]: Swezey, 1950; [?] unknown.

Carl (India), 1971 ; 0.48: Hirose (Thailand), 1989). During laboratory maintenance of *C. menes*, Carl (1971) noted a rapid change towards males within five generations, maybe due to mating problems. Murai (1988ab) also recorded a gradual change in sex ratio in the laboratory: after few generations only parthenogenetically reproducing females remained. In laboratory cultures originating from European strains during four years of rearing, only one single male has been found (Loomans pers. comm.). The background of this difference between these unisexual and bisexual populations remains unclear.

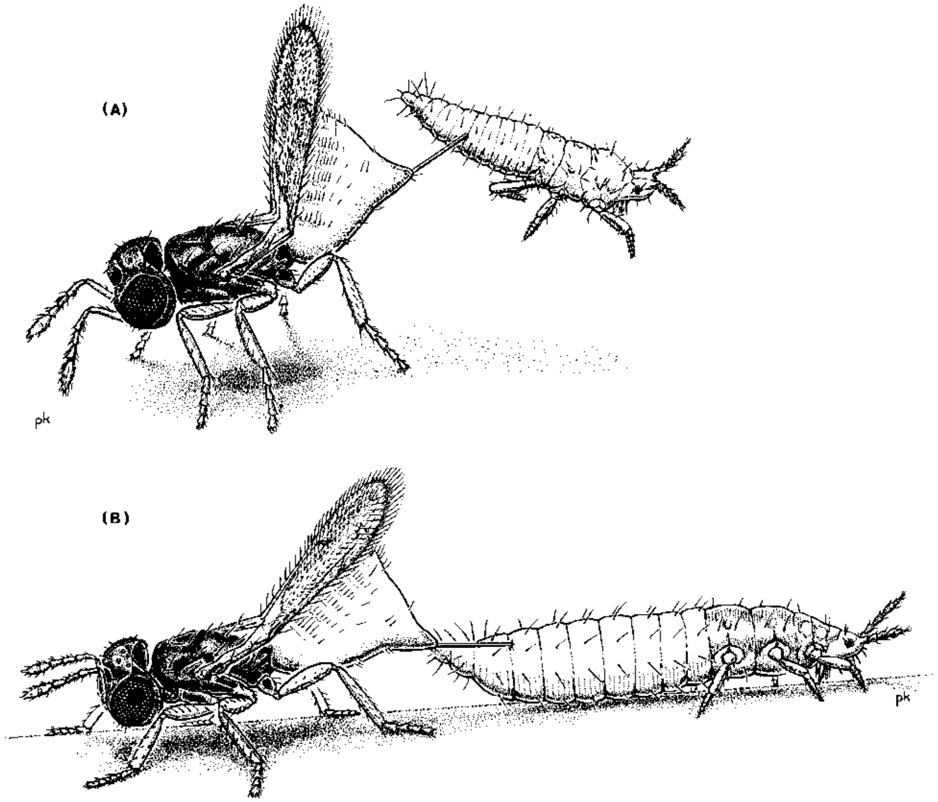

Fig. 3. *Ceranisus menes* oviposition postures (A) lifting, (B) tailing or dragging (original).

Searching and host handling behaviour of *C. menes* is similar for various host-parasitoid combinations. Once a host is encountered and examined with the antennae, the ovipositor is inserted into the hosts body after a short struggle, usually the thorax (Sakimura, 1937a) or abdomen (Saxena, 1971). Almost immediately the female turns 180°C, lifting the vigorously moving larvae up in the air (Carl, 1971; Murai, 1988; Loomans, 1991; Galazzi & Bazzocchi, 1993), a constant characteristic for *C. menes* (i.c. hanging head-down from the underside of a leaf, see figure 3a), although it was not mentioned as such by Sakimura (1937a) and Daniel (1986). Especially with large sized larvae, wasps often are standing tail-to-tail to their host (figure 3b) (Loomans et al., 1992). Once inserted a first stage larva becomes paralyzed (Daniel, 1986; Loomans, 1991) and a single egg is deposited. An oviposition varied from 8 – 230 for a brown colour-type, and from 3 – 150 seconds for a yellow one, but when hostfeeding occurs hosthandling can take up to 12 minutes (Loomans 1991; Loomans et al., 1993). Times handling larvae from other host species varied from 17-69 seconds (Hirose 1989) for *T. palmi*, 30-60 seconds (Carl, 1971) and 60-180 seconds (Sakimura 1937) for *T. tabaci*, 30-40 seconds parasitizing *Z. ricini* and *R. syriacus* (Daniel, 1986).

C. menes attacked both larval stages of *K. pisivorus* (Bühl, 1937). According to Sakimura (1937a) it also did not prefer any particular size or age of *T. tabaci* larvae, but Saxena (1971) noted a preference for second stage larvae. Daniel noted a preference of *C. menes* for late first and early second stage larvae of *T. ricinus*, *Z. ricini* and *R. syriacus* (Daniel et al, 1983; 1986; Daniel, 1986). Laboratory studies showed that acceptance of *F. occidentalis* decreased with age (Loomans et al., 1992) and size (Loomans et al., 1993) of the host larvae, young and small sized hosts being preferred. Although it will even oviposit in prepupae and pupae, parasitization is not successful (Sakimura, 1937a; Daniel, 1986; Murai, 1988; Loomans, 1991) or in some cases in *F. intonsa* wingless females developed which do not reproduce (Murai, pers. comm.). Thripine hosts however usually pupate in the soil or other hidden places, exposure to *C. menes* is therefore rare. Behavioural defense reactions (abdominal movements, anal exudates, escape) of old and large *F. occidentalis* larvae however could prohibit successful parasitization (Loomans et al., 1992) or if insertion occurred, the larva dragged the female wasp behind her, trying to escape (figure 3b). Asian strains of *C. menes* attacked all sizes of larvae of *F. intonsa* (Sakimura 1937a) and *T. tabaci* (Carl, 1971; Sakimura, 1937a) indiscriminately, and showed no violent defense measures. Daniel (1986) noted a preference for late first or early second stage larvae of two panchaetothripine species, that only escaped from being parasitized when the first attack failed. Sakimura (1937a) noted oviposition failures on *Haplothrips subtilissimus* f. *floricola* Pr. (Tubulifera: Phlaeothripidae) in the laboratory due to violent defense measures and large sized larvae of *T. tabaci* often escaped parasitization (Saxena 1971; Carl, 1971), because of vehement defense. According to Carl (1971) and Hirose (1989), *C. menes* did not attack parasitized larvae of *T. tabaci* and *T. palmi* respectively.

Once a host larvae has been parasitized, larval stages of the parasitized hosts cannot be distinguished externally from unparasitized ones. Egg and larval stages of the wasp are completed before prepupation of the host (Sakimura, 1937, Bühl, 1937). Only at that time parasitism first becomes evident. The pupation process has extensively been described for *C. menes* by Sakimura (1937), parasitizing *Thrips tabaci* Lind. and is similar to *F. occidentalis* (Loomans, pers. obs.; cf. Greene & Parrella, 1993) and other hosts (Daniel, 1986; Murai, 1988). Summarized it is as follows. The absence of prepupal wing pads is a first indication of parasitism of the host. The next day the body gets swollen, becomes creamy white in colour with an orange spot in the center (figure 4A-C). When ready to pupate, the host skin splits anteriorly (figure 4A-B), and the parasitoid pupa becomes visible and gradually works itself out of the host skin remains (arrow figure 4B). Except for the orange cylinder C, newly formed pupae of *C. menes* are almost white A, and change within a few hours from bluish to dark brown. The host skin B, at first lying behind the parasitoid pupa, soon dries and shrivels, holding the pupa to the surface at the tip of the abdomen. Yellow and brown colour-types can already be distinguished from each other by the size and colour (Loomans, unpublished data) of the maturing pupa. Size of the parasitoid pupae was also related to the thrips host: 0.98 mm in *F. intonsa*, 0.82 mm in *T. tabaci* and *T. hawaiiensis* (Murai, 1988a). Pupation development takes place outside the host body, in the same place as where the thrips

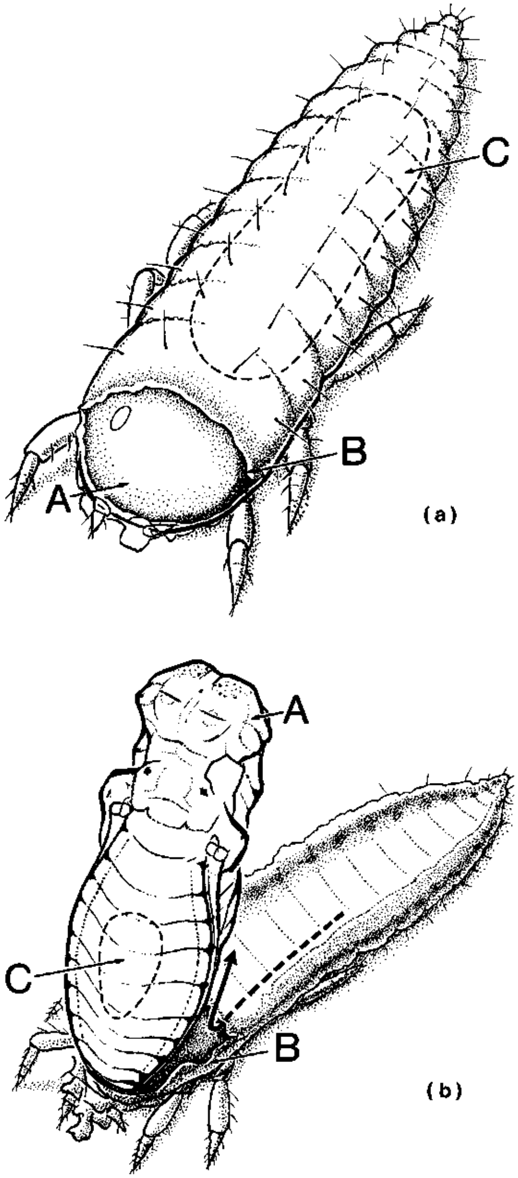

Fig. 4. (a) Prepupa at the moment of pupation and (b) emerged pupa of *Ceranisus menes*. A = pupa, B = host skin, C = orange/red central spot. The way by which the pupa emerged from the host skin, is indicated by the arrow (original).

host pupates, for thripine species usually the soil. In the panchaetothripine species *Z. ricini*, both host and parasitoid pupate in the soil too (Daniel et al., 1983); what happens when host pupae stay on the leaf like in *R. syriacus*, is not reported (Daniel et al., 1983; Daniel, 1986).

Developmental time of *C. menes* is highly variable, and is influenced both by the host and parasitoid and by climatic conditions:

* Developmental time of *C. menes* is related to the thrips species that has been parasitized. In the univoltine host *K. pisivorus*, *C. menes* developed one generation a year, overwintering as pupae whereas the host overwintered as full-grown second stage larvae (Bühl, 1937). Parasitizing multivoltine host species like *F. occidentalis*, *F. intonsa*, *T. tabaci*, etc., developmental time varied slightly between species (see table 5) at the same conditions, producing many generations a year. Development of *C. menes* is much longer than that of the recorded thripine hosts species, like e.g. *F. occidentalis*, 25.6 days at 20°C and 12.9 days at 25°C (Robb, 1989). Daniel (1986) recorded a very short developmental time with the panchaetothripine species *Z. vicini* and *R. syriacus* as hosts, much shorter than that of the hosts: *Z. ricini* takes 16-20 days at 28°C to complete its life-cycle (Daniel et al., 1983), whereas *C. menes* took 10.8 days. *R. syriacus* takes 21-32 days (including 3-5 days pre-oviposition above 26°C in Israel; Rivnay, 1939) and *C. menes* 16.3 days; but since this is the only record of this subfamily, data need confirmation.

* Within a single host species, developmental time can vary widely too. Sakimura (1937a) found that developmental time of the egg and larval stages of the parasitoid varied widely with the age of the *T. tabaci* larva on which the egg was laid: the younger the host, the longer the parasitoid stages were. Although parasitoids hatched 1-2 days earlier from male *F. intonsa* larvae, variation in developmental time was similar in *F. intonsa* larvae of both gender (Murai, 1988a). Different de-

Table 5. Developmental time (days ± standard deviation) of *C. menes* on various thrips hosts at different temperatures

Temp. (°C)	thrips host	developmental time egg+larvae	pupa	total	reference
15	*F. intonsa*	22.8 ± 0.9	107.1 ± 14.7	129.9	Murai, 1988, 1990
17.5	*F. intonsa*	18.2 ± 1.6	109.5 ± 18.2	127.7	Murai, 1990
	T. tabaci	18.5 ± 0.6	112.0 ± 14.6	130.5	
	T. hawaiiensis	14.3 ± 0.9	113.5 ± 14.2	127.8	
20	*F. intonsa*	13.5 ± 1.0	112.0 ± 14.6	125.5	Murai, 1988, 1990
20	*F. occidentalis*			28-34	Loomans, 1991[2]
22.5	*F. intonsa*	10.3 ± 1.0	38.2 ± 8.3	48.5	Murai, 1988, 1990
25	*F. intonsa*	8.4 ± 0.8	38.5 ± 7.4	46.9	Murai, 1988, 1990
25	*T. tabaci*			25-28	Carl, 1971[2]
25	*F. occidentalis*			23-30	Loomans, 1991[2]
25	*F. occidentalis*			35.6	Galazzi et al., 1992
17.2*	*T. tabaci*	12.7	24.1	36.8	Sakimura, 1937a
22.0*	*T. tabaci*	11.3			
23.2*	*T. tabaci*	9.2			
25.7*	*T. tabaci*	8.7	14.0	22.7	
??*	*T. palmi*	>6.2	13.3	>19.5	Hirose, 1989[1]
??*	*T. tabaci*	9	7-14	16-23	Narayanan, 1971
28?*	*Z. vicini*	5.8	5.0 ± 1.2	10.8	Daniel, 1986
	R. syriacus	8.0	8.3 ± 0.9	16.3	

* = insectary temperature, [1] = from field collected larvae, [2] = incomplete from rearing units

grees of parasitism on different geographical host strains have not well been evaluated (cf. Sakimura, 1937a).

* The length of the immature stages varied according to the sex of the offspring, males developing faster than females (*T. tabaci*, Sakimura, 1937a): from 13.6 days (♂) and 14.8 (♀) at 24.7°C during the summer months to 23.4 days (♂) and 24.5 (♀) days at 18.2 °C in autumn. This variation was also found by Murai (1988a, 1990) with *F. intonsa* as a host in the pupal stage.

* Recent results indicate that developmental time on *F. occidentalis* varied between parasitoid strains, according to their phenotypic appearance (abdominal colour-types: yellow and brown) and geographical origin. Yellow strains show a large variation in overall developmental time, brown types did not (Loomans et al., in press). Also Murai recorded a marked variation in pupal development of *C. menes* for both sexes 25-90 days at 22.5°C (Murai, 1988a, 1990) for a yellow strain on *F. intonsa* in Japan (figure 5). Similarly Galazzi et al. (1992) found a large variation in developmental time with *F. occidentalis* as a host in Italy: 78% in 28-34 days, 22% in 46-64 days for females of a yellow type *C. menes*. Pupal duration of the parent had no relation to that of its offspring (Murai, 1988a). This indicates that possibly different biotypes or geographical races of *C. menes* are involved.

* Temperature strongly mediates developmental time and pupal development in particular. At 20°C or lower, life-cycles are very long (table 5), especially Dutch strains had a very long pupal developmental time (Loomans et al., in press). With the advance of cold temperatures Sakimura (1937b) noticed an increase of the number of specimens that did not emerge ('hibernated'). At low temperatures pupae probably are not in diapause, but in a quiescent state: pupae readily started hatching when transferred to higher temperatures (Murai, 1988a).

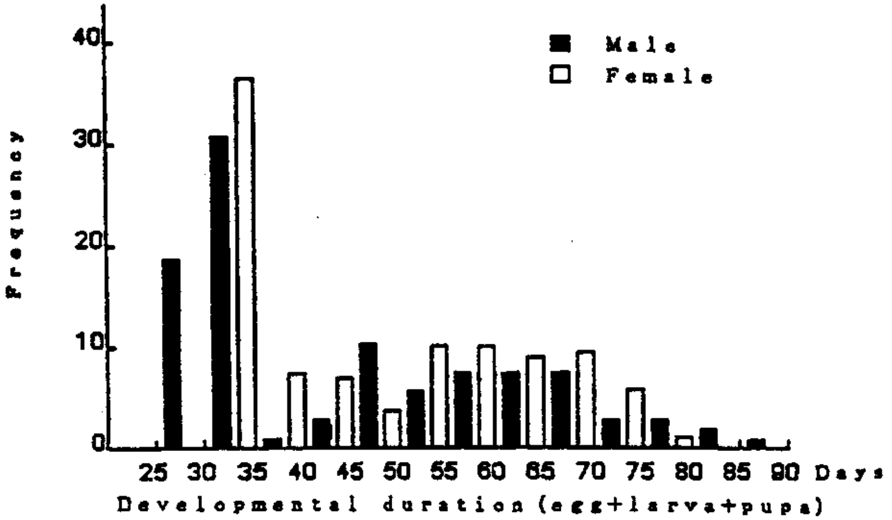

Fig. 5. Adult parasitoid eclosure (days after parasitization) for males and females of *C. menes* (Japan), at 22.5°C (from Murai, 1990).

Life history parameters for *C. menes* differed according to temperature, the thrips host species parasitized and origin and strain of the parasitoid. In Russia, females lived for 5-7 days, but 8-15 days when fed additionally with sugars (Antsiferova & Timraleev, 1974). When provided with honey and water, without any hosts, longevity of adults at a mean of 21.5°C, varied from 14-22 days, with a mean of 19.1 days for females and 20.2 for males (Sakimura, 1937a). Average longevity of *C. menes* parasitizing *F. intonsa* in Japan (Murai, 1988a; 1990) did not differ very much with temperature, 9.2 days at 20°C and 10.4 days at 25°C. *C. menes* is synovigenic: it can start ovipositing on the day of emergence (Murai, 1988a; Loomans, 1991), but Sakimura (1937a) recorded a pre-oviposition period of 1-2 days and Daniel (1986) mentioned 2-3 days. According to Sakimura (1937a) several oocytes mature within 24 hours after emergence. Full grown oocytes per female varied from 29-48 with an average of 38.6 (op. cit.). The post-oviposition period is also short. Adult females can lay 20 to 25 (Murai, 1988a, 1990) eggs per day on *F. intonsa* at 25°C, but at 20°C this was only half the amount. In both cases numbers gradually decreased with age. Parasitizing *Z. ricini* and *R. syriacus*, an average maximum of 46±2.6 eggs per day (Daniel, 1986, reared in groups of five) was laid (Daniel, 1986) in India. Fecundity was significantly affected by temperature: 61.0 eggs per female at 20°C and 161.8 at 25°C. Reproduction capacity of European *C. menes* was strongly related to the thrips-parasitoid combination: 89.6 – 105.0 pupal offspring were found for brown colour-types and 36.8 for a yellow strain parasitizing *F. schultzei* (Loomans, 1991) at 25°C. Fecundity rate was much lower on *F. occidentalis*: up to 24.5 offspring per female were produced when reared in groups (Loomans, 1991).

The net reproduction (R_o) and the intrinsic rate of increase (r_m) varied largely with temperature, mainly due to differences in developmental period. The r_m values, 0.047 and 0.098 at 20°C and 25°C respectively, for a Japanese strain of *C. menes*, parasitizing *F. intonsa*, were much lower than that of its host (Murai, 1988a, 1990). E.g. the intrinsic rate of *F. intonsa* was 0.158 at 25°C (Murai, 1990) and that of *F. occidentalis* 0.095 at 20 °C on chrysanthemum and 0.171 at 25°C (Robb, 1989).

Rearing

For rearing *C. menes* and their thrips hosts, a number of methods has been applied. Sakimura (1937b) reared field collected larvae of *T. tabaci* on onion leaves in glass vials and Hirose (1989) used eggplant leaves in cages, for rearing field collected larvae of *T. palmi*. For laboratory propagation of thrips and parasitoids, Loomans (1991) based on Narayanan (1971), described a bean pod method, using fresh beans (*Phaseolus vulgaris*) and additional bee pollen, using *T. tabaci*, *F. occidentalis* and *F. schultzei* as hosts. Murai & Ishii (1982) developed an artificial method for flower inhabiting thrips species (*T. tabaci*, *T. hawaiiensis*, *T. setosus*, *F. intonsa* etc.) (Murai, 1988ab; 1990). This method was adopted later for *F. occidentalis* and *F. schultzei* (Loomans, 1991), and modified again by Galazzi et al. (1992) and Murai (pers. comm.), using a honey-solution and plant pollen. Methods were used for stock as well as experimental rearing of thrips hosts and parasitoids, applying different devices respectively. In general each method consisted of four parts: an oviposition unit were adult thrips were allowed to lay eggs during a fixed amount of time, a rearing unit for parasitized and unparasitized larvae, an incubation unit for parasitoid pupae and a storage unit for adult parasitoids. Both methods allowed synchronization of host larvae to age; the artificial method also allows users to check a wide variety of larvae of thrips feeding on pollen, originating from various host plants for parasitism, which is more difficult when using bean pods.

Field incidence

High levels of parasitization have been reported from Asia. Sakimura (1937b) in a well documented three-year survey of *T. tabaci* infestations in the vicinity of Tokyo – Japan, found that parasitoid occurrence was well synchronized with the host population. Adults emerged from overwintering pupae in late May and completed 4 generations, parasitized host larvae hibernated from late October onwards. The rate of parasitism went up to 79.9% late July 1932, on single sites larvae were parasitized almost 100% by the end of October 1933. Parasitoids were present when average monthly temperature means were above 20°C (35°N.L.). During the low temperature period, *T. tabaci* was capable to develop to a well established population in June. During the first half of the season, *C. menes* levels were not yet high enough to be an efficient mortality factor, but during the latter half of all three years *T. tabaci* populations were kept in check (Sakimura, 1937b). Regression analysis of Sakimura's sampling data shows a clear positive density-dependent relationship (figure 6: $y = 15.84 + 0.047\ x$, $R^2 = 0.442$), but as also stated by Lewis

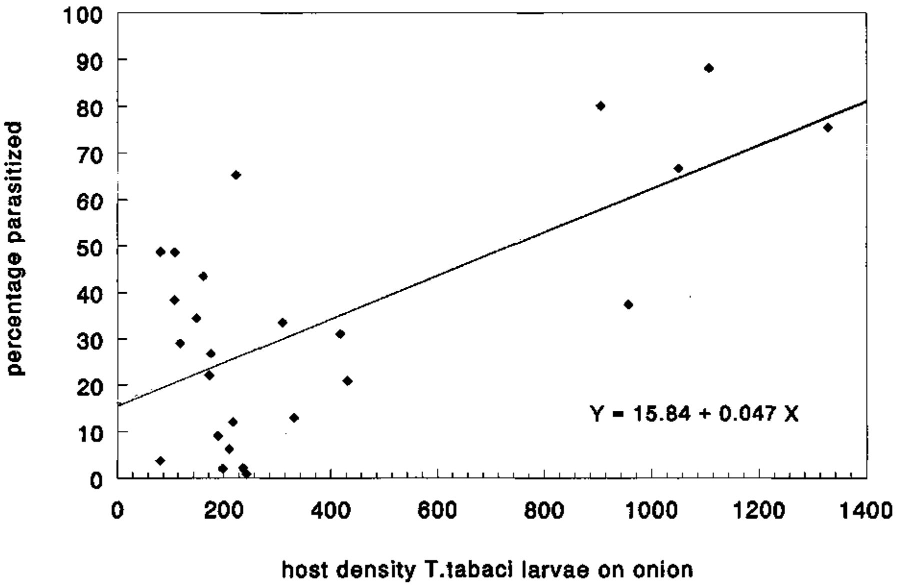

Fig. 6. Relationship between the host density of *Thrips tabaci* on onion and percentage parasitism by *Ceranisus menes* (Japan) (data from Sakimura, 1937c).

(1973), it is not clear if this increase in parasitism with host density was due to an numerical response (aggregative or reproductive) or to a functional response.

Parasitism by *C. menes* of *T. palmi* larvae infesting leaves of eggplants in home and commercial gardens near Fukuoka – Japan, was very localized (Hirose, 1990; Hirose et al., 1992). Parasitism was found in 7 of the 20 home gardens, but in only 1 of the 7 commercial gardens, where pesticide sprays were common. Parasitism rates increased from an average of 8.1% and 31.6% from August to October and reached a maximum of 75% (ibid.). In an extensive survey of eggplant fields in several districts in Thailand during December 1987-February 1988, parasitism of *T. palmi* larvae by *C. menes* ranged from 0-60% (Hirose, 1989, 1990; Hirose et al., 1993). A high percentage (40-60) parasitism was frequently observed in unsprayed, small-scale home gardens, while the level was significantly lower in pesticide treated gardens. In a 7.2 m^2 test plot consisting of 45 plotted eggplants, parasitism reached 40-50% in the first half of February, followed by a sharp decline in adult and larval *T. palmi* abundance (op. cit.).

Parasitism rates quoted for other regions were not so high. Van Heurn (1923) checked infestations by *T. tabaci* in a greenhouse at Buitenzorg, Bogor – Java, Indonesia, and noticed a decline in host numbers in January coinciding with an increase in *C. menes*, but parasitism was very rare on onion in September at Singladoet, Java (Franssen & van Heurn, 1932). In India incidence of *C. menes* was also seasonal. Parasitism was absent during the wet period from June till October when temperatures were above 30°C. The percentage parasitism of *T. tabaci* by *C. menes*, appearing in February in onion fields in Rajastan, varied from 12-18% in the months of March-April which coincided with the peak period of the pest (Saxena, 1971). Near Bangalore, up to 10% of *T. tabaci* larvae were attacked by *C. menes* in some fields, but none in others nearby (Narayanan, 1971). Parasitoids remained active up to 37°C. A decline in population of *T. tabaci* set in due to a rise of temperature and incidence of parasitoids (Saxena, 1981). Beyond the second week of April the parasitoid population declined due to intense heat.

On *Ricinus communis* (Euphorbiaceae) around Madras – India, inhabited by a mixed population of 7 species (Anathakrishnan, 1984), *C. menes* had a substantial impact on population dynamics of *Z. ricini* infesting the mature leaves and *Toxothrips ricinus* inside young buds, but had no impact on the population of the simultaneously occurring *R. syriacus*. *C. menes* population build up started in November and peak parasitization on *Z. ricini* was 48% in January/February, one month after *Z. ricini* reached its maximum, 50% on *T. ricinus* in February and 20% on *R. syriacus* in March. In the field it preferred *Z. ricini* and *T. ricini* over the simultaneously occurring *R. syriacus*, but when the first species were absent it switched over to *R. syriacus*, sustained itself but did not increase until the removal of the crop early June (Daniel et al., 1983, 1986; Daniel, 1986).

In Europe, parasitization levels have been reported only occasionally. Although occurring regularly on *T. tabaci* on onion in Italy (Domenichini, pers. comm.) and Bulgaria (Pelov, pers. comm.), collections in onion fields in Central Europe resulted in fairly low numbers (Carl, 1971); in others (Vuillet, 1914 and Bühl, 1937, working on *K. pisivorus*) high numbers were found. Bühl (1937) found a single generation of *C. menes*, when it parasitized the univoltine host *K. pisivorus* near Kiel, Germany, and 35.1% of the overwintering population was parasitized. Parasitoids were present in pea fields during one month. First adults occurred from the third week of June till the third week of July, and soon reached 10% parasitism and 40% at its peak beginning of July, but *C. menes* did not contribute significantly to thrips control. Sampling home gardens in that area in 1992, Teulon et al. (1992), did not find any signs of parasitism. In Russia, East of Moscow, up to 17% of the *Kakothrips* larvae were infected (Antsiferova & Timraleev, 1974), the rate depending on the number of flowers. Sampling flowers of various host plants, infected with thripine host species in France and Italy, Loomans (1991) recorded 8-25% parasitism by *C. menes*, but often also found no parasitism. *C. menes* was rare in the Mediterranean Area of Spain in August-September when most of the vegetation had dried (Loomans, 1991; Riudavets, pers. coll.), but common on weeds in spring and early summer (Lacasa, pers. comm.).

There have been few attempts to use *C. menes* in biological control. In 1932-1934 some 44,000 pupae of *C. menes* were introduced from Japan into Hawaii and 41,617 were released as adults for the control of *T. tabaci* on various islands (Sakimura, 1937c; Swezey et al., 1939). Parasitoids established and were recovered later occasionally (Swezey, 1936, 1937, 1950; Yoshimoto, 1965), but no accounts have been published regarding increase and spread, or on its influence in reducing populations of *T. tabaci* (Clausen, 1978). Later several shipments were made to Hokkaido, but *C. menes* did not establish there (Ishii, 1940), although Yasumatsu & Watanabe (1964) mentioned its occurrence later. Attempts to introduce *C. menes* from India into Barbados (Narayanan, 1971; Alam, 1974) for the control of *T. tabaci* were started, but shipments failed. An extensive searching and monitoring in the field in Hawaii during recent years, showed a very low rate of parasitism (Lai, in Hirose, 1990). Its effect on *T. palmi* and *F. occidentalis* which have recently been introduced into Hawaii, and caused severe losses, is probably low and re-introductions of *C. menes* are considered (Early, pers. comm., 1990). In Florida *C. menes* recently has been introduced from Thailand and Japan for the control of *T. palmi* (Baranowski, pers.comm., 1993; see also table 18), results are not yet known.

3.2.1.1.2 Ceranisus pacuvius Walker 1842.

Synonymy

Thripoctenus kutteri Ferrière 1936
Entedon acestor Walker 1839
Cirrospilus pacuvius Walker 1838
Derostenus clavicornis Thomson 1878
Ganahlia clavicornis (Thomson) Dalla Torre 1898

Taxonomy

Female as well as males measure 0.7 – 1.0 mm (Ferrière, 1936), the male (0.85 mm) somewhat smaller than the female (0.90 mm) (Bakkendorf, 1957). Male and

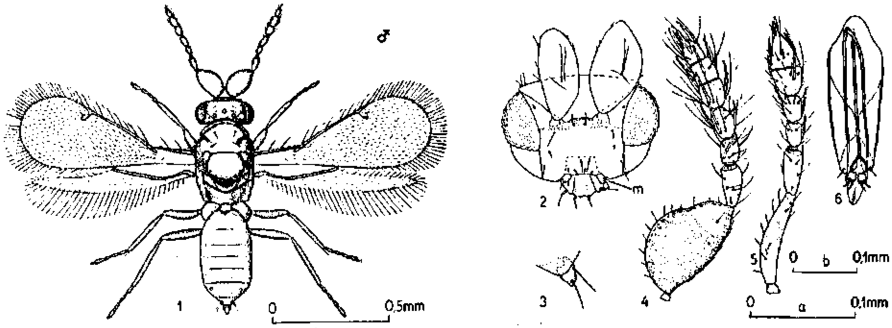

Fig. 7. *Ceranisus pacuvius* (Walker): ♂: 1. adult image; 2. head frontal view, from below; 3. mandible; 4. antenna; 6. genitalia; ♀: 5. antenna. a. scale 3.6.; b. scale 2.4.5 (from Bakkendorf, 1957).

female can be distinguished by the swollen first segment of the scape (figure 7). Both sexes are uniform black, with antennae and legs yellow-brown. A detailed taxonomic description of the species can be found in Ferrière (1936) and Bakkendorf (1957).

Distribution, hosts, host plant associations
Ceranisus pacuvius (Kutter) is palearctic in its distribution, and only recorded from Europe (see figure 8, table 6). It is mainly found in the temperate climatic part of it. Although Kutter (1937) and Franssen (1960) recorded high numbers, it is nowhere common. Records are known from England (Walker 1838; Graham, 1963; BMNH 1970), Ireland (Walker, 1839), Scotland (Teulon et al., 1992), The Netherlands (Franssen, 1960), Denmark (Bakkendorf, 1957), Sweden (Tompson, 1878; Hedqvist, 1978pc), Germany, Austria (Kirchner 1867), Switzerland (Kutter, 1934, 1935, 1936ab, 1937; Teulon et al., 1992), Czechia (Kirchner, 1867; Boucek, 1957), Hungary (Erdös, 1971), Poland (Miczulski, 1968) and Moldavia (Boucek, 1961). De Stefani Perez (1905) collected *Ganahlia clavicornis* (Thoms.) (synomymized as *Derostenus clavicornis* Thomson by Dalla Torre 1898, which is a synonym of *Ceranisus pacuvius* (Walker) (Boucek & Graham 1978, Hansson 1991)) from galls of *Andricus (= Callirhytis?) glandium* Giraud (Hymenoptera: Cynipidae) in May and galls of (?) *Braueriella phyllireae* Timb. (Diptera: Cecidomyiidae) in April in Italy, but as already stated by Boucek & Askew (1968), these records are rather doubtful. Some of the published data by Boucek & Askew (1968) may concern *Tetrastichus crino* Walker or other species, which were incorrectly identified by Erdös (1956).

C. pacuvius has a very narrow host range. Its distribution is probably closely linked to its univoltine host, the pea thrips *Kakothrips pisivorus* Westwood, occasionally an important pest of peas, *Pisum sativum* (Kutter 1935, 1936ab; 1937), or beans (Faber, 1973) in Europe up to the Kaukasus and Anatolia (Priesner, 1964). Bühl (1937) however in his studies on this pest in the Kiel area (Germany), Vuillet (1914) in France and Antsiferova & Timraleev (1974) in the Mordovin district (Russia) only found parasitization by *C. menes*. The only other host it has been associated with is *Odontothrips ulicis* Haliday (BMHN, 1977) and a yet unidentified thrips species (Teulon et al., 1992) both found on broom, *Cityscus scoparius* (L.). Other records are related to its presence in the calyx of flowers of different Fabaceae (except *Pisum sativum*, also from *Vicia cracca, Trifolium repens, Lathyrus tuberosus*) (table 6) or have resulted from sweepnet collections from flowering *Brassica napus* (Miczulski, 1968), *Anethum graveolens* (Boucek, 1961) or from low bushes in a mixed forest (Bakkendorf, 1957) and near forest edges (Jenser, 1992pc).

Biology

Data about biology and behaviour of *C. pacuvius* are mainly known by the observations made by Kutter (1936ab, 1937), who recorded significant levels of parasitism on *K. pisivorus* in the Rheintal, Switzerland. It has one generation a year, its occurrence is closely related to the phenology of its host *K. pisivorus*. First appearance of adult wasps coincided with the peak presence of second stage host larvae.

Fig. 8. Distribution of *Ceranisus pacuvius* (Walker) in Europe.

Tabel 6. Survey of thrips parasitoids belonging to *Ceranisus pacuvius* Walker. Distribution, host plant and host species.

Distribution	host species	host plant	date	reference	Syn.
England, London				Walker 1838	1
England, London			1838	Walker 1839/40	4
Ireland				Walker 1839/40	2
England				Graham 1959	2
Austria, Mödling				Kirchner 1867	2
Germany, Aachen				Kirchner 1867	2
Czechia, Kaplice				Kirchner 1867	2
Czechoslovakia				Boucek 1957	2
Sweden, Sälsynt, Skåne				Thomson 1878	5
Sweden		sweep net		Hedqvist 1978pc	2
Denmark, North Sealand-		forest	1926.v	Bakkendorf 1957	2
Ryget			1926.vi		
Denmark, North Sealand-		low bushes	1955.vi		
Fortunens Indelukke		(forest)	1955.vi		
Moldavia, Kishinev		*Anethum graveolens*	1958.vii	Boucek 1961	2
Poland, Czechów		*Brassica napus* (w)	1953.vi	Miczulski 1968	2
Slawin		*Brassica napus* (w)	1953.vi		
Felin		*Brassica napus* (w)	1955.vii		
Slawin		*Brassica napus* (s)	1953.vii		
Hungary, Tompá, Mátrá			v-vii	Erdös 1971	2
Kalocsá, Mecsek					
England, Dorking			1970.vi	BMNH (Boucek)	2
			1971.vii	BMNH (Boucek)	2
Switzerland, Rheintal		sticky trap	1932.vi	Kutter 1936ab	3
Rheintal	*Kakothrips pisivorus*	*Vicia cracca*	1933.vii	Kutter 1936ab,	
		Pisum sativum	1933.vi.vii	Kutter 1935	
		Trifolium repens	1933.vii		
Rheintal		*Pisum sativum*	1934.vi		
Rheintal	*Kakothrips pisivorus*	*Pisum sativum*	1935.vi-vii		
Rheintal	*Kakothrips pisivorus*	*Pisum sativum*	1936.vi-vii	Kutter 1937	
Flawil	*Kakothrips pisivorus*	*Pisum sativum*	1936.vi		
Switzerland, Diepoldsau	*Kakothrips pisivorus*	*Pisum sativum*	1992.vii	Teulon et al.	2
Netherlands, Goeree	*Kakothrips pisivorus*	*Pisum sativum*	1957.vi	Franssen 1960	3
Hungary, Nagykovácsi	*Kakothrips pisivorus*	*Lathyrus tuberosus* (forest edge)	1989.vi.vii	Jenser 1993pc	2
England, Southampton	*Odonthothrips ulicis*	*Cytiscus scoparius*	1977.v	BMNH (Noyes) Teulon et al. 1992	2
Scotland, Flotterstone	unidentified thrips	*Cytiscus scoparius*	1992.vi	Teulon et al. 1992	2

Synonym, 1: *Cirrospilus pacuvius*, 2: *Ceranisus pacuvius*, 4: *Entedon acestor*, 3: *Thripoctenus kutteri*, 5: *Derostenus clavicornis*. w = winterrape, s = summerrape

Males occur somewhat earlier than the females (Kutter, 1936a), but all records have been made between the end of May and beginning of July (table 6). Mating takes only seconds, on leaves and flowers of pea. It preferably attacks large, second stage larvae (Kutter, 1935, 1936a). Kutter (1936a) gives an extended description of egg and larval development of the parasitoid inside its host's body, which very much resembles the developmental process in other *Ceranisus* species (*menes*, *americensis, russelli, nubilipennis, vinctus*, see 3.2.1.1.1). Developmental time from egg till pupa takes about 18 days (derived from dissection of field collected larvae). The parasitoid overwinters in the pupal stage, whereas the host overwinters as a full-grown larva in the soil. Also Bühl (1937) noted a similar univoltine development on *K. pisivorus* for *C. menes* (see 3.2.1.1.1).

Its impact on its host population is not clear. Although from 1933-1936, locally 68% (Kutter, 1936a) or even 92% (Kutter, 1937) of the host larvae population had been parasitized, on other places the parasitization level was very low. Also Franssen (1960) frequently noticed the presence of parasitoids in pea crops in The Netherlands. The number of parasitoids found however was related to the infestation level by *K. pisivorus* the year before (Kutter, 1937), and was fluctuating over the years. As Kutter (1936a) states, the preferred second stage larvae occur from the second half of June until the second half of July, *C. pacuvius* adults were present over a number of years between June 14th-July 5th, coinciding with the peak presence of second stage host larvae, but a significant part of the larvae could escape from parasitization (see also 3.2.1.1.1; Bühl, 1937). Heavy rainfalls during the flowering period seem the have the largest impact on thrips population dynamics (Faber, 1973). Recently Teulon et al. (1992) sampled populations of *K. pisivorus* in private gardens in the second half of June in the same area of the Rheintal. Although on a number of occasions second stage thrips larvae were abundant on pea pods, only a single ♀ specimen of *C. pacuvius* was found. From field collections made by the same author in England, Germany and Scotland, there was no evidence of parasitism in any cleared thrips larvae.

Its effect on other, multivoltine pest species from the thripine subfamily, like the genera *Thrips* and *Frankliniella*, is unknown, but based on its phenology and registered host range, it probably is low.

3.2.1.1.3 Ceranisus russelli (Crawford)

Synonymy

Thripoctenus russelli Crawford 1911

Taxonomy

The genus *Thripoctenus* and *T. russelli* in particular was first described by Crawford (1911). Only females are known, about 0.6 mm in length (figure 10-1); head and thorax black, smooth, polished; abdomen brown with a large basal flavous spot; antennae and legs testaceous, pedicel longer than two funicular joints combined; wings hyaline, longest marginal fringes two-thirds as long as greatest wing width (cf. *C. americensis*).

Distribution, hosts, host plant associations

Ceranisus russelli (Crawford) is nearctic, and found in California U.S.A. in particular (figure 9). It was originally found in Compton, Whittier and Puente (Russell, 1911, 1912ab; Howard, 1911), which are all part of Los Angeles nowadays. Later it was found in other parts of California too (Horton, 1918; Bailey, 1933; McKenzie, 1935). Bagnall (1914) described a black and white chalcid parasitoid associated with thrips from England, which he described as ' almost certainly' *C.* (*Thripoctenus*) *russelli*. His identification however is doubtful (Graham, 1993 pers. comm.), although Bagnall identified it after comparing it with material sent to him by Russell, *C. russelli* was the only thrips parasitoid which had been described at that time. It probably concerns the brown colour-type of *C. menes*, but as Bagnall's material is lost (Graham pers. comm.), this cannot be verified. The New Zealand records of *C. russelli*, e.g. in Valentine (1967), seem to concern *C. menes* (Boucek, 1988) as well.

C. russelli has been reported mainly from the bean-thrips *Caliothrips fasciatus* (Panchaetothripinae: Thripidae) (Russell, 1911, 1912ab; Horton, 1918; Bailey, 1933) infesting *Phaseolus vulgaris*, lima bean (*Phaseolus lunatus*) and wild plants like prickly lettuce (*Lactuca scariola*), sow-thistle (*Sonchus oleraceus*), and filaree (*Nicotiana glauca*) surrounding bean fields. The same author also recorded parasitization of *T. tabaci* on turnip foliage (*Brassica napus*) (table 7). In the laboratory it also attacked and inserted larvae of *H. haemorrhoidalis* and *Hercinothrips (Heliothrips) femoralis*, but no parasitization followed (Russell, 1912b). In the laboratory it attacked an developed on *Frankliniella tritici* (Fitch) (referred to as *Euthrips tritici* Fitch: Russell, 1912b). Although Russell (1912b) could not confirm this with field observations, Horton (1918) found that it affected *F. tritici* in San Joaquin Valley. McKenzie (1935) quotes Bailey that *C. russelli* was taken on gladiolus

Table 7. Survey of *Ceranisus russelli* (Crawford): distribution, host species and host plant associations.

Distribution	host species	host plant	date	reference
Calif., Compton LA	*Caliothrips fasciatus*	*Phaseolus vulgaris*	1910.xi	Russell 1911, 1912a Crawford 1911
Calif., Compton LA	*Caliothrips fasciatus*	*Phaseolus vulgaris*	1911.vi-ix	Russell 1911, 1912b
		Lactuca scariola	1911.viii	
	Thrips tabaci	*Brassica napus* (turnip)	1911.viii-ix	
Calif., Hollywood	*Caliothrips fasciatus*	*Phaseolus vulgaris*	1911.vi-viii	Russell 1911, 1912b
	Caliothrips fasciatus	*Lactuca scariola*	1911.viii	
		Phaseolus lunatus	1911.viii	
Calif., Puente LA	*Caliothrips fasciatus*	*Phaseolus vulgaris*	1911.viii-ix	Russell 1912b
		Sonchus oleraceus	1911.x	
		Nicotiana glauca	1911.x	
Calif., Whittier LA	*Caliothrips fasciatus*	*Phaseolus vulgaris*	1911.vii	Russell 1912b
	Frankliniella tritici [1]	lab. test		
Calif., San Joaquin V.	*Caliothrips fasciatus*			Horton 1918
	Frankliniella tritici [1]			
Calif., Central	*Caliothrips fasciatus*		1929.vi-viii 1930.vi-vii	Bailey 1933
Calif., Sacramento	*Thrips simplex*			McKenzie 1935

[1]: Referred to as 'the wheat thrips *Euthrips tritici* Fitch' (Russell, 1912b), 'the flower thrips (*Frankliniella tritici* Fitch)' (Horton, 1918). In that time *Euthrips tritici* (Fitch) has been used as a synonym for *Frankliniella occidentalis* (Pergande) too (e.g. Daniel, 1904; Crawford, 1909). Also Bryan & Smith (1956) mentioned Crawford's description as a synonym of *F. occidentalis*, but the specific name as used by Russell (1912b) is referring to *Frankliniella tritici* (Fitch) (Jacot-Guillarmod, 1974, 7(3): 825).

thrips, *Taeniothrips gladioli* (= *Thrips simplex*) (Thripinae: Thripidae).

A number of hosts have erroneously been mentioned in literature as being parasitized by *C. russelli*. An erroneous record of *Taeniothrips inconsequens* Uzel as a host has been referred to as such in Lewis (1973) and Ananthakrishnan (1984). Foster & Jones (1915) however mentioned *C. russelli* only as a potential but not as an actual parasitoid of this thrips species. The citrus thrips, *Scirtothrips citri* Moulton, was not attacked by *C. russelli* (Horton, 1918), although it occurred in close association with the flower thrips *F. tritici*, on orange trees. As already mentioned above, hosts found in association with a parasitoid – *T. tabaci*, *F. intonsa*, *Thrips paluster* on *Pedicularia palustris*, *Taeniothrips picipes*, *Taeniothrips atratus* in *Linaria* flowers and *Taeniothrips* (= *Ceratothrips*) *ericae* on heather – by Bagnall (1914) in England, are very likely not related to *C. russelli*, but to *C. menes*.

Biology

Almost all accounts about the biology, the habits and occurrence in the field of *C. russelli* have been registered by Russell and Graf in 1910-1911 (Russell, 1911, 1912ab) and Bailey (1933, 1937). Recent data are not available. The pre-oviposition period is very short: oviposition can take place within a few hours after emergence. The parasitoid does not seem to prefer any particular size of larva, as it has been seen to oviposit in all sizes, from larvae not over a day or two old to larvae ready to change to prepupae (Russell, 1912b), although Bailey (1933) observed that it oviposited in large larvae only. The degree of maturity bears some relation to the length of time between oviposition and indication of parasitism in the host. In larvae that were nearly full-grown either the parasitic larvae did not develop or the duration for their development was lengthened a number of days (Russell, 1912b).

The same author described the searching behaviour for *C. russelli*, completed by Bailey (1933). While searching for hosts, the female crawls very slowly over the leaf with her antennae diverging but horizontal and constantly moving from side to side, until she comes into contact with a larva of *C. fasciatus*. At that point the antennae were drawn closely together and moved carefully and slowly over the larva from one end to the other; then the antennae were dropped downward, touching the larva. The abdomen was curved under the body and the ovipositor was quickly thrust in the body of the thrips larva, and as soon as the egg was deposited the ovipositor was withdrawn. Generally this was easily done, but in a few cases a short struggle was necessary before it could be accomplished. Eggs are deposited both in the thorax and abdomen of the thrips larva but usually at the side of the abdomen (Bailey 1933). Although it has been frequently observed that this parasitoid would oviposit in the same host two or even three times, only one adult has been reared from these double-parasitized specimens, and in nearly every case only one parasitoid larva developed in them (Russell, 1912b). In the majority of cases the larvae of *C. fasciatus* did not seem to be in the least disturbed by this action (Russell, 1912b), although Bailey (1933) states that attempts to oviposit were many times unsuccessful owing to the violent struggle of the (second stage) larva. Oviposition in the larvae of *T. tabaci* and *F. tritici* was identical with that of *C. fasciatus*, but the thrips larvae were more active and more easily alarmed so that they either moved away or violently threw the tip of the abdomen around. In the open, where larvae are more scattered, searching six square inches of leaf surface took 40 minutes, finding and ovipositing in only 4 larvae. Its searching behaviour differed according to the type of leaf surface, moving with rapidity on smooth, glaucous surfaces like leaves of cabbage, turnip, wild lettuce, or delayed on hairy or sticky leafage like that of nasturtium or Chinese gourd (Russell, 1912b). *C. russelli*, observed in the open on a croton leaf, attempting to oviposit in the larva of *Heliothrips haemorrhoidalis*, was frequently caught by the sticky excrement of its host, and only with great difficulty succeeded in freeing itself (Russell, 1912b).

The act of oviposition ranged from 15 seconds to 4 minutes (Bailey, 1933), according to Russell (1912b) it required from 20-50 seconds. Russell (1912b) recorded 38 eggs laid in 36 larvae within 60 minutes; it is difficult however to estimate the egg-laying capacity of *C. russelli*, the few observations mention a minimum of 56-91 parasitized offspring for a single female and a longevity of 3-10 days. Host feeding has been observed as well (Bailey, 1933). Parasitism first becomes evident two or three days after the thrips larvae have changed to the prepupal stage and development into prepupal and pupal stage closely resembles this process as described for *C. menes*. The inner coloured cylinder in the prepupa however varies according to the host: deep crimson in *C. fasciatus* and yellow in *T. tabaci* and *F. tritici* (Russell, 1912b). *C. fasciatus* pupates in rubbish, in cracks or under clods of earth, when this species is the host of *C. russelli*, the latter will be found to form its pupae in the same places (Russell, 1912b).

Developmental time of the parasitoid on *C. fasciatus* shows a large variation in all stages. In the insectarium with fluctuating temperatures (see table 8), it took 10.2 days from oviposition to the first indication of parasitism and duration of the prepupal and pupal stage lasted 3.6 and 19.8 days respectively: in total 33.6 days (range 28-44 days), about the same time when parasitizing *T. tabaci* (Russell, 1912b) and within the same range as *C. menes* on *T. tabaci* (see table 5). In June/July 1931 the length of the egg/larval stage averaged about 7.5 days, pupal period 14 days (Bailey, 1933, 1937). Developmental time of *C. fasciatus* and the parasitoid are about the same (see table 8), that of *T. tabaci* is much shorter.

Parasitism levels of *C. fasciatus* showed a large variation and ranged as high as 70% in southern California in 1911 (Russell, 1912b). During the seasons 1929-1931 about 5% parasitism by *C. russelli* was observed in central California by Bailey (1933, 1937). In different collections of *T. tabaci* parasitization levels ranged

Table 8. Average developmental times of *C. russelli* and its host *C. fasciatus* in California USA, at an average temperature of 65°F = 18-19°C, 1911^{r} (after Russell, 1912b), and summer 1931^{b}, 72°F = 22.2°C (Bailey, 1933).

species	period	eggs + larvae	prepupa	pupa	Total
C. fasciatus	July-Aug 1911	13-19 + 10-12	------ 7-12	-----	30-44^{r}
	June-Aug 1931	7 + 10	------ 5	-----	22.0^{b}
C. russelli	July-Sept 1911	10.2	3.6	19.8	33.6^{r}
	June-July 1931	------------ 7.5	------------	14.0	21.5^{b}

from 15-60%, with an average of 33.5% (Russell, 1912b). There appears, however, to be a gradual seasonal increase in the number of parasitoids, reaching a maximum in the late fall: low levels in June-August – 0.9% from over 10,000 larvae collected –, a much higher level in the fall with the falling-off of the thrips population. Adults have been found in the open in association with the bean thrips during every month of the year (Bailey, 1933). During the winter adults have been found among the hibernating adult thrips on the underside of the leaves of various hosts. In the spring they are to be seen actively running about among the first generation of thrips larva on prickly lettuce, filaree, sow-thistle, etc. During the summer they appear to be even more scarce than in the spring. Russell (1912ab) noticed first appearance of adults on June 15, and a last appearance in fall November 10, 1910; *C. russelli* passes the winter in the pupal stage, few adults emerged after October 5, adults however being present and active during October, parasitized larvae were found as late as December 8, 1911. The number of generations (March 15- November 10) within 210 seasonal days, is varied from 5 up to 8, depending on the developmental time.

In 1930/1931, Sakimura (1932) introduced *C. russelli* into Hawaii from LA county California for the control of *T. tabaci*. It was reared in considerable numbers at Riverside Ca and shipped to Hawaii in an attempt to control the onion thrips. The plan has proven unsuccessful (Bailey, 1937): a definitive hibernation period (*T. tabaci* shows no hibernation during winter months at 22.2°C) and the length of its pupal period, resulting in a much longer life-cycle, made it ineffective in Hawaiian climatic conditions (Sakimura, 1932).

3.2.1.1.4 Ceranisus americensis (Girault)

Synonymy
Thripoctenus americensis Girault 1917

Taxonomy
Girault (1917c) described *T. americensis* from females only. They are about 0.75 mm (Girault, 1917) till 0.95 mm in length: body black, scaly, proximal half of abdomen orange yellow and the distal half brown; antennae and legs (except coxae) pale, dusky; pedicel longer than second funicular joint; wings subhyaline, longest marginal fringes forewing one-fourth of greatest wing width (figure 1-4) It resembles *C. russelli* very much (Crawford, 1911) and somewhat the brown colour-type of *C. menes*, but the basal spot is more clear in *C. americensis*.

Distribution, hosts, host plant associations
Until recently few data were available about *C. americensis*. Its distribution seems restricted to the Western part of North America (figure 9). Girault (1917c) first collected it from alfalfa in Utah, August 1912 and identified it as *Thripoctenus americensis*. In 1920 it was found on alfalfa in association with *F. occidentalis*, in Alberta – Canada (Seamans, 1923). Only recently it has been collected again from wild mustard, alfalfa, clover, etc. infested with a.o. *F. occidentalis* in various places in

Fig. 9. Worldwide distribution of *Ceranisus* spp. (other than *C. menes*).
a = *americensis*, r = *russelli*, nu = *nubilipennis*, ni = *nigrifemora*, L = *lepidotus*, P = *planitianus*, mc = *maculatus*, j = *javae*, V = *vinctus*, f = *femoratus*, bi = *bicoloratus*, m = *margiscutum*, * = unidentified *Ceranisus* sp. (other than *C. menes*).

California and Arizona (table 9; Loomans 1993, pers. coll.). Parasitoids collected from alfalfa infested with *F. occidentalis* in California and referred to as *Ceranisus* sp. by Greene & Parrella (1993), partly consisted of *C. menes* and *C. americensis* (Loomans, pers.id.).

Biology

Until recently little was known about *C. americensis*. Its biology has been subject of study only since 1993. What follows (Loomans, unpublished data) is an excerpt from a more elaborate report that will be published elsewhere.

C. americensis is a solitary endoparasitoid of larval stages of thrips, and exhibits thelytokous parthenogenesis, only females are produced. *C. americensis* has a short pre-oviposition period of a few hours only and a female can lay up to 160-170 eggs on average. First stages and to a less extent second larval stages of thrips species of the thripine subfamily are preferred as hosts. In the laboratory *F. occidentalis*, *F. intonsa*, *T. tabaci* and *F. schultzei* were preferred in decreasing order. Its stinging and oviposition behaviour is like that of *C. russelli* described by Russell (1912b) and can easily be distinguished from that of *C. menes*, described above: standing on its legs, it extends its ovipositor between them, stinging the host larva in a curved position and remaining like that during oviposition. Host-feeding has been observed as well. Like in other *Ceranisus* spp., parasitized larvae can move about freely and feed normally, and the development of prepupa and pupa is alike: the prepupal central spot is orange red, the pupa is creamish white when newly hatched, becoming grey very quickly and blackbrown before emergence. The life-cycle is completed in 27-28 days on average at 25 °C (cf. Greene & Parrella, 1993), but like in *C. menes* it is much longer at 20°C, showing a large variation: 40-125 days.

3.2.1.1.5 Ceranisus vinctus (Gahan)

Synonymy

Thripoctenus vinctus Gahan 1932

Taxonomy

Gahan (1932) considered *C. vinctus* 'very close to *T. brui* Vuillet (= *C. menes*) but slightly smaller, with the second funicle joint globose, the wings somewhat narrower, and the abdomen mostly blackish with the base pale'. Except for the funicle, these characteristics are not solid (see below). Gahan's additional description of the details of its morphology (Gahan, 1932), e.g. wing structure, presence of a bare surface of the wing behind the submarginal vein edged by a sigmoid row of cilia also fits descriptions of *C. menes* (wing: subcubital vein is curved, and all legs are yellow). Compared with Ishii's description of *C. menes* from Japan (Ishii, 1933) and because of his remark that he examined a specimen bred by Fullaway from *T. tabaci*, and thus considered it as occurring in the Philippines, there is circumstantial evidence that *C. vinctus* likely is a colour-type of *C. menes*. Since all (field-collected) parasitoids of *C. vinctus* were females, it was said to reproduce partheno-

Table 9: Survey of thrips parasitoid species belonging to the genus *Ceranisus* Walker. Distribution, host species and host plant associations; (): thrips species found in association with parasitoids.

Distribution	host species	host plant	date	reference
Ceranisus americensis				
USA, Utah	?	alfalfa, swept	1912.vii	Girault, 1917a
Canada, Alberta	(*Frankliniella occidentalis*)	alfalfa, swept	1921/22	Seamans, 1923
USA, California	*Frankliniella occidentalis*	wild mustard	1993.v	Loomans, 1993pc
	unid. thrips	wild mustard		
USA, Arizona – Willcox,	unid. thrips	*Trifolium* sp.	1993.v	Loomans, 1993pc
CampVerde	unid. thrips	*Melilothus officinalis*		
Ceranisus vinctus				
Philippines, Luzon	*Megalurothrips usitatus*	flowers lima bean	1931.vii	Gahan, 1932
Philippines, Los Banos	*Megalurothrips usitatus*	flowers cowpea, lima bean	1931.vii	Fullaway & Dobroscky, 1934
Ceranisus bicoloratus				
Japan, Nagasaki – Ikiriki	thrips (Tubulifera?)	leaves *Piper futokadzura*	1926	Ishii, 1933
Japan, Shimane – Sada	*Liothrips wasabiae*	leaves/roots wasabe (forest)	1990.viii	Murai, pc
Ceranisus nubilipennis				
USA, Massachusetts – Forest Hills	*Cryptothrips rectangularis* *Megalothrips spinosus*	galls willow (swampy spot)	1915.vii	Williams, 1916
Ceranisus femoratus				
Philippines, Luzon	(*Megalurothrips usitatus*)	flowers lima bean	1931.vii	Gahan, 1932
Ceranisus nigrifemora				
Argentina, Tucumán	?	forest	1960.iii	DeSantis, 1961
Ceranisus lepidotus				
England, Wytham	?	?	1952.vi	Graham, 1963
Britain, unloc.	?		18??	(Haliday coll.)
Spain, Murcia	*Limothrips cerealium*	*Hordeum*	1990.v/vi	Lacasa, pc
	(*Stenothrips denticornis*)	*vulgare*	1993.v/vi	
	(*Frankliniella occidentalis*)	weeds		
Ceranisus planitianus				
Central Europe	?	?		Graham, 1963
Hungary, Szöd	?	grasses	1922.ix	Erdös, 1966
Kalocsá			1943.v	
Foktö			1943.vi	
Hajdúböszörmény			1959.ix	
Czechoslovakia				Erdös, 1971
Spain, Castellon-Benicasim			1974.vi	BMNH (Boucek)
Ceranisus margiscutum				
Australia,				
NSW, Chindara	?	mangrove/river	1914.v	Girault, 1915
QLD, Indooroopilly	?	window house	1932.xii	Girault, 1934
Ceranisus javae				
Indonesia, Salatiga	*Thrips* sp.	cacao	191?.vii	Girault, 1917b
Ceranisus maculatus				
India, Lyallpur – Punjab	*Rhipiphorothrips cruentatus*	vine	1929.xi	Waterston, 1930
Ceranisus **sp.**				
Taiwan, Pingtung	*Rhipiphorothrips cruentatus*	wax apple	1982-83	Chiu, 1984

genetically (Fullaway & Dobroscky, 1934), but not each parasitoid was checked for sex. However, adult *C. menes* specimens collected by Tamò in the field from e.g. *Cajanus cajan* (pigeon pea) and *M. usitatus* at Los Banos, April 1991, were all females (Tamò, pers. coll.), but reproduced sexually in the laboratory (Loomans, pers. comm.), but only comparison of the holotype specimens can give full proof.

Distribution, hosts, host plant associations

Ceranisus vinctus has been recorded only from The Philippines (figure 9), from July till November 1931 (Gahan, 1932; Fullaway, 1933; table 9), when field surveys were made to find parasitoids attacking *T. tabaci*, in order to introduce them into Hawaii for its control (table 18). *T. tabaci* was only found in low numbers in the field and no evidence of parasitism was found. The parasitoids found however, *C. vinctus* and a single female of *Ceranisus femoratus* (Gahan), were parasitizing larvae of *Taeniothrips longistylus* Karny (= *Megalurothrips usitatus* Bagnall). Both were collected from flowers of lima bean (*Phaseolus lunatus*) and cowpea (*Vigna unguiculata*) at Los Banos (Fullaway & Dobroscky, 1934).

Biology

A short, though incomplete account of its biology is given by Fullaway & Dobroscky (1934). Successful parasitism was obtained only when the young larval stages were used, occupying about one week in the life of the thrips host, *M. usitatus*. A larva of a size as large as the parasitoid was able to shake the latter of its back, regardless repeated efforts of the parasitoid to thrust the ovipositor into the abdomen of the larva. The time between oviposition and first signs of parasitism took 7-9 days under laboratory conditions and development evolved as described earlier for *C. menes*. The prepupal period lasted 1-2 days, the pupal period was from 10 to 12 days, the complete life-cycle 18-23, the average being 22 days for a single adult to emerge. The life-cycle of the host, *M. usitatus*, also lasted 3 weeks or less, when reared on bean stems.

For rearing and shipping purposes, a single field-collected female was placed in a jar of 900 cl, with 50 *M. usitatus* larvae feeding on bean stems. The highest number of parasitoid pupae obtained from one vial was 23 (46%). Females lived for 3-4, occasionally 8 days. Several shipments of *C. vinctus* reared to pupae on *M. usitatus* were sent from Manilla to Hawaii by boat, for the control of *T. tabaci*. First attempts to retard development of the pupae, by keeping them at 5 °C, only resulted in their death. In later attempts to expose emerging parasitoids to onion plants infested with *T. tabaci* and *Taeniothrips* sp., embarked in Kobe – Japan, during the trip, *C. vinctus* could not be reared from either of these hosts (Fullaway & Dobroscky, 1934) and introductions failed (Clausen, 1978; table 18).

3.2.1.1.6 Ceranisus maculatus (Waterston)

Synonymy

Thripoctenus maculatus Waterston 1930

Taxonomy

According to the description of Waterston (1930), head and thorax are shining black, abdomen nearly white with some blackish spots at the sides, antennae of both females and males very much alike, the scape being only a little swollen in the latter; antennae and legs pale, coxae of forelegs black, females 0.8-0.9 mm and males 0.7-0.75 mm long. A transverse second funicular joint separates it from other *Ceranisus* spp. (see figure 11, compare however the description of *Thripobius semiluteus*, Boucek 1976).

Distribution, hosts, host plant associations

Distribution of *Ceranisus maculatus* (Waterston) is oriental, and India in specific (figure 9). It has only been recorded from Lyallpur, Punjab (Waterston, 1930; Ramakrishna Ayyar & Margabandhu, 1934) in 1929-1930, parasitizing *Rhipiphorothrips cruentatus* Hood (Panchaetothripinae) on grape-vine leaves (Rahman & Bhardway, 1937).

Biology

What is known about its biology, has shortly been described by Rahman & Bhardway (1937). Adults copulate on the leaves, a pre-oviposition period followed of 3-5 days. First and second stage larvae are both accepted as hosts, and a single egg is laid in them. The number of eggs laid per female varied from 30 to 105, her longevity is unknown. During the active season (March-November 1929), eggs hatch within 5-10 days, the larval stage lasts 3-6 days. Parasitized larvae move about freely and feed normally, development of prepupa and pupa like in other *Ceranisus* sp.; the prepupal central spot is deep red, the pupa is deep red when newly formed, becoming piceous before emergence. The prepupal and pupal stage, which both stay on the leaf, lasts 15-29 days. The life-cycle is completed in 23-45 days. The life-cycle of *R. cruentatus* is much shorter, 14-33 days, excluding a pre-oviposition period varying from 6-14 days. Longevity ranged up to 20 days, depositing 2 eggs per day in spring/autumn, 5-6 eggs during summer. Life-history values varied with the season: low in June-July, high in spring and autumn at fluctuating temperatures (for laboratory data of *R. cruentatus* at constant temperatures, see Chiu, 1984). The hibernation period of *C. maculatus* is synchronized with its host, the parasitoid hibernating as pupae on the host plants and the host as pupae in the soil, from November-December till March-April. Towards the end of the season, middle of November, parasitoid numbers can go up to 340 pupae per leaf.

In southern Taiwan, Chiu (1984) found a *Ceranisus* sp. occurring in wax apple fields infested with *R. cruentatus*. His records of developmental characteristics and times are almost exactly the same as for *C. maculatus* from Punjab. It has tentatively been identified in 1991 as *T. semiluteus* (Loomans pers. comm.), but its characteristics are also close to *Ceranisus javae* (Girault, 1917; see below). Like in Punjab, populations of *R. cruentatus* were largely affected by temperature and to some extent parasitism and rainfall. Regression equations between thrips populations and % parasitism for two experimental fields were Y = 308.4153 – 5.7678 X (r=0.5984) and Y = 308.2598 – 3.5338 X (r=0.6012) respectively. In winter, when thrips levels were low, parasitism was as high as 77.2 % in January, at a density of 2.1-3.5 parasitoids per leaf. In Taiwan *R. cruentatus* did not hibernate in the soil. Parasitoids gathered on leaves with high densities of the host. However during summer, when a maximum of 52% parasitism was found, it was not able to control thrips population outbreaks.

3.2.1.1.7 Ceranisus bicoloratus (Ishii), *Ceranisus nubilipennis* (Williams)

Synonymy
Thripoctenus bicoloratus Ishii 1933
Synonymy
Thripoctenus nubilipennis Williams 1916, *Cryptomphale nubilipennis* Girault 1917

Taxonomy
Both sexes of *C. nubilipennis* are uniform black in colour, highly polished, wings dusky with very long dark cilia; antennae dark translucent with white hairs, ♂ scape broader and whorls of bristles on the flagellum; length 0.7-0.9 mm. Of *C. bicoloratus* only 3 females are known, the type specimens however are lost (Murai, pers. comm.). Females, dark brown, 0.99 mm in length; antennae pale brown except for first funicular joint which is whitish and covered with long bristles and hairs, club unjointed; legs brownish except the tip of fore-femora, tibiae and tarsi of fore and mid-legs which are whitish; wings hyaline (Ishii, 1933, figure 10).

Distribution, hosts, host plant associations
Because their taxonomy and host range are similar, both species will be discussed together. From *Ceranisus bicoloratus* (Ishii), females have been recorded from Japan, bred by Ishii from a thrips on the leaves of *Piper futokadzura* at Ikiriki, Nagasaki, in 1926 (Ishii, 1933). Murai (pers. comm.) reared the same species from larvae of *Liothrips wasabiae* Haga et Okajima (Tubulifera: Phlaeothripidae) collected in a forest from leaves and roots of wasabe (Cruciferae), august 1990 in Sada, Shimane – Japan (table 9).

Ceranisus nubilipennis (Williams) has been recorded from a swampy spot near Forest Hills, Massachusetts, USA (Williams, 1916). Males and females were repeatedly collected from willow galls occupied by *Cryptothrips rectangularis* Hood and *Megalothrips spinosus* Hood (Tubulifera: Phlaeothripidae), summer 1915.

Biology
C. nubilipennis attacks both larval stages, pupa occasionally. When searching for hosts in the laboratory, it first briefly examines the body of the thrips larva with the antennae, after any slight movement of the host the female immediately thrusts its ovipositor forward between its legs and punctures the larva. The host larva is generally rather quiescent, sometimes crawl about, managing to escape; occasionally the female follow the host sidling along, still holding-on when dragged head-long, or circumvented its victim by mounting on its back. Host larvae, and particularly pupal forms, defended themselves by violently contorting their abdomen, excreting

anal droplets. Oviposition lasted 10-15 minutes, sometimes 30; hostfeeding occurred regularly. The number of hosts attacked, during 4-5 days they stayed alive, was not ascertained. One or two days after parasitism became clear in an advanced larval stage of the thrips host, the larva grew mottled and waxy in colour. Successful multiple parasitism seems to be the rule: 2-3 or even more pupae can emerge after 11-13 days from a single host, ♂ and ♀ are present in the same host. In *C. bicoloratus* multiple parasitism also occurs parasitizing another plaeothripid, *L. wasabiae* (Murai, pers. comm.) and also Ishii (1933) states that his 3 females came from 'a thrips on the leaves of *P. futokadzura*'. Takahashi (1934: in Lewis, 1973) recorded the plaeothripid *Gynaikothrips kuwani* causing galls on *P. futokadzura*. Plaeothripid species involved are quite large, about 3 mm in length when fullgrown. From the latter parasitoid species no further data are known.

3.2.1.1.9 Odd records of *Ceranisus* spp.

A number of *Ceranisus* species have been described from a few specimens only, and except for their collection data (see figure 9, table 9), nothing is known about them.

Ceranisus femoratus (Gahan) (= *Thripoctenus femoratus* Gahan), has been described from a single female, 1 mm long, collected in Laguna – Luzon, The Philippines (Gahan, 1932). It resembles *C. vinctus*, except for the size of its wings, its blackish coxa, femora and abdomen and may possibly be merely a variety of that species (Gahan, 1932), see also discussion *C. menes*. It was collected from lima bean flowers (*P. lunatus*) infested with *M. usitatus*, July 1931. Since the only ♀ specimen was used as type, it was never introduced into Hawaii as stated by Clausen (1978).

Ceranisus lepidotus Graham 1963 was described from two females, 0.95 mm long, originating from Berkshire, England collected in may 1952 and the holotype from an unlocalized place in Britain in the 1800's. See Graham (1963) for its description. In 1990, the first author received 6 females on alcohol, collected near Murcia, Spain, which were identified as *C. lepidotus* (LaSalle pers. comm.). It was found in association with *Limothrips cerealium* and *Stenothrips denticornis* in *Hordeum vulgare* during May 1990 (Lacasa pers. comm.), and was seen to attack larvae of the first species in the laboratory. Although this species has been collected again since then, further biological data are not known.

Ceranisus margiscutum (Girault) has been swept as a single female from mangrove/bushes in New South Wales, Australia by Girault (1915), described as *Entedonomphale margiscutum* Girault and as a female of *Entedonomphale stalini* Girault (1934) from a window at home in Indooroopilly, Queensland, Australia. Both names have been synonymized by Boucek (1988).

A single female and two males are known from *Ceranisus nigrifemora* DeSantis, described by DeSantis 1961 from a forestry reserve in Tucuman, Argentina and is closely related to *C. pacuvius*. Like in *C. pacuvius* (Walker, 1940; Ferrière, 1936; Bakkendorf, 1959, see figure 7), the male, 0.86 mm long, is characterized by the strongly swollen scape of the antenna. Its biology is unknown.

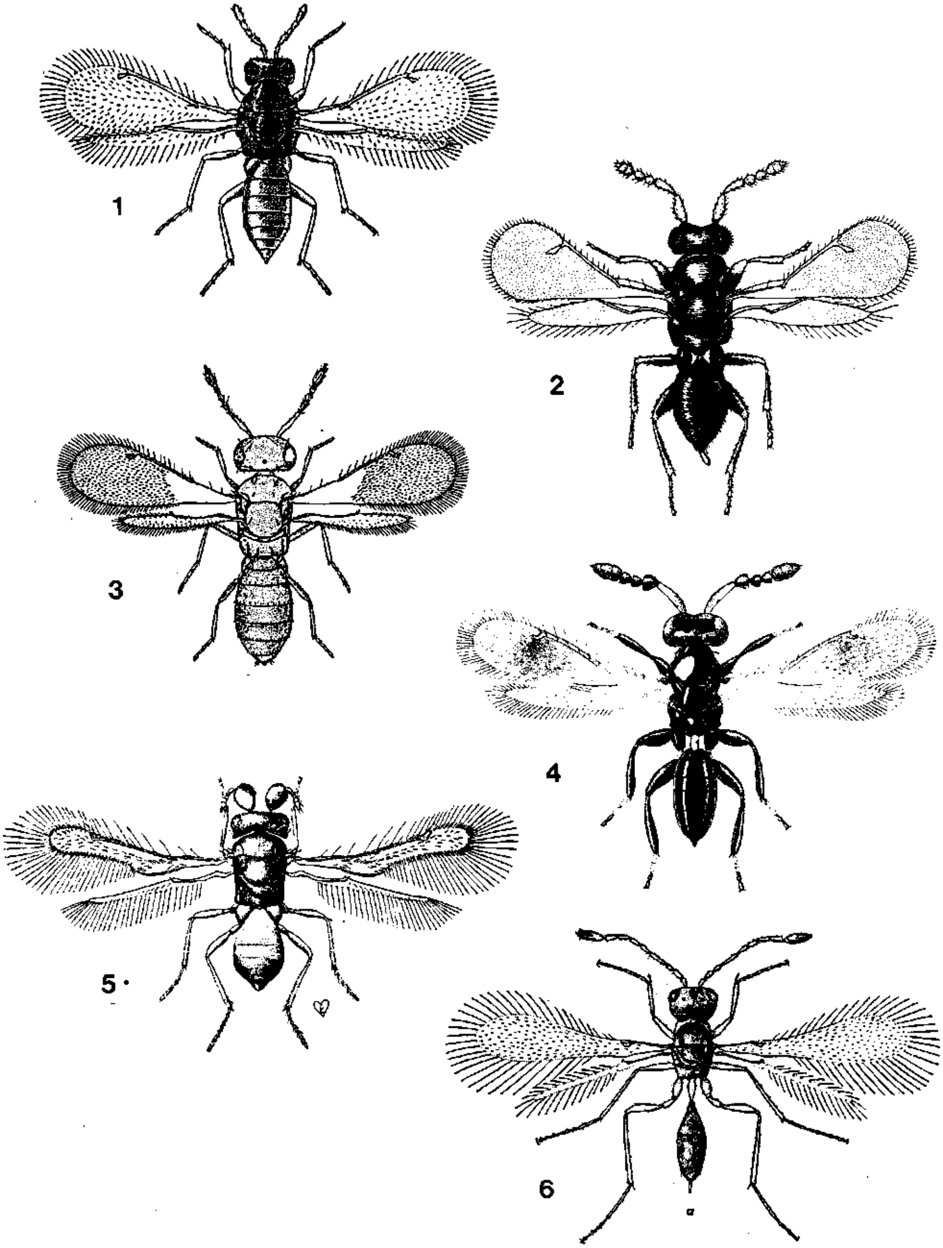

Fig. 10. Image of adult thrips parasitoids. Eulophidae: 1. *Ceranisus russelli* ♀ (Russell, 1912b); 2. *Ceranisus planitianus* ♀ (Erdös, 1971); 3. *Ceranisus bicoloratus* ♀ (Ishii, 1933); 4. *Entedonastichus carbonarius* ♀ (Erdös, 1971); 5. *Goetheana shakespearei* ♂ (Gahan, 1928); Mymaridae: 6. *Polynema indica* ♀ (Narayanan & Subba Rao, 1961).

Ceranisus planitianus Erdös is known from a few specimens, all collected in Europe. A female was first described by Graham (1963, as *Ceranisus* sp. indet.) collected in Central Europe. Later Erdös (1966) identified and described both females, 0.98 mm long, and males, 0.89-0.96 mm long (figure 10), collected from grasses on several places in Hungary. The only other records are from Czechoslovakia (Erdös, 1971) and from a single male collected in Spain in 1974 (BMNH, Boucek).

Finally, *Ceranisus javae* (Girault) (= *Epomphale javae* Girault 1917). Females, 0.6 mm long, were reared from *Thrips* (likely *Heliothrips* or *Selenothrips*, see Entwistle, 1972) on cacao, Salatiga – Midden Java, Indonesia by W. Roepke; it differs from *C. menes* (as described for *Epomphale auriventris* by Girault (1915)) by a two spotted abdomen, the structure of the antennae and wings, the colour of coxae (purple) and antennae and mandibles absent. Except for the length of the pedicel, Girault's description of *C. javae* is very close to that of *C. maculatus* (Waterston, 1930) and that of *Thripobius semiluteus* (Boucek, 1976, see below) and also their host range is similar. Both *Ceranisus* species were not included in Boucek's revision of Australasian Chalcidoidea (Boucek, 1988), and since the descriptions made by Girault (1917) and Waterston (1930) are short, their specific status remains unclear until type specimens have been compared.

Ceranisus (Thripoctenus) sp. that had been named as such prior to their proper identification has already been mentioned above (Greene & Parrella, 1993; Siddipaji & Reddy, 1974; Saxena, 1971, 1981). Others have not been identified to species yet, e.g. the *Ceranisus* (near *russelli*) (Osborne pers. comm., 1990) attacking *Frankliniella bispinosa* in Florida and *Ceranisus* spp. reported by Schauff (1991) from California. Others probably are new to science (Murai, 1992 pers. coll.: collected from tea in Japan; Tamò, 1992 pers. coll.: from cowpea in Zambia; Loomans, 1993 pers. coll.: ♂♀ population collected from lupine, Arizona and *Brassica nigra*, California).

3.2.1.2 Genus *Thripobius* Ferrière

Synonymy

Thripobius hirticornis Ferrière, 1938
Thripobius semiluteus Boucek, 1976

Taxonomy

Females of *T. semiluteus* are 0.6 mm in size, head and thorax purpleblack the latter strongly convex in lateral view, wings hyaline with a slightly curved subcubital vein (figure 11); abdomen, legs (except for coxae) and antennae pale yellow, gaster with 1-2 small dark spots sublaterally; male of *T. semiluteus* is unknown (for details see Boucek, 1976). Female and male of *T. hirticornis* are 0.6-0.9 mm long, body black, antennae and legs yellow, abdomen with a yellow base; antennae of the male with narrower joints and more bristly than that of the female (see Ferrière, 1938).

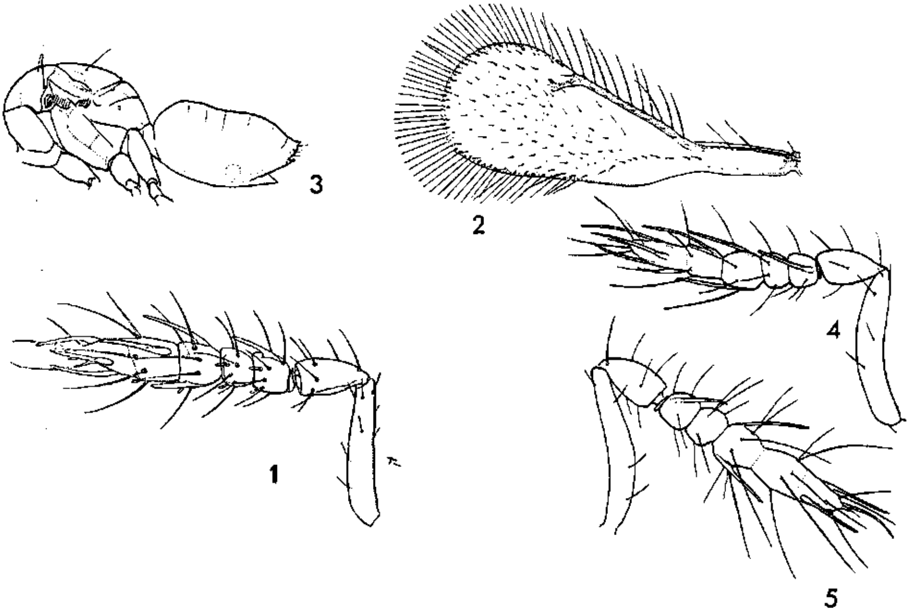

Fig. 11. *Thripobius semiluteus* Boucek. ♀: 2. forewing; 3. body laterally (except head); 4. antenna ♀ Sao Tomé; 5. antenna ♀ Bangalore, India (Boucek, 1976). *Ceranisus maculatus* (Waterston), 1. antenna ♀, Lyallpur, India (Waterston, 1923).

Distribution, hosts, host plant associations

Specimens belonging to this genus were first collected in Africa in 1931. Preliminarily referred to as *Thripoctenus* (= *Ceranisus*) sp. (Ritchie, 1932; 1933), it was later identified as a separate genus *Thripobius* (Ferrière, 1938). Both species belonging to this genus are recorded from tropical and subtropical areas of Africa, Asia and Australia (see table 10, figure 12). Whereas *Thripobius hirticornis* Ferrière only occurs in Africa (Ghana, Tanzania, Uganda, Zimbabwe, Kenya), *Thripobius semiluteus* has been reported from Africa (Sao Tomé: Boucek, 1976; South Africa: Steyn et al., 1993), Asia (India: Boucek, 1976; Siddapaji & Reddy, 1974 (as *Ceranisus* sp.), Japan: BMNH), Australia (Boucek, 1988) and South America (Brazil: LaSalle & McMurtry, 1989). Field collected material send from Taiwan to Wageningen, recorded as *Ceranisus* sp. (Chiu, 1984), probably belongs to this species too (Loomans, pers. comm.). It has been introduced into California (McMurtry, 1988), Hawaii USA (Early, pers. comm.) and Israel (Wysocki, pers. comm.) (table 18).

Thrips species which have been recorded as hosts for *T. hirticornis* as well as *T. semiluteus* all belong to the subfamily Panchaetothripinae (Thripidae). From *T. hirticornis* it is only known to parasitize *Retithrips syriacus*. For *T. semiluteus*, important pest species like *Heliothrips*, and especially the greenhouse thrips *Heliothrips haemorrhoidalis*, is often reported as a host (Boucek, 1976; 1988; Steyn et al., 1993; McMurtry et al., 1993). But also closely related species like *Pan-*

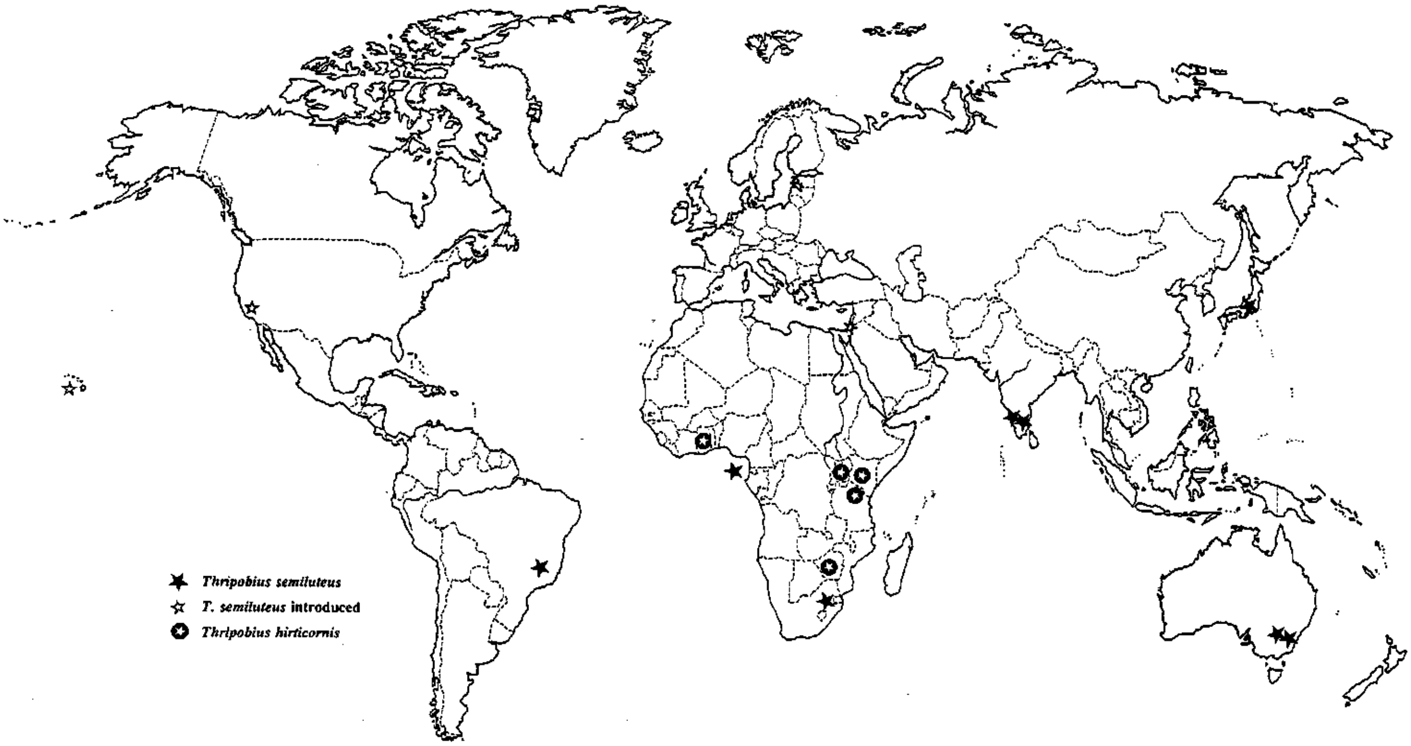

Fig. 12. Worldwide distribution of species belonging to the genus *Thripobius* (Boucek) (Hymenoptera: Eulophidae). Star: *T. semiluteus* (endemic and imported); circled star: *T. hirticornis.*

chaetothrips indicus (Boucek, 1976; Siddapaji & Reddy, 1974 as *Ceranisus* sp.), *Brachyurothrips anomalus* (Boucek, 1976), *Selenothrips rubrocinctus* (Early, pers. comm.), and maybe *Rhipiphorothrips cruentatus* (as *Ceranisus* sp., Chiu 1984), are recorded as hosts. In the laboratory it also parasitized *Hercinothrips femoralis* (Early, pers. comm.), but species like *F. occidentalis*, belonging to the Thripinae (Thripidae), were not accepted as hosts (Ramakers, pers. comm.; Loomans, 1991), contrary to what is mentioned by Albert & Schneller (1993). The relation of *T. hirticornis* and *T. semiluteus* with the host plant species is yet unknown: host plants from which they have been collected all are evergreen shrubs and trees belonging to different families with host infestations on mature, thick, waxy leaves (*T. semiluteus*: cardamom, croton, hibiscus, liquid amber, Valencia oranges, macadamia, avocado, *T. hirticornis*: coffee, rose) (see table 10).

Biology

Whereas from *T. hirticornis* both sexes have been found (Ferrière, 1938), *T. semiluteus* is uniparental (McMurtry et al., 1993), only females are produced. Searching for hosts the female of *T. semiluteus* walks slowly sideways ('crabwalk', Loomans pers. obs.) over the leaf surface. First and early second stage larvae are preferred as hosts (Newberger & McMurtry, 1992; McMurtry et al., 1993). Late second stage larvae were less favourable for parasitoid development, as more than 50% of the pupae developing from these hosts failed to develop. No parasitoids developed in the thrips prepupal or pupal stages. The mature second stage larva is killed by the parasitoid and transforms to a black pupa which remains on the surface where the parasitized thrips larva has been feeding (Newberger & McMurtry, 1992). Developmental time of *T. semiluteus* averages 23.6 (22-25) days at 23 °C, whereas the greenhouse thrips has a longer life-cycle: 35.6 (34-39) days at 23 °C. From *T. hirticornis* no biological data are available.

Newberger & McMurtry (1992) described a technique for mass rearing *T. semiluteus*. The procedure is summarized as follows: The thrips host, *H. haemorrhoidalis*, is allowed to oviposit for 2-3 days on the unwaxed top-surface of silvergreen lemons (*Citrus limon* var. Lisbon or var. Ureka), in units of about 80 fruits arranged in 2 layers infested with 1000 adult greenhouse thrips. When thrips larvae are 2-4 days post-emerged from the egg, newly emerged parasitoids are introduced. After approximately three weeks incubation at 22-25 °C, the black parasitoid pupae are brushed off the fruit into a vial, 250 each. Pupae are stored for a maximum of 2 weeks, at a temperature of 17-18 °C, for field colonization, or for establishing new sting units.

Biological control

In 1986 *T. semiluteus* was introduced from Australia (McMurtry, 1988; McMurtry et al., 1993) and in 1988 from Brazil (LaSalle & McMurtry, 1989) into California to achieve biological control of greenhouse thrips, *H. haemorrhoidalis* in avocado and citrus orchards. Release of more than 500,000 *T. semiluteus* from September 1986 to April 1990 in 50 different avocado orchards in Southern California, resulted in the establishment in many orchards, surviving both cold and hot weather ex-

Table 10. Survey of thrips parasitoid species belonging to the genus *Thripobius* Boucek. Distribution, host species and host plant associations.

Distribution	host species	host plant	date	reference
Thripobius semiluteus				
Africa, Sao Tomé	*Brachyurothrips anomalus*	Hibiscus	1975.ii	Boucek 1976
India, Bangalore	*Heliothrips* sp.	croton	1971.i	Boucek 1976
India, Bangalore	*Heliothrips* sp.	croton	1974.i	Boucek 1976
India, Mudigere	*Panchaetothrips indicus*		1972	Boucek 1976
India, Mudigere	*Panchaetothrips indicus*	cardamom	197?.xi	Siddapaji & Reddy 1974[1]
Japan	*Heliothrips haemorrhoidalis*	(rearing USA[2a])	1988.ix	BMNH (Boucek)
Australia, NS Wales	*Heliothrips haemorrhoidalis*	liquid amber orange	1986.iv	Boucek 1988
Australia, NS Wales	*Heliothrips haemorrhoidalis*	liquid amber (sweet gum)	1986	McMurtry & Badii 1990
Australia, NS Wales			1991	BMNH (LaSalle)
Brazil, Minas Gerais	*Heliothrips* spp.	croton avocado	1988.v	LaSalle & McMurtry 1989
S.Africa, Nelspruit	*Heliothrips haemorrhoidalis*	croton	1993.i	Steyn et al. 1993
USA, California	*Heliothrips haemorrhoidalis*	avocado	1986-9	McMurtry et al. 1991[2a]
USA, Hawaii	*Heliothrips haemorrhoidalis* *Selenothrips rubrocinctus*	macadamia croton ornamentals	1988	Early 1990pc[2b]
	Hercinothrips femoralis	lab. trial		
Israel	*Heliothrips haemorrhoidalis*	avocado bot. garden	1991/92	Wysocki pc[2a]
Thripobius hirticornis				
Uganda, Kampala	thrips nymphs	coffee	1923.x	BMNH, Ferrière
Tanzania, Usa, N.Prov.	*Retithrips syriacus*	coffee	1931.xii	Ritchie 1932, 1933 Ferrière 1938
Ghana, Adeiso, E.Prov.	*Retithrips syriacus*	?	1935.vi	Ferrière 1938
Kenya, c. Makuyii 22	*Retithrips syriacus*	?	1945.iv	BMNH
Zimbabwe, Salisbury	*Retithrips syriacus*	rose	1959.iv	BMNH (Kerrich)

[1]: recorded as *Ceranisus* sp.; [2a]: introduced for control, [2b]: introduced accidentally

tremes. Within 3 years after the release of 20,000 *T. semiluteus* at Irvine Ca, the parasitoid had established and spread to adjacent fields (total 7.3 ac). In San Diego, widespread establishment and up to 63% parasitization occurred within 2 years, following the release of 11,000 wasps in a 6 ac orchard (McMurtry & Badii, 1991; McMurtry et al., 1993). Results indicated that thrips populations declined when the parasitization rate increased up to 50-60%. However, its ability to spread within and between orchards and its carry over at low host densities have not been determined yet. The parasitoid is now produced commercially by several producers of natural enemies in the USA (Hunter, 1992), for $60 per 1,000 pupae (Vandriesche, Biocontrol Flash, Univ. Mass., 11-7-1990). *T. semiluteus* is released for the control of greenhouse thrips in avocado orchards using up to 2000 pupae per acre (two vials per tree with 500 pupae each in four locations). Concentrated releases, e.g. 4 * 250 pupae per tree, are advised in case of isolated trees with heavy infestations of greenhouse trips (News Bulletin FAR company, 1990). In 1991 this parasitoid was imported from California into Israel for the control of greenhouse trips, *H. haemorrhoidalis* in avocado orchards and results suggest that *T. semiluteus* can suppress thrips populations to a large extent (Wysocki, pers. comm.).

3.2.1.3 Genus *Goetheana* Girault

Synonymy
Goetheana Girault 1920
Dasyscapus Gahan 1927

Synonymy species
Dasyscapus parvipennis Gahan 1927
Goetheana parvipennis Ferrière 1931
Dasyscapus thripsivorous Narayanan, Rao & Rao 1960

Taxonomy
Two species have been recorded thus far from the genus *Goetheana*: *Goetheana shakespearei* Girault and *Goetheana incerta* Annecke. Both female and male of *G. shakespearei* are about 0.5 mm – 0.6 mm long (Gahan, 1928; Annecke, 1962; Narayanan et al., 1960). The forewing is very narrow, with long marginal fringes, sexes can be distinguished easily because of the greatly swollen first antennal segment of the male (see figures 10 and 13). Like in *G. shakespearei*, both sexes of *G. incerta* are of the same size, with head and thorax black, and the abdomen yellow/white. The male scape however is not so much swollen as in *G. shakespearei* (Annecke, 1962).

G. shakespearei was first recorded from Cairns, Australia by Girault (1920), who placed it in the Mymaridae. It was associated with thrips first from Java, Indonesia, (Van Heurn, 1923) and identified as *Dasyscapus parvipennis* Gahan in 1927, although it almost exactly fitted Girault's description of *Goetheana* (Gahan 1928). Girault (1930) synonymized *Dasyscapus* Gahan with *Goetheana* Girault in 1930, but until the early sixties (Annecke, 1962) most papers mention its records under the genus name *Dasyscapus*. Narayanan et al. (1960) collected *G. shakespearei* near Bombay, India in 1959 with unidentified thrips and described it under the name *Dasyscapus thripsivorous* Narayanan, Rao & Rao. Although specimens from different origins differ in small features (Annecke, 1962; Narayanan et al., 1960), Boucek (1988) recently synonymized both names to *G. shakespearei*. Boucek (1976) distinguishes it from the closely related genera *Ceranisus*, *Thripobius* and *Entodonastichus* by its minute size, and its very narrow wings with long marginal fringes. A good description of both species is given by Gahan (1928), Annecke (1962) and Viggiani and Nieves-Aldrey (1993). An excellent summary on the knowledge of this genus until 1970 is given by Entwistle (1972).

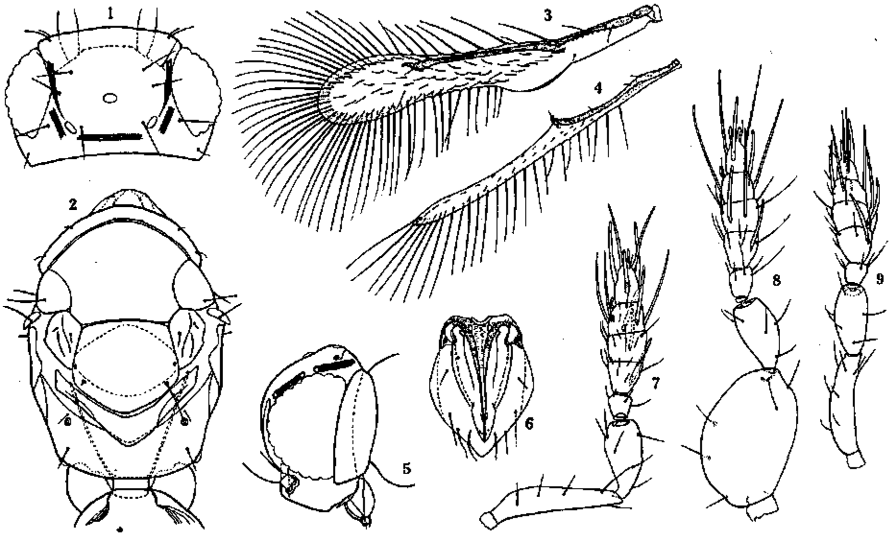

Fig. 13. *Goetheana shakespearei* (Girault), ♀: 1. head, dorsal; 2. thorax, dorsal; 3. left forewing; 4. left hind wing; 5. head, lateral side, without setae; 6. genitalia; 7. right antenna, inner lateral view; ♂: 8. antenna. 9. *Goetheana incerta* Annecke, antenna ♂ (from Annecke, 1962).

Distribution, hosts, host plant associations

The distribution of *G. shakespearei* is australian, aethiopian, oriental and neotropical with a few records from the palearctic. Records are made from tropical and subtropical climates (see figure 14). Except from Australia (Girault, 1920), Indonesia (Van Heurn, 1923), India (Narayanan et al., 1960; Daniel, 1983) and Japan (Takagi, 1988 as *Goetheana* sp., identified by LaSalle as *G. shakespearei*), it has been recorded from Ghana (Cotterell, 1927, 1928), South Africa (Annecke, 1962) and Benin (Tamò, pers, comm.). In 1925 it was recorded from Gold Coast (Ghana), Africa, where it was effectively controlling the cacao thrips *Selenothrips rubrocinctus* (Giard) on cacao (Cotterell, 1927, 1928). In the thirties *G. shakespearei* was shipped from Ghana into Trinidad in 1935 (Adamson, 1936; Cotterell, 1936) and between 1936 and 1942 from Trinidad into Jamaica, Puerto Rico, Bermuda, Grenada, Canada and Hawaii (Callan, 1943) and Maryland-USA (Strong, 1936; Bartlett, 1939). In 1962 it was introduced into California for the control of *Heliothrips haemorrhoidalis* (McMurtry & Johnson, 1963) (see table 18). Based on collections however made from *S. rubrocinctus* at El Valle (Caracas), Venezuela in 1943 (Annecke, 1962) and the Bahamas (Bennett & Baranowski, 1982), were it had not been released deliberately, it probably was already present in the neotropics prior to the biocontrol releases. Also Kaden's report on the occurrence of (pupae of) an unidentified hymenopterous parasitoid attacking *S. rubrocinctus* on cacao in Costa Rica, could indicate its original presence there (Kaden, 1934). Recently *Goetheana* also has been recorded from Europe: an unidentified species from Bulgaria (Pelov, pers. comm.) in 1985 and *G. shakespearei* from Spain in 1989 (Viggiani & Nieves-Aldrey, 1993). The only other

Fig. 14. Worldwide distribution of *Goetheana shakespearei* Girault and *Goetheana incerta* Annecke (Hymenoptera: Eulophidae)

species known, *Goetheana incerta* Annecke, has been described from material collected in a suction trap at Kruger National Park, South Africa (Annecke, 1962).

As shown in table 11, most hosts in field records of *G. shakespearei*, belong to species of the panchaetothripine subfamily (Thripidae) and host plant records are related to these hosts: *Selenothrips rubrocinctus* (Giard) (on cacao, cashew, mango, tropical almond, *Acalypha wilkesiana*), *H. haemorrhoidalis* (croton (*Codiaeum*: Euphorbiaceae), avocado, orange), *Caliothrips insularis* (Hood), *Caliothrips indicus* (Bagnall) (groundnut, *Achyranthes aspera*) and occasionally *Hercinothrips femoralis* (passionfruit, bougainvillaea) and *Dinurothrips hookeri* Hood (laboratory only: Callan, 1951). In its first record however it was associated with *T. tabaci*, (Van Heurn, 1923). Also other authors report on hosts belonging to the thripine group: from *Pseudodendrothrips mori* (Niwa) on mulberry in Japan (Takagi, 1988). Field records from *T. tabaci* however are scarce and parasitization levels are low (Waterston, 1938; Bartlett, 1939), mostly it has been reared from this host under laboratory conditions (Bartlett, 1939; Callan, 1943). Adamson (1936) and Bartlett (1939) also reared *G. shakespearei* on two other unidentified species of thrips in Trinidad. Ananthakrishnan (1984) mentions the cacao flower thrips, *Frankliniella parvula* Hood and *Frankliniella formosa* (= *F. intonsa*), as a host, but Billes (1941) reported that the first was not attacked by *G. shakespearei*, the latter probably has been erroneously mentioned as such.

Biology

G. shakespearei is a solitary endoparsitoid, exhibiting arrhenotoky, producing both sexes. For host acceptance. the adult female can attack both larval stages, but small to medium-sized larvae appear to be required for successful parasitization. *G. shakespearei* selected the late first larvae of *C. indicus* and rarely attacked the second stage larvae, prepupae and pupae (Daniel, 1986). Whenever *G. shakespearei* oviposited in host pupae, the parasitoid could not develop, but adult *C. indicus* which emerged normally, lived only for 2-3 days (Daniel, 1986). In the laboratory when all stages of *H. haemorrhoidalis* were available, the parasitoid examined each host larva contacted, but usually preferred the early second stage larva for oviposition. Sometimes first or late second stage larvae were also stung, but mostly it rejected larger-sized larvae. When confined with only large thrips larvae or prepupa, some of the parasitoids deposited eggs in them, but none of the progeny completed development (McMurtry & Johnson, 1963; Hessein & McMurtry, 1989). The same was found for *S. rubrocinctus* (Dohanian, 1937b), although Bartlett (1939) reported that the percentage of parasitism in newly hatched thrips was nearly double that in fully developed *S. rubrocinctus* larvae in Puerto Rico. Above mentioned panchaetothripine host larvae are more sluggish than host larvae of thripine species, like *T. tabaci* and *F. occidentalis*. Takagi (1988) mentioned that *G. shakespearei* lays its eggs in first and second instar larvae of *P. mori*. No details are known about *T. tabaci*, but Billes (1941) states that the very active larvae of *F. parvula* renders them probably immune from attacks by *G. shakespearei*.

Searching for a suitable host, *G. shakespearei* pounced on it, attacking the host larva by inserting its ovipositor standing laterally to the anterior part of the ab-

Tabel 11. Survey of thrips parasitoid species belonging to the genus *Goetheana* Girault. Distribution, host plant and host species.

Distribution	host species	host plant	date	reference	Syn.
Australia, Cairns	?		1919.i	Girault 1920a	1
Indonesia, Java	*Thrips tabaci*	onion, (greenhouse)	1922.i	Van Heurn 1923 Gahan 1927	2
India, Bombay State	unid. thrips	groundnut	1959.ii	Narayanan, Rao & Rao 1960	4
India, Madras	*Caliothrips indicus*	groundnut *Achyranthes*	1982/3	Daniel 1983	4
Japan, Tokyo area	*Pseudodendrothrips mori*	mulberry	1984.vii-x	Takagi 1988	5
				(LaSalle pc)	1
Ghana, Abuxi	*Selenothrips rubrocinctus*	cacao	1925	Cotterell 1927, Cotterell 1928 BMNH 1928	2
Ghana, E.Prov.	*Selenothrips rubrocinctus*	cacao	1929	Ferrière 1931	2
Benin	*Selenothrips rubrocinctus*	mango	1992	Tamò, pc	2
	Hercinothrips femoralis	bougainvillaea passionfruit			
Trinidad[1]	*Selenothrips rubrocinctus*	cashew, cacao	1935/6	Adamson 1936	2
	2 unid. thrips spp.	lab. test			
	Thrips tabaci	lab. test			
Trinidad[1]	*Selenothrips rubrocinctus* *Caliothrips insularis* *Heliothrips haemorrhoidalis*	cashew, cacao	1935-43	Callan 1943	2
Trinidad, Ch.Fleur	*Selenothrips rubrocinctus*	cashew	1968	Yaseen 1971	2
Jamaica, Hope[2]	*Selenothrips rubrocinctus*	mango	1942	Callan 1943	2
				Edwards 1938, 1939	
	unknown thrips	*A. wilkesiana*	1960.iv	Cock 1985	2
Puerto Rico[1]	*Selenothrips rubrocinctus*	mango	1936.v/xii	Dohanian 1937ab	2
	Selenothrips rubrocinctus	almond	1936/7	Bartlett 1939	2
	Thrips tabaci	onion	1936.ix	Bartlett 1939	2
Venezuela, Caracas	*Selenothrips rubrocinctus*	mango	1943.ix	Annecke 1962	2
Bahamas, Nassau	*Heliothrips haemorrhoidalis*	croton	1980.ix	Bennett & Baranowski 1982	2
USA, California[3]	*Heliothrips haemorrhoidalis*	rearing lab.	1962	McMurtry & Johnson 1963	2
USA, California[4]	*Heliothrips haemorrhoidalis*	avocado lab.	1982	Hessein & McMurtry 1989	3
Bulgaria, Varna	unknown thrips	leaves	1985	Pelov pc	5
Spain, Madrid		Malaise trap	1989.vii- 1989.ix	Viggiani & Nieves 1993	1
South Africa, Skukuza (Kruger Ntl. Park)		riverine forest (suction trap)	1959.xii- 1960.iii	Annecke 1962	2 6

Syn. = synonym used: 1 = *Goetheana shakespearei*, 2 = *Dasyscapus parvipennis*, 3 = *Goetheana parvipennis*, 4 = *Dasyscapus thripsivora*, 5 = *Goetheana* spec.; 6 = *Goetheana incerta*

[1]: introduced 1937, [2]: introduced 1936, [3]: introduced from Trinidad, [4]: introduced from Bahamas

domen (Hessein & McMurtry, 1989; Daniel, 1986). If the larval host escaped during the first attempt, the same larva was attacked repeatedly. A single egg is laid (McMurtry & Johnson, 1963; Daniel, 1986), which hatches in about 24 hours (Dohanian, 1937b) or 3-4 days after parasitization (Daniel, 1986). Superparasitism occurs occasionally, but usually one of the pupae could complete its development (Daniel, 1986; Hessein & McMurtry, 1989). Oviposition time ranged from 20-48 seconds, stung hosts being motionless within a few seconds (Hessein & McMurtry, 1989; Daniel, 1986). A single female can sting up to 25 host larvae in a period of 10-25 minutes, oviposition alternating with short cleaning intervals. Parasitization becomes visible in the last larval or prepupal stage (Dohanian, 1937b), 7-9 days after oviposition (table 12). In this prepupal stage, the host is motionless, a slightly swollen, creamish white cylinder with no wing buds (Takagi, 1988; Dohanian, 1937b). In 2 days a pupa emerges, gradually turning brown, the posterior end of the pupa sticking to the leaf surface hanging head downwards from the skin of the host (Entwistle, 1972, Daniel, 1986). The pupa is shining jet black (Dohanian, 1937b) and has a duration of 8-12.5 days (table 12). The mature parasitoid emerges anteriorly from the host, through a slit between the prothorax and mesothorax (Hessein & McMurtry, 1989).

Life-history notes on *G. shakespearei* presented in table 12, although performed under a variety of conditions, show that developmental time, percentage of adult emergence, longevity and sex-ratio is largely mediated by temperature. The whole

Table 12. Biological parameters for *G. shakespearei* at different temperatures, parasitizing different panchaetothripine hosts: *C. indicus* (Daniel, 1986), *S. rubrocinctus* (Dohanian, 1937b; Bartlett, 1939), *H. haemorrhoidalis* (McMurtry & Johnson, 1963; Hessein & McMurtry, 1989).

Host	Temp.	developmental time (days) egg/ larva	prepupa	pupa	total	range	longevity	sex-ratio
C indicus India	28?	9.1	*	9.5	18.6	17-20	3-4	$2:1^{f}$ $4:1^{f}$
S. rubrocinctus Trinidad	??	7	2	10-11		17-21	4-5	
	$??^{e0}$	8	2	10	20		4-9	
H. haemorrhoidalis California	12.8						11.3 (3-27)♀ 21.7 (2-46)♂	
	17.8	no development			-		16.6 (2-36)♀ 20.8 (2-42)♂	
	21.1^{e1} -24.4^{1}	11.0	4.7	12.5	27.8♂ 28.3♀	27-29 27-29		6.5:1
	22.2				31.6	31-33	9.3 (4-20)♀ 12.4 (4-28)♂	2.0:1
	23.9			8-10	20♂ 21♀		(7-10)	
	29.4^{e2}				20.3	17-26	1.1 (2- 6)♀ 2.8 (2-15)♂	4.8:1

??: temperature unknown, tropical insectary conditions; ^{f}: field results December and February resp.; ^{1} : early 2nd larvae as hosts on avocado leaves, others on Valencia oranges (Hessein & McMurtry, 1989); ^{e0}: 83-87 % emergence, ^{e1}: 75.5 % emergence, ^{e2}: 59.1 % emergence.

life-cycle takes about 17-21 days at temperatures above 24 °C, but is much longer at lower temperatures. At 17.8 °C, the parasitoid did not reach the pupal stage (Hessein & McMurtry, 1989). Adult longevity is short, 3-5 days, but is positively affected when sugar solution (Dohanian, 1937b) or honey is provided (Hessein & McMurtry, 1989). Mean longevity of males exceeds that of females at different temperatures, but both are considerably reduced at higher temperatures (ibid.). Compared to *G. shakespearei* developmental time of their hosts is shorter: *S. rubrocinctus* takes 13-16 days in a tropical climate (Entwistle, 1972) and producing about 50 eggs at an adult longevity of 17-30 days, and *C. indicus* completes its life-cycle in 11-14 days (Ananthakrishnan, 1984). In subtropical zones developmental times of both cacao thrips and parasitoid are about equal: 4 weeks. The total life-cycle of *H. haemorrhoidalis* is much longer, including a pre-oviposition period of 5-6 days: 31 days at 23.3 °C (Hessein & McMurtry, 1989 on Valencia oranges), 35.6 (34-39) days at 22.7 °C (McMurtry et al., 1991 on citrus lemon), 36-42 days (Rivnay, 1935 on citrus) at 23-25 °C and an adult longevity of 40.6 days, producing 45-50 eggs on citrus (op. cit.) or an average of 38.3 per female (Ebeling, 1959) on avocado leaves. Under most favourable conditions, at 26-28 °C, the life-cycle lasts 30-33 days (Rivnay, 1935).

Adamson (1936) and Dohanian (1937b) described a technique for rearing *G. shakespearei* in the laboratory in Trinidad. Newly emerged *G. shakespearei* males and females (10:15) were placed into glass cylinder cages (12.7 cm by 24.5 cm) for mating, closed by moist muslin at both ends and provided with food: cut raisins and 10% sugar solution on paper. Cashew (*Anacardium occidentale*) leaves with young *S. rubrocinctus* larvae collected in the field, were introduced into these cylinders, 20-200 larvae per parasitoid female. After 24 hours exposure leaves were replaced, and placed in a humid atmosphere in battery jars of 30.5 cm by 23 by 18 cm. In this way stocks numbered 10,000-12,000 pupae in the 5th-7th generation. Necessitated by local conditions, Bartlett (1939) slightly modified this technique by exposing four infested tropical almond (*Terminalia catappa*) leaves to 5 ♂ and 5 ♀ in each cage; four infested leaves were added on the second and another four on the fourth day. Uninfested leaves were added as food for thrips, all foliage remaining in the cylinder during the entire period. In this way *G. shakespearei* was reared for 33 generations, resulting in 88,315 pupae. For propagation on *H. haemorrhoidalis*, McMurtry & Johnson (1963) exposed the host insect to orange fruits for oviposition during 10 days. A few days after thrips larvae hatched, single fruits were exposed to *G. shakespearei* (10♂:10♀). Parasitoid pupae were collected from the fruits into small vials until emergence of adults (cf. rearing technique for *T. semiluteus* described above).

Information on the reproduction capacity is limited. In Trinidad up to 70 offspring have been obtained from a single female parasitizing *S. rubrocinctus* (Adamson, 1936). In Puerto Rico the highest increase obtained in any single generation was 24.2 offspring per female, and for any single cage 53.2, reared during 33 generations in the laboratory on tropical almond (Bartlett, 1939). Dohanian (1937) obtained 25.5 pupae/female during five days when breeding *G. shakespearei* on *S. rubrocinctus* on cashew leaves. Progeny yield per female was highly variable parasitizing *H. haemorrhoidalis*. Yields of 40:1 were common with a maximum of 60:1 (McMurtry & Johnson, 1963). Mean progeny production of *G. shakespearei* parasitizing *H. haemorrhoidalis* on avocado leaves in the laboratory was lower: 25.3 offspring/female for 3 days. But when Valencia oranges were used as host substrate this was different: 10.1 (7-13) at 22.2°C and 3.43 (1.4-5.7) at 29.4°C (Hessein & McMurtry, 1989). In India, when parasitizing *C. indicus* in the laboratory, a single female of *G. shakespearei* laid an average of 78 ± 3.1 eggs per day, with a range of 53-105 parasitized offspring per day on *Arachis hypogea*, adults living for 2-3 days. Hessein & McMurtry (1989) suggested that the host plant might have an effect on progeny production and sex-ratio for *G. shakespearei*. All authors mentioned however performed their experiments in different conditions, offering different numbers of host larvae to groups of 5-15 females (added with males) during different periods (1-5 days).

In the field, large variations have been found in the percentage of hosts attacked by *G. shakespearei*. High levels of parasitism occurred on cacao infested by *S. rubrocinctus* in Ghana (Cotterell, 1927, 1928), up to 70-80% were parasitized in 1925, leading to the ultimate control of the cacao thrips. At peak periods whole colonies of 50-60 individuals on a single leaf were completely parasitized. In Benin (Tamò, pers. comm.) *G. shakespearei* controls *S. rubrocinctus* infestations on mango and keeps populations of *H. femoralis* in check on bougainvillaea and passionfruit. Attacking *P. mori* on mulberry trees parasitization levels up to 58.6% have been registered in Japan in one orchard in September, but only reached 19.5% in another (Takagi, 1988). In India, Daniel (1986) recorded parasitism rates up to 92% during winter months by *G. shakespearei* in *Arachis hypogea* fields on the weed *Achyranthes aspera*, infested by *C. indicus*, resulting in a gradual decline of the thrips population in the latter.

Biological control

Several attempts have been carried out to control various thrips species with *G. shakespearei* (table 18). Initial shipments arrived from Ghana into Trinidad in 1935 (Adamson, 1936; Cotterell, 1936), using cool storage at 10°C during transfer by ship. Between 1936 and 1942 after multiplication of the initial 250 live parasitoids, *G. shakespearei* consignments were sent from Trinidad onto various islands in the Caribbean, by air: in 1936 into Puerto Rico (Dohanian, 1937ab), in 1937 into Jamaica (Edwards, 1938, 1939), into Bermuda and Granada (Callan, 1943), for the control of *S. rubrocinctus*. Shipments followed into the United States, Canada, Hawaii (Callan, 1943) for the control of various species of thrips (table 18). *G. shakespearei* was mostly shipped and released as pupae, at first attached to the original leaves, later pupae were dislodged from leaves and glued onto cards either by plain water (Dohanian, 1937b) or 'gloy' (Bennett in Lewis, 1973).

Although it has been successfully established in Trinidad, after release of about 26,000 pupae (Adamson, 1936), Puerto Rico (Bartlett, 1937, 1939: 57,000 pupae) and Jamaica (Callan, 1943), recoveries comprised only small numbers on mango, but had no regulatory effect on populations of *S. rubrocinctus* on cacao and cashew (Callan, 1943). On cacao plants in a semi-open greenhouse in Trinidad nearly

100% was parasitized late 1942, controlling cacao thrips until April 1943, but counts in very restricted areas of a few cacao trees gave parasitism rates from 20 to 30% (ibid.). It could not be found on cacao during cursory searches in the 1950's and 1960's, but was reared on several occasions from *S. rubrocinctus* on cashew (Yaseen, 1971; Cock, 1985). More recently Bennett (1970) failed to find *G. shakespearei* in Trinidad despite several attempts and in Jamaica it was seasonally (July) very scarce on high *S. rubrocinctus* infestations on mango, cashew and tropical almond (Bennett, 1970; Bennett & Alam, 1974).

In a second series of introductions during 1936-1939, *G. shakespearei* was consigned by the CIBC from Trinidad and Jamaica for the control of *T. tabaci* in onion into Hawaii, Puerto Rico, Bermuda and Barbados (table 18), but recoveries were made only soon after releases and establishment and economic control did not occur. Another series of introductions concerned the control of *H. haemorrhoidalis* in the USA. *G. shakespearei* was dispatched to Maryland in 1936 (Bartlett, 1939) for experimental breeding work and to California in 1962 from Trinidad and 1983 from the Bahamas for releases in avocado orchards, and although recoveries were made initially, it did not become established (McMurtry & Johnson, 1963; Hessein & McMurtry, 1989) (table 18). In April 1960 Bennett sent 225 pupae of *G. shakespearei* collected from thrips infested *Acalypha wilkesiana* Müll.Arg. (Euphorbiaceae) in Jamaica to control *Gynaikothrips ficorum* on *Ficus* sp. in Bermuda. Although releases were made, no subsequent recoveries have been reported (Cock, 1985). It is unknown however, if *G. ficorum* actually is parasitized by *G. shakespearei*.

Although *G. shakespearei* is able to control thrips host populations, and *S. rubrocinctus* in particular under some conditions, the reasons for its relative overall failure in biological control are still speculative. Weather conditions have a strong influence on thrips populations (Lewis, 1973; Ananthakrishnan, 1984), which indirectly influences parasitoid occurrences (Entwistle, 1972), but it is unknown what direct influence it has on the parasitoid. Wolcott (1948) mentioned that *G. shakespearei* is of little value in the biocontrol of thrips pests, because the parasitoid builds up its population only during wet-weather conditions, whereas thrips infestations reach their peak during the dry season of the year. Natural incidence of *G. shakespearei* is indeed highly seasonal, numbers being very low in spring and summer (Bennett, 1970), common from September onwards, reaching its peak in the main dry season January-February in Ghana (Cotterell, 1927), Benin (Tamò, pers. comm.) and the Caribbean. Also the host plant might influence the parasitoid searching efficiency. In India (Daniel, 1986) parasitoids occurred in 2-3 months (September-November) on the groundnut crop and 5-6 months (September-February) on the reservoir weed; compared to the weed the incidence on the crop was low, and mainly governed by host availability.

From laboratory studies (e.g. Hessein & McMurtry, 1989), it is obvious also that this parasitoid, coming from the tropics, might be more successful in tropical areas, where temperature ranges are moderate. This parasitoid would be of less value in the control of thrips attacking such temperate-climate crops as chrysanthemums or even warm-temperature crops like sweet pepper. Apparently higher temperatures, such as prevail in the tropics, are necessary for the development of this parasitoid. Thripine species are not preferred as hosts and biocontrol attempts to control *T. tabaci* with *G. shakespearei* failed. If it is adapted well enough to maintaining itself on *F. occidentalis* or other thripine pest species in European greenhouses and if it will be able to significantly reduce its numbers is therefore doubtful.

3.2.1.4 Genus *Entedonastichus* Girault

Synonymy
Entedonastichus Girault 1920
Pirenoidea Girault 1922)
Thripoctenoides Erdös 1954

Taxonomy

This genus was first described by Girault in 1921 from Australia. In Europe the first record was made in 1957 in Germany (Gauss 1957, Ferrière 1958). The single male specimen of *Thripoctenoides thione* (Walker) (= *Pteropterix thione* Walker), mentioned in most review lists of parasitoids of thrips (e.g. Boucek & Askew, 1968; Lewis 1973; Ananthakrishnan 1984), appeared to be a dwarf specimen of *Asecodes coronis* (Walker), in Britain a common grass dweller (Boucek & Graham (1978). Since Boucek's revision in 1988, this genus comprises six species (for synonyms of individual species see appendix 1a).

Distribution, hosts, host plant associations

Distribution and host range are not well been documented, records are rather scarce: only from *Entedonastichus (Thripoctenoides) carbonarius* (figure 10-4) thysanopteran hosts are known (Dyadechko, 1964, 1967; table 13). As can be seen from figure 15, species belonging to the genus *Entedonastichus* have a palearctic (*E. albicoxus, E. gaussi, E. carbonarius*), nearctic (*E. kaulbarsi*) or australian (*E. dei, E. mirus*) distribution. From *E. carbonarius* one ♂ specimen is also known from Australia (Boucek, 1988). Most species however have been recorded from Central Europe: *E. gaussi* from Germany (Gauss, 1957; Ferrière, 1958) and the Ukraine (Dyadechko, 1964, 1967), *E. carbonarius* from Hungary (Erdös, 1954, 1956a, 1971, figure 8), South Slovakia (Boucek, 1957), Bulgaria (Pelov, pers. comm.), and *E. albicoxis* from Hungary (Szelényi, 1982). Specimens belonging to *Entodonastichus* have been found in Sweden (Hedqvist, letter to Nedstam, 1978) and Russia (Trjapitzin pers. comm.), but were not yet identified to the species level. Three species are known from Australia (*E. dei, E. mirus* (also in New Zealand), *E. carbonarius*) and a single brachypterous species (*E. kaulbarsi*) from Canada and Florida (Yoshimoto, 1981).

Most specimens have been collected from grassy areas (*E. carbonarius, E. albicoxis, E. dei, E. kaulbarsi*) and forests (*E. gaussi, E. mirus*) or from a combination of both (see table 13). Boucek (1988) mentioned collections of *E. dei* from rose, *Discaria* and *Juncus* too. Only from *E. gaussi* hosts have been recorded. They all are plaeothripids living on leaves and bark (*Liothips setinodis* Reuter) (Dyadechko, 1964, 1967) or on the bark and under peeling bark (*Crypothrips nigripes* Reuter,

Fig. 15. Worldwide distibution of species belonging to the genus *Entodonastichus (albicoxis, carbonarius, dei, gaussi, kaulbarsi* and *mirus).*

Table 13. Survey of thrips parasitoid species belonging to the genus *Entedonastichus*. Distribution, (associated) host species and locations.

Distribution	host species	host plant	date	reference
Entedonastichus gaussi				
Germany, Lahr	*Liothrips setinodis*	pine	1957.x	Ferrière 1958
Ukrain, Kiev, Volynsk	*Phlaeothrips coriaceus* *Acantothrips nodicornis* *Cryptothrips nigripes* *Liothrips setinodis* *Phlaeothrips pillichianus*		1957	Dyadechko 1964 Dyadechko 1967
Entedonastichus kaulbarsi				
Canada, Chatterton Ontario		meadow	1967.vii	BMNH
Canada, Belleville Ontario		meadow	1968.ix	BMNH
Canada, Riceville Ontario		emergence trap (pine/herbs)	1979.vi	Yoshimoto 1981
Canada, Lac Roddick Quebec			1980.vi/vii	Yoshimoto 1981
USA, Florida				Yoshimoto 1981
Entedonastichus mirus				
Australia, Qld, Irvinebank		forest	1919.iii	Girault 1920b
Australia, Ipswich distr.			1980.vi	Boucek 1988
Entedonastichus dei				
Australia, Brisbane		warehouse	1921.v	Girault 1922
New Zealand, Coromandel		tussock/grasses	1981.i	Boucek 1988
New Zealand, Otago Lakes		tussock/grasses	1981.i	Boucek 1988
Entedonastichus carbonarius				
Hungary, Tompa		grass stems	1949.iv/vi	Erdös 1954
		Silene otites	1950.vi-vii 1952.vii	Erdös 1956a
Hungary, Kelebia, Baja, Bátorliget, Nagyszénos		forest grassy areas *Stipa capillata*	1950.iv/vii iv-vii	Erdös 1971
Slovakia, South				Boucek 1957
Bulgaria		sweepnet		Pelov 1990pc
Australia, Horseshoe Lookout			1981.iv	Boucek 1988
Entedonastichus albicoxis				
Hyngary, Nagyiván, (Hortobágy N.P.)		bird's nest	1972.vi	Szelényi 1982
Entedonastichus *sp.*				
Russia, St.Petersburg			1981.vii	Trjapitzin 1993pc
Sweden (spp.)				Hedqvist 1978pc

Acanthothrips nodicornis Reuter, *Phloeothrips coriaceus* Hal. and *Hoplandrothrips pillichianus* Pr.), (Dyadechko, 1964) of needle-leaved and broad-leaved trees (Priesner, 1964; Schliephake & Klimt, 1979). Species mentioned are often found in groups of mixed combinations (ibid.). *E. gaussi* parasitizes larvae of the second stage of *L. setinodis*, *C. nigripes*, *A. nodicornis*, *P. coriaceus* and *H. pillichianus*, etc. The parasitized larvae become less mobile. The emerging wasps escape by making a small hole in the abdominal wall of the prepupae or pupae (Dyadechko, 1964). In some years *E. gaussi* is assumed to have great importance in keeping down the number of thrips. In 1957 in the Feofanya area, in the neighbourhood of Kiev, 34% of the total *P. coriaceus* population and 87.6% of the *L. setinodis* population had been parasitized by *E. gaussi* (Dyadechko, 1964; 1967).

3.2.1.5 Genus *Pediobius* Walker

Synonymy
Pleurotropis Förster

Distribution, hosts, host plant associations

Pediobius thysanopterous Burks was described by Burks in 1971 as an internal parasitoid from *Gynaikothrips ficorum* (Marchal), living in leaf rolls on fig. Female specimens, 0.8-0.9 mm in length, were reared from material originating from Rehovot, Israel (September 1966) and Giza, Egypt (September 1955). In 1961, Tawfik (1967) recorded a *Pediobius* sp. parasitizing the larval stages of *G. ficorum* inside terminal leaf rolls of *Ficus nitida* Thunb.-Hort. (= *Ficus retusa* L.) trees in the Giza region. His data probably refer to the same species as described by Burks. The only other record of another *Pediobius* associated with thrips, was made by Risbec (1958). In 1952, he reared 11 males, 0.75-1.0 mm in length, of *Pediobius dipterae* (Risbec), from leaf galls of *Psiadia* sp., infested with larva of thrips and collected from the Mahageby forest (Morafenobé) in Madagascar. *P. (Pleurotropis) dipterae* was originally described by Risbec (1951) from females and males parasitizing dipterous and lepidopterous leafminers from M'Bambey, Senegal. As has been pointed out by Burks (1971), the figures of the radius and (post)marginal parts of the wing given by Risbec in his papers (1951, 1958) do not look the same, so two different species might be involved.

Biology

The only notes about the biology of *Pediobius* parasitizing thrips, have been recorded by Tawfik (1967). A single female of *Pediobius* sp., when present in a roll, can parasitize most of the thrips larvae. When all stages of *G. ficorum* are present, numbers can go up to more than 30-40 larvae per roll in September (Rivnay, 1947; Tawfik, 1967). Usually, the female oviposits in the first and second larval stages. In the newly hatched larva she can oviposit without mounting on its back. The oviposition process lasts on average 45 (40-60) seconds. The attacked host sometimes responds to the sting by twisting the posterior end of the body towards the ovipositing female, but more often this movement fails in dislodging her. Oviposition occurs more than once in the same host or another parasitized larva when attacked within few minutes, but only a single parasitoid emerges from each host. When parasitized the waxy-white colour of the larva gradually takes a purple hue. When the parasitoid larva becomes mature, it appears opaque through the transparent integument of the host, the head directed anteriorly. The dark brown or black pupa stays inside the host integument and measures 1.13 mm in length and 0.56 mm in width. Emergence of the adult parasitoid takes place through a round exit hole made by the emerging individual in the integument of the host larva at its antero-dorsal region. No details are given about developmental time, reproduction, etc.

Tawfik (1967) also registered the seasonal fluctuations in thrips and parasitoid populations. Taking a monthly sample of 50 leaf-rolls of *F. nitida* during 1961, the *G. ficorum* numbers remained low (2-4 ind./roll) during most time of the year. A steady rise in number started from July onwards, reaching a peak (40 ind./roll) in September at 24.5 °C and 63% RH. In Israel (Rivnay, 1947), development of *G. ficorum* takes about one month at 21 °C and producing 8 generations per year, only interrupted by cold winters. In fall an obvious fall in the number of thrips was observed coinciding with an increase in numbers of the parasitoid (and predators). *Pediobius* sp. was present during most time of the year except for May and June when temperatures were high 29 °C and RH low 45%. *Pediobius* reached its peak (4 pupae/roll) in November/December at 14.0 °C and 78% RH. Population fluctuations of both host and parasitoid however probably are largely governed by climatic conditions.

3.2.2 Eulophidae, Tetrastichinae

3.2.2.1 Genus *Thripastichus* Graham 1987: *Thripastichus gentilei* (Del Guercio)

Synonymy
Tetrastichus gentilei Del Guercio 1911
Tetrastichus rhipophorathripscidis Narayanan, Rao & Rao 1960
Tetrastichus thripophonus Waterston 1923
Tetrastichus tatei Dozier 1937

Taxonomy
T. gentilei females are 1-1.4 mm (Del Guercio, 1911; Waterston, 1923; Dozier, 1937), their body dull brown (Burks, 1943; Bournier, 1967) to black with weak metallic tints (Graham, 1987), legs and antennae yellowish brown, wings hyaline; mandibles bidentate (Melis, 1935; Graham, 1987); abdomen with a large pale subbasal spot; in contrary to Burks (1979), the ♂ has been recorded from Europe (Del Guercio, 1911; Melis, 1935) and India (Narayanan et al., 1960) and is similar to the ♀, except for their densely hairy antennae and its smaller size (figure 16). The genus has been synonymized by Burks (1943), Domenichini (1965, 1966), Graham (1987) and Boucek (1988).

The genus *Thripastichus*, comprises one single species, *Thripastichus gentilei*. It formerly belonged of the genus *Tetrastichus* Walker, but being the single thrips parasitizing species, not closely related to the European genera, it was redescribed by Graham (1987) with an additional synonym of Boucek (1988). According to

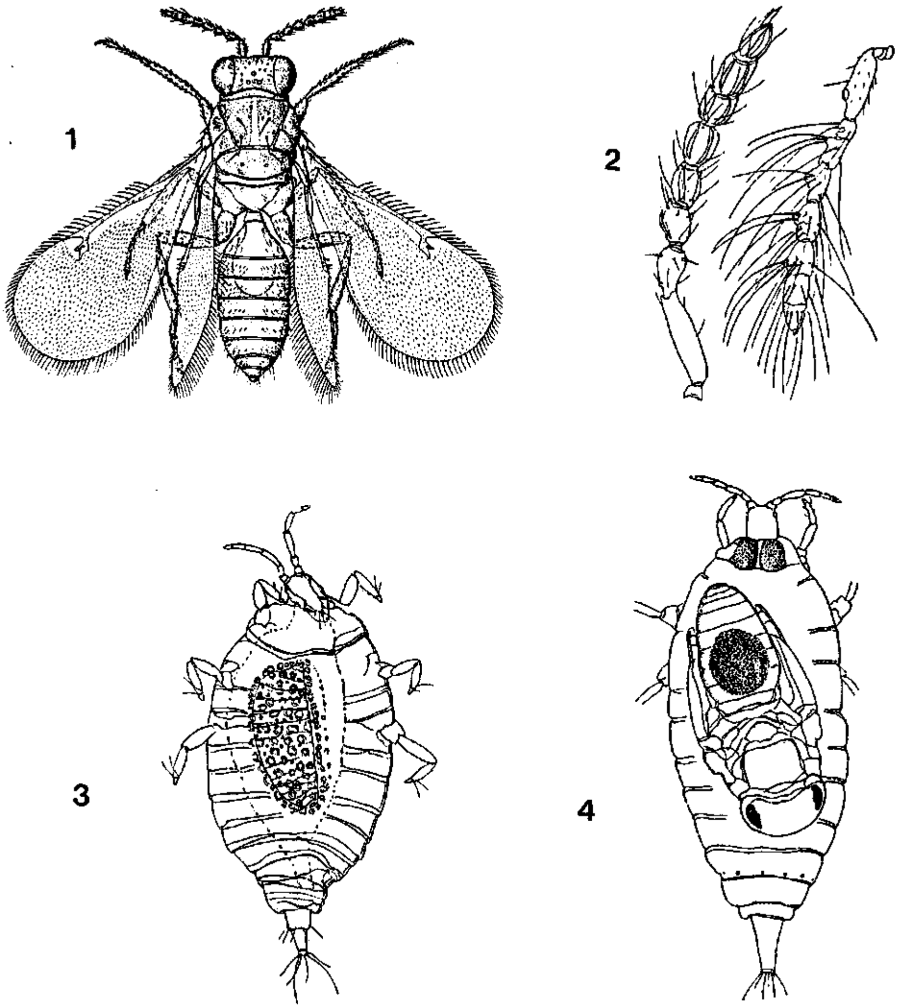

Fig. 16. *Thripastichus gentilei* (Del Guercio). 1. adult ♀ (from Melis, 1935); 2. antennae ♀, ♂; 3. parasitized larva of *Liothrips oleae* (Costa); 4. parasitoid pupa inside host body (from Paoli, 1931).

Graham (1987) it probably did not evolve inside the palearctic region, and was probably introduced into Europe (however see below).

Distribution, host range, host plant associations
T. gentilei is considered as cosmopolitan (Krombein et al., 1979), but it has been recorded under various synonyms (Graham, 1987) only from coastal areas and islands from the Mediterranean Area (*T. gentilei*: Del Guercio, 1911; Paoli, 1931; Melis, 1935; Tominic, 1950; Domenichini, 1965; Bournier, 1967; Alexandrakis, 1986), the Caribbean area (*T. thripophonus*: Mason, 1922; Yothers & Mason, 1924; Simmonds, 1933; Cock, 1982b; *T. tatei*: Dozier, 1937) and India (*T. rhi-*

Fig. 17. Worldwide distribution of *Thripastichus gentilei* (Del Guercio) (Hymenoptera: Eulophidae, Tetrastichinae).

pophorathripscidis: Narayanan et al., 1960; *T. thripophonus*: Ananthakrishnan & Swaminathan, 1977) on the northern hemisphere (figure 17). From the southern hemisphere it has been recorded only from Brazil (Bennett, 1965) as *T. thripophonus*, but it is not clear if it has been (recently) introduced with its hosts or not (see e.g. Bennett, 1965).

Except for a single record from *R. cruentatus* (Thripidae: Panchaetothripinae) (Narayanan et al., 1960) all host records are from species belonging to *Liothrips*, *Gynaikothrips ficorum*, *Manothrips floridensis*, *Hoplothrips pedicularius*, *Schedothrips orientalis* and a number of other species from India, all Phlaeothripidae (table 14). *Gynaikothrips uzeli* (Zimmerman) has often been mentioned as a host as well (Dozier, 1937, cited in Burks, 1943; Domenichini, 1965, 1966; Cock, 1982b) curling the foliage of *Ficus nitida* but as has been pointed out by Wolcott (1948), and confirmed by Jacot-Guillarmod & Brothers (1986) all records of infestations on Cuban laurel refer to *G. ficorum*, the former presumably restricted to *F. benjamina* as a host. It also parasitizes the plaeothripid predator *Androthrips flavipes* Schmutz, both in the laboratory and in the field (Ananthakrishnan & Swaminathan, 1977; Varadarasan & Ananthakrishnan, 1981), one of the controlling factors of gall inhabiting thrips in India. Lewis (1973) mentioned another species, *Tetrastichus atratulus* (Nees), in his list of thrips parasitoids, parasitizing *Liothrips setinodis* (Reuter) in Germany, but many species have been described under this name and it remains unclear which one it is, as the type is lost (Domenichini, 1965).

Thrips of the genus *Liothrips* are important pests, some injurious others beneficial. *L. oleae* is a major pest on olives in the European Mediterranean Area. *L. urichi* has been used in the biological control of *Clidemia hirta* with success, particularly in Fiji (Simmonds, 1937; Cock, 1982b) and *L. mikaniae* was advised as an agent for the control of the strangler vine, *Mikania micrantha* in Southeast Asia (Cock, 1982b). *Liothrips* spp. are leaf-feeding species, all stages of thrips are found around the terminal bud and the new shoots, hatching on the newly unfolding leaves, others also feed on new growth (Mason, 1922) of olive, bays, camphor trees and various shrubs, or like *L. oleae* hide in the galleries made by Scolitid beetles (Melis, 1935). All other plaeothripid host species are cecidogenous (Raman & Ananthakrishnan, 1984): causing and inhabiting galls of young, undifferentiated leaves of either *Ficus* spp. (Moraceae) or various other trees and shrubs (table 14). Emergence of adult thrips synchronizing with the formation of young leaf buds (Varadarasan & Ananthakrishnan, 1981), attacks causing severe distortion, leaf curling and eventually defoliation (Cock, 1985).

Biology

T. gentilei is a solitary endoparasitoid of larvae (Del Guercio, 1931; Bournier, 1967), and although occasionally 2-3 eggs are laid in the host usually only one develops (Melis, 1935; Ananthakrishnan & Swaminathan, 1977). Searching for hosts, the female either slowly entered galleries made by scolitids, occupied by *L. oleae* larvae or going after them on branches, leaves and fruits (Del Guercio, 1911). With *G. ficorum* as a host, the female laid her eggs preferably inside young larvae and never attacked second stage larvae, prepupae or pupae (Bournier, 1967), in *L. oleae*

Tabel 14. Survey of the thrips parasitoid species *Thripastichus gentilei* (Del Guercio). Distribution, host plant and host species.

Distribution	host species	host plant	date	reference	Syn.
Italy, Liguria Toscane	*Liothrips oleae*	olive	1910	Del Guercio 1911	0
Italy, Imperia	*Liothrips oleae*	olive		Paoli 1931	1
Italy, Toscane	*Liothrips oleae*	olive	1930.iv-ix	Del Guercio 1931	1
Italy, Versilia Lucchese	*Liothrips oleae*	olive	1933.iv-x	Melis 1934	1
Croatia	*Liothrips oleae*	olive	1947-1948	Tominic 1950	1
Greece	*Liothrips oleae*	olive		Alexandrakis 1986	1
France, Montpellier	*Gynaikothrips ficorum*	*Ficus nitida*	1962.ix	Bournier 1967	1
			1962.x	Domenichini 1965	1
Germany	*Hoplothrips pedicularius*			Domenichini 1965	1
Lebanon	*Gynaikothrips ficorum*			Zur Strassen pc	
Spain	*Gynaikothrips ficorum*			Lacasa pc	
USA, Florida	*Liothrips laureli*	bay tree	1921.ix	Mason 1922	5
USA, Florida	*Manothrips floridensis*	camphora tree		Yothers et al. 1924	5
Trinidad	unid.thrips	*Clidemia* sp.	1922	Waterston 1923	2
	Liothrips urichi	*Clidemia hirta*	1920	Simmonds 1930	2
North	*Liothrips mikaniae*	*Mikania micrantha*	1981	Cock 1982b	1
St. August.	*Liothrips varicornis*	*Hibiscus rosa-sinensis*	1981.x		
C. Rica, Gualpes	*Liothrips mikaniae*			Cock 1982b	1
P. Rico, Mayagüez	*Gynaikothrips ficorum*	*Ficus nitida*	1936,iii-iv	Dozier 1937	3
Bermuda[1]	*Gynaikothrips ficorum*	*Ficus* spp.	1963	Bennett 1964	2
Brasil	*Gynaikothrips ficorum*			Silva 1962	2
Campinas	*Gynaikothrips ficorum*	*Ficus nitida*	1962.x	DeSantis 1965	2
Rio Janeiro	*Gynaikothrips ficorum*	*Ficus nitida*	1963.iii	Bennett 1965	2
Porto Alegre		*Ficus nitida*	iii-iv		
India, Delhi	*Rhipiphorothrips cruentatus*		1958.vi	Narayanan et al. 1960	4
India, Delhi	*Mallothrips indicus*	*Eugenia jambolana*	1962.v-vii 1963.v-vii	Sharma et al. 1965	4
India, Tamil Nadu	*Schedothrips orientalis*	*Ventilago maderasapatana*	1976.ix-xii 1977.vii	Ananthakrishnan & Swaminathan 1977	2
	Androthrips flavipes (pred.)				
India, Tamil Nadu	*Arrhenothrips ramakrishnae*	*Miusops elengi*		Varadarasan & Ananthakrishnan 1981	2
	Schedothrips orientalis	*V. maderasapatana*			
	Thilakothrips babuli	*Acacia leucophloea*			
	Androthrips flavipes (pred.)				
	(*Teuchothrips longus*)	lab. tests			
	(*Crotonothrips dantahusta*)	not in nature			
	(*Gynaikothrips flaviantennatus*)				

Sn.= synonym used: 0 = *Eulophus gentilei*; 1 = *Tetrastichus gentilei*, 2 = *Tetrastichus thripophonus*, 3 = *Tetrastichus tatei*, 4 = *Tetrastichus rhipophorathripscidis*, 5 = *Tetrastichus* sp. ; [1]: introduced, not established

newly hatched and old larvae were not attacked (Del Guercio, 1911). Parasitizing *S. orientalis*, host selection appeared restricted to second stage larvae, although occasionally prepupae and pupae were affected (Ananthakrishnan & Swaminathan, 1977). In *L. laureli*, the female lays her eggs inside both larval stages (Mason, 1922).

The ovipositor is inserted in the pronotum of the thorax. Sharma et al., (1965) distinguishes three well marked larval stages in addition to the egg, prepupa (1.13 mm x 0.52 mm) and pupal stages. The egg hatches within 2-3 days (Bournier, 1967). 5-6 days after that *L. oleae* larvae stop feeding and hide under bark or underside of dead leaves of olive (Melis, 1935). Parasitized larvae, besides being deformed, stopped moulting and showed gradual swelling of the body leading to immobility. The host is dead by the time of pupation of the parasitoid 2 days later, its skin remains sticking on the leaf with its ventral surface (*R. cruentatus*: Sharma et al., 1965; *G. ficorum*: Bournier, 1967). With *G. ficorum* some individuals emerge and pupate within the curled leaf (Bennet, 1965). According to Waterston (1923), Burks (1943) and Bennett (1965), the prepupal stage is affected for *L. laureli* and *G. ficorum*, but Cock (1982b) reared *T. gentilei* from mummified second-stage larvae of *L. mikaniae* and *L. varicornis*, as did Bournier (1967) from *G. ficorum*. The newly formed pupa is creamy white during the first 4 days (Melis, 1935), but later becomes black brown (Sharma et al., 1965). *Thripastichus* larvae exhibited peristaltic and slight up and down movements within the host (Ananthakrishnan & Swaminathan, 1977; Melis, 1935). Shortly before adult emergence the parasitoid displayed a rotation of 180° within the host's body, facing its hind end (Del Guercio 1931; Bournier, 1967; Ananthakrishnan & Swaminathan, 1977; figure 16). Emergence of the parasitoid from the host occurred on the 8-10th day of pupation through a wide slit on the ventral side of *Schedothrips* larvae between thoracic and 6th abdominal segments (op.cit.) or from *L. laureli* after a week from a hole cut through the host integument near the end of the abdomen (Mason, 1922). Emergence of the adult is quick, about 20 seconds (Bournier, 1967). In India approximately 12-14 days were required to complete the life-cycle on *R. cruentatus* (Sharma et al., 1965) and in Europe at temperatures of 20-25 °C *T. gentilei*, parasitizing *L. oleae* or *G. ficorum*, completed its life-cycle in about 20 days (Silvestri, 1934; Melis, 1935; Bournier, 1967). This is much faster than most of its hosts: 30-35 days from egg till egg-laying adult (including a long pre-oviposition period of the thrips host) of *L. oleae* (Melis, 1935), 30 days or more for *L. laureli* (Mason, 1922) and *G. ficorum* (Rivnay, 1947) and 35 days for *L. mikaniae* (Cock, 1982b). Total life span of adult parasitoids was 2-3 days in the laboratory (Ananthakrishnan & Swaminathan, 1977), up to 10 days in field cages (Melis, 1935), much shorter than most of its hosts. Data on egg-laying capacity are not available. The sex-ratio is nearly 1:1. Within 24 hours after emergence, mating started which lasted for 15 minutes.

T. gentilei hibernates, as a larva or pupa in diapause induced by its host *L. oleae*, which itself passes winter (October-April) in diapause as adults (Del Guercio, 1911; Melis, 1935). In the greenhouse at constant temperatures of 20-25 °C, no diapause occurred when parasitizing *G. ficorum* (Bournier, 1967).

T. gentilei is an important natural enemy of a number of pest species. It is the most important natural control agent of *L. oleae* in the Mediterranean Area (Del Guerçio, 1911, 1931; Melis, 1935). In Italy, first adults appear in April-May and there are 5 generations a year, whereas the host has 3. Parasitization was low in spring (Melis, 1935; Bournier, 1967) but at the end of the season, it parasitized 60-70% (Del Guercio, 1931), sometimes up to 75% (Melis, 1935) or 90% of the larvae (Del Guercio, 1911), controlling the thrips population almost completely in August-September (Paoli, 1931; Del Guercio, 1931). In Trinidad it is common and levels of 40% have been found on *L. mikaniae*, infesting the strangler vine, *Mikania micrantha* (Compositae), but it was found on only one occasion on *L. urichi* infesting *Clidemia hirta* (Melostomaceae) (Simmonds, 1933). Parasitizing *G. ficorum*, 75% parasitization was found in autumn by Bournier (1967) in a greenhouse in France, and Bennett (1965) recorded that it was abundant on *G. ficorum* at some sites in Brazil. It has been introduced as a potential biological control agent of *G. ficorum* on *Ficus* spp. in Bermuda, but failed to establish (Bennett, 1965). In North Africa *G. ficorum* is an important pest of *Ficus* spp. too, but ther are no data about any parasitoids.

Sharma et al., (1965) regarded *T. gentilei* as an important natural control agent of *M. indicus* in the area of New Delhi, parasitizing up to 73.6% of the host population in June, occurring in the second week of May. Later the pest population declined rapidly and after the last week of July both the parasitoid and the pest were not found in the field. In the Madras region, *T. gentilei* was recorded in nature in a high incidence in galls of *Schedothrips orientalis* Ananthakrishnan; population trends show a significant decline immediately following the increase in the parasitoid population (starting from July onwards) in September, remaining in the field until December. *T. gentilei* was more abundant in galls on *V. madreasapatana*, parasitizing as much as 20 % of *S. orientalis* population. The incidence was very low in galls of *Arrhenothrips ramakrishnae* Hood and *Thilakothrips babuli* Ramakrishna. Parasitization of *A. ramakrishnae* was restricted to individuals at the base of the galls, which were the only places were the parasitoid could come into contact with the host larvae. On *T. babuli* parasitization was observed only in the outer whorls of the rosette galls of *A. leucophloea*, host larvae being present in good numbers in the inner whorls too. Though parasitization of second stage larvae of various gall thrips was successful under laboratory conditions, they were never found in galls induced by *Teuchothrips longus* (Schmutz), *Crotonothrips dantahasta* (Ramakrishna) and *Gynaikothrips flaviantennatus* Moulton on their host plant in nature. The reason for its absence in galls of the latter species is not clear, their galls have less compact folds which could facilitate their entry (Ananthakrishnan & Swaminathan, 1977; Varadarasan & Ananthakrishnan, 1981; Raman & Ananthakrishnan, 1984).

3.2.3 Unidentified parasitoid specimens

Hukkinen (1936) when studying the detrimental effects of *Chirothrips hamatus* Tryb., which damaged the kernels of *Alopecurus pratensis* L., registered a parasitoid attacking larvae and pupae of *C. hamatus* on various places in Finland, up to 58.2%, in 1934 and 1935. Hukkinen tentatively identified it as belonging to the Proctotrupidae, its biology and identity remains unknown. The family is characterized by 13 segmented antennae and most host records involve larvae of Coleoptera, some species parasitize fungus gnats (Diptera) or centipedes, but there is no record from thrips (Krombein, et al., 1979).

Kratochvil & Farsky (1942) observed in many larvae of *Taeniothrips laricivorus* infesting the end shoots of larch near Brno – Czechia, a few chalcidoid parasitoids, but did not establish quantity nor the identity of the species.

Searching for natural enemies of *Taeniothrips inconsequens* in Central Europe, Carl et al. (1989) found larvae to be parasitized by an internal eulophid parasitoid in low numbers. Surveying cherry orchards end of May, 1989, 1 out of 100 larvae checked at Rauenthal (Wiesbaden, Germany) was parasitized and 4% parasitism was found from a collection near Stockach (Bavaria, Germany), but the identity of the species could not be established. Mature parasitoid larvae left their host after this had entered the soil. They pupated and remained in dormancy, probably until the following year, as the last surviving pupae were still observed in October. The parasitoid apparently was univoltine like its host and did not depend on host alternation. How well it is synchronized with *T. inconsequens* and its effect on this host in low and high densities remains to be ascertained.

3.3 Egg parasitoids

Egg parasitoids all belong to the genus *Megaphragma* (Trichogrammatidae) and a single species described in the genus *Polynema* (Mymaridae). *Megaphragma* can be ranged amongst the smallest insects (0.17 – 0.35 mm), and because are too small to recognize by the eye they are easily overlooked and makes collection of these egg parasitoids troublesome. Tamò (1991) and Tamò et al. (1993) recovered *Oligosita* sp. (Trichogrammatidae) from eggs of *Megalurothrips* in Benin. Because elsewhere they are have been reared from eggs of hispid beetles (Coleoptera), cicadellids, mirids (Homoptera), and tettigoniids (Orthoptera) and of pupae of Diptera (Noyes & Valentine, 1989), this record needs at least confirmation. The identification of species of the *Megaphragma* genus also is greatly hampered be-

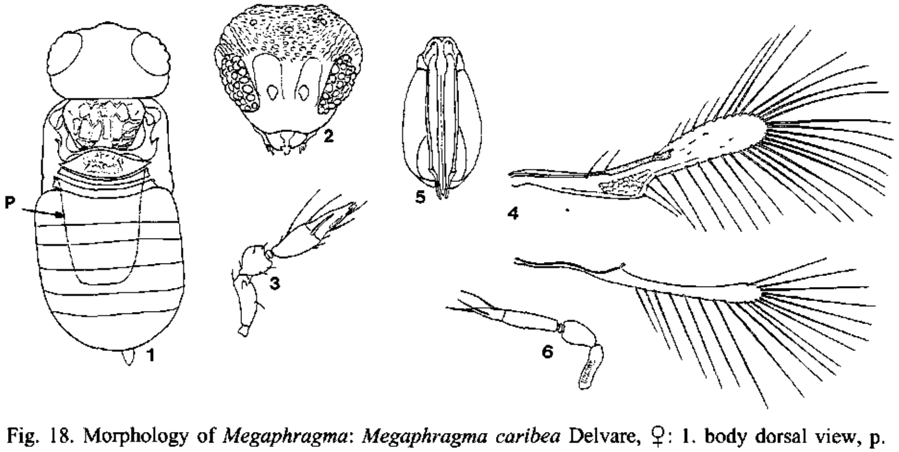

Fig. 18. Morphology of *Megaphragma*: *Megaphragma caribea* Delvare, ♀: 1. body dorsal view, p. phragma; 2. head front view; 3. antenna; 4. wings; 5. genitalia. 6. antenna ♂ (from Delvare, 1993).

Fig. 19. Worldwide distribution of egg parasitizing species belonging to the genus *Megaphragma* (Hymenoptera: Trichogrammatidae).

cause of this and revision of this thrips parasitizing genus is badly needed (Polaszek, pers. comm.; Delvare, 1993). Egg parasitoids have only been recorded from thrips whose eggs are embedded in the leaf tissue, i.c. species belonging to the family Thripidae. Tubulifera usually lay their eggs on the substrate and not embedded inside the host plant material. Eggs are relatively large, e.g. eggs of *L. laureli* are 0.46 x 0.20 mm (Mason, 1922) and of *L. mikaniae* 0.42-0.48 mm (Cock, 1982b). But most of species belonging to the family Phlaeothripidae, are not injurious and not well investigated.

3.3.1 Trichogrammatidae

3.3.1.1 Genus *Megaphragma* Timberlake

Synonymy
Megaphragma Timberlake 1924
Sethosiella Kryger 1932
Paramegaphragma Lin 1992

Taxonomy
Up till 1993, 12 species of egg parasitoids belonging to the genus *Megaphragma*, have been described (table 15ab). A number of specimens collected recently have not yet been described to the species level (table 15c). A key to some species of *Megaphragma* is provided by Ghesquière (1939), Yousuf & Shafee (1987) and Subba Rao (1969) and additional notes on taxonomy can be found in Timberlake (1924), Lin (1992) and Delvare (1993). *Megaphragma*, characterized by its small flattened body size, having the wings linear and very long-fringed and an extremely large phragma (see figure 18), is not closely related to any other genus, but features of the antennae and wings suggest (Doutt & Viggiani, 1968) a derivation from the same stock that gave rise to the *Oligosita* complex of genera. It was also first identified by Ghesquière (1939) as such. Because not many biological data are available from *Megaphragma*, all species will be discussed as a group.

Distribution, host range, host plant associations
Collections of *Megaphragma* specimens have been recorded worldwide in the tropics and subtropics, as far north as Japan (Takagi, 1988) and Bulgaria (Pelov, pers. comm.) and as far south as Chile (DeSantis, 1965), South Africa (Doutt & Viggiani, 1968) and New Zealand (Noyes & Valentine, 1989), see figure 19.

The first specimens of *Megaphragma* were collected in 1920 in Hawaii by Pemberton (1930) and described as *Megaphragma mymaripenne* by Timberlake (1924). It was reported again by Swezey (1929) and Pemberton (1930). Later this species was recorded from other parts of the nearctic (Haiti: Dozier, 1932; California: Boyce & Mabry, 1937; Ebeling, 1959), neotropics (Chile: Olalquiaga Faure, 1962; DeSantis, 1965; Guadeloupe: Delvare, 1993) and also the aethiopean area (Benin: Polaszek, pers. comm.). Material collected in Mexico and the Galapagos Islands probably also belong to this genus (BMNH: Polaszek, pers. comm.). Ghes-

Tabel 15a. Survey of egg parasitoid species belonging to *Megaphragma mymaripenne* Timberlake: distribution, host species and host plant associations.

Distribution	host species	host plant	date	reference
Megaphragma mymaripenne Timberlake				
USA, Hawaii-Mt.View	unid. thrips	leaves forest tree	1920.i	Timberlake 1924
USA, Hawaii-Honolulu	unid. thrips	*Codiaeum variegatum*	1927.iii	Swezey 1929
USA, Hawaii-Honolulu	*Heliothrips haemorrhoidalis*	*Brassaia actinophylla* *Codiaeum variegatum*	1930.v	Pemberton 1931
USA, Ca- Santa Fé	*Heliothrips haemorrhoidalis*	Valencia oranges	1936.vi-viii	Boyce & Mabry 1937
USA, Ca-Santa Barbara	*Heliothrips haemorrhoidalis*	avocado	1960.ix-x	McMurtry 1961
Ca-San Diego	*Heliothrips haemorrhoidalis*			
USA, Ca-Irvine	*Heliothrips haemorrhoidalis*	avocado	1985-1986	Hessein & McMurtry 1988
Ca-Santa Barbara	*Heliothrips haemorrhoidalis*		1984-1985	
Chile, La Cruz	*Heliothrips haemorrhoidalis*		1962.v	Olalquiaga 1962
Haiti, Port-au-Prince	*Leucothrips* (cf. *piercei*)	*Codiaeum* sp.	1931.v	Dozier 1932
Guadeloupe, Pt. Bourg	*Selenothrips rubrocinctus* *Heliothrips haemorrhoidalis*	*Inga ingoides*	1989.xi	Delvare 1993
Benin, Center, South	*Megalurothrips sjöstedti*	*Vigna unguiculata*	1989.vi-viii	Tamò 1991;
		Vigna unguiculata	1988/9.x-xii	Tamò et al. 1993
		Cajanus cajan	1989.xi-xii	
		Centrosema pubescens	1989.xi-xii	
		Pueraria phaseoloides	1989.xii-i	
Ecuador, Galapagos Isl.		guava thicket	1985.v-vii	Polaszek pc [?]
Mexico, Vera Cruz		(sweeping)	1981.vii	Polaszek pc [?]

[?] : labelled *?mymaripenne*

quière (1939) erroneously mentioned, and this was quoted as a record later by Doutt & Viggiani (1968), that it was found by Dozier in 1932 in Louisiana – USA. This author however, only mentioned that its host *Heliothrips haemorrhoidalis* had been found there (Dozier, 1932).

Other *Megaphragma* species are less widespread and have been collected more regionally. *Megaphragma ghesquièrei* Nowicki and *Megaphragma priesneri* (Kr.) Nowicki are recorded from Zaire (Ghesquière, 1939) and Egypt (Kryger, 1932) respectively. Rivnay (1939) reared the latter species from thrips eggs in Israel too. From India three species have been described: *Megaphragma longiciliatum* Subba Rao (Subba Rao, 1969), *Megaphragma aligharensis* Yousuf & Shafee and *Megaphragma magniclava* Yousuf & Shafee (Yousuf & Shafee, 1987). In 1992 Lin described five new species from the Fujian and Guangdong provinces of China: *Megaphragma deflectum*, *Megaphragma decochaetum*, *Megaphragma polychaetum*, *Megaphragma macrostigmum* and *Megaphragma stenopterum*. One of them, *M. deflectum*, is probably present in Japan as well: some material sent by Takagi to the first author and collected from the *Megaphragma* complex present in tea plantations (Takagi, 1988), was identified as such (Polaszek, pers. comm.). In 1993 Delvare described a another new species *Megaphragma caribea* from Guade-

Tabel 15b. Survey of egg parasitoid species belonging to the genus *Megaphragma* (Trichogrammatidae): distribution, host species and host plant associations.

Distribution	host species	host plant	date	reference
Megaphragma ghesquièrei Nowicki				
Zaire, Rutshuru	*Panchaetothrips noxius*	*Coffea arabica*	1938.i	Ghesquière 1939
Megaphragma priesneri (Kr.) Nowicki				
Egypt, Tanta	*Retithrips syriacus* Mayet	vine leaves	1930/1.xi-i	Kryger 1932
Israel, Rehovot	*Retithrips syriacus* Mayet	?		Rivnay 1939
Megaphragma longiciliatum Subba Rao				
India, Bangalore-Avati	*Frankliniella lilivora*	*Polyanthes tuberosa*	1968.x	Subba Rao 1969
Megaphragma aligharensis Yousuf & Shafee				
India, Uttar Pradesh	'thrips'	wild plant	1985.ix	Yousuf-Shafee 1987
Megaphragma magniclava Yousuf & Shafee				
India, Uttar Pradesh		(sweeping)	1985.ix	Yousuf-Shafee 1987
Megaphragma deflectum Lin				
China, Fujian-Mt.Wuyi		(yellow pan)	1987.x	Lin 1992
Fujian-Laincheng County			1986.vii	
Fujian-Fuzhou, Longyan			1987.v	
Japan, Ibaraki, Shizoka	*Scirtothrips dorsalis*	tea	1985	Takagi 1988
Yamaguchi, Nagasaki				(Polaszek pc)
Megaphragma decochaetum Lin				
China, Fujian-Fuzhou		(yellow pan)	1987.vi	Lin 1992
Fujian-Xianyu County			1987.viii	
Fujian-Yuxi County			1987.viii	
Megaphragma polychaetum Lin				
China, Fujian-Mt.Wuyi		(yellow pan)	1987.vii	Lin 1992
Megaphragma macrostigmum (Lin)				
China, Fujian-Fuzhou		(yellow pan)	1987.viii	Lin 1992
Guangdong-Guangzhou			1985.xi	
Megaphragma stenopterum (Lin)				
China, Fujian-Fuzhou		(yellow pan)	1987.xi-xii	Lin 1992
Fujian-Fuan County			1986.vii	
Megaphragma caribea Delvare				
Guadeloupe, Vx Hab.	*Selenothrips rubrocinctus*	*Psidium gujava*	1988.xi	Delvare, 1993

loupe, and missing the antennal funicle segment, is very closely related to *M. macrostigmum* and *stenopterum*.

Megaphragma species have been recorded from a wide range of habitats, cultivated evergreen crops like tea (Kenya, Taiwan, Japan), coffee (Zaire), citrus (Japan), guava (Guadeloupe, Galapagos Isl.), mulberry (Japan), annuals like eggplant (Thailand) and cowpea (Benin), as well as wild plants like Leguminosae (Benin) and Liliacae (India), infested with a wide range of host species, both Panchaetothripinae as well as Thripinae (Thripidae) (see table 15). From a number of records the host-plant-association is not known, they have been collected in yellow pans (Lin, 1992), malaise traps (Noyes & Valentine, 1989), sticky traps (Takagi, 1988), emergence cages (Tamò, pers. comm.) or by sweeping vegetation (Yousuf & Shafee, 1987; unidentified specimens BMNH). For *M. mymaripenne*, most thrips species which have been recorded as hosts belong to the Panchaetothripinae. It has been reported from *H. haemorrhoidalis* in California, Hawaii, Guadeloupe

Tabel 15c. Survey of unidentified/undescribed egg parasitoid species belonging to the genus *Megaphragma* (Trichogrammatidae): distribution, host species and host plant associations.

Distribution	host species	host plant	date	reference
Mexico, Campeche		(screen sweeping)	1984.vii	Polaszek pc
Benin, Mono Prov.	*Megalurothrips sjostedti*	cowpea	1988.xi	Polaszek pc ^{AB}
Zouzouvou	*Megalurothrips sjostedti*	cowpea	1989.vii-ix	
Tchi-Ahomadegbe	*Megalurothrips sjostedti*	cowpea	1989.vii-ix	
Djoho/Tannouwo	*Megalurothrips sjostedti*	*Cajanus cajan*	1989.xi-xii	
		Centrosema pubescens	1989.xi-xii	
Sehoue/Agon	*Megalurothrips sjostedti*	*Pueraria phaseoloides*	1989.xii-1990.ii	
Kenya, Meru		tea	1965.iv	Polaszek pc
South Africa				Doutt-Viggiani 1968
Japan,	*Scirtothrips dorsalis*	?	1979	Hirose 1979
Japan, Ibaraki,Shizoka	*Scirtothrips dorsalis*	tea, citrus	1985	Takagi 1988 ^{ABC}
Yamaguchi, Nagasaki		(stickey trap)	1985	
Japan	*Pseudodendrothrips mori*	mulberry	1985	Takagi 1988
Taiwan	?*Empoasca formosana*?	tea		Lin, 1981
Thailand, Chiang Mai	*Thrips palmi*	eggplant	1987.ix	Hirose 1989,
Thailand, Chiang Mai,	*Thrips palmi*	eggplant	1988.i-ii	Hirose et al. 1993
Bangkok, Nakhon Pathom		eggplant	1988.i-ii	
India, Bangalore,	*Heliothrips haemorrhoidalis*	croton		Narayanan 1971
Hebbal	*Helioth(r)i(p)s*		1971.i	Polaszek pc
New Guinea, Pt.Moresby	forest edge		1986.i	Polaszek pc
		(screen sweeping)		
New Guinea, Pt.Moresby	*Eucalyptus* grassland		1986.i	Polaszek pc
		(screen sweeping)		
New Zealand, Lynfield		(malaise trap)	1981.iv	Noyes & ^{AB}
New Zealand, Massey,		(malaise trap)	1979.xii	Valentine 1989
Lynfield			1981.i	
Bulgaria		(sweeping)		Pelov pc

$^{AB, ABC}$: a mixture of different unidentified species.

and Chile, and on *S. rubrocinctus* from Guadeloupe (see table 15a), infesting cultivated host habitats like avocado, Valencia oranges and wild plants like croton, *Inga ingoides*. Also Thripinae are reported as hosts: Dozier (1932) reared numerous females from croton foliage infested with *Leucothrips* sp. and Tamò et al. (1993) recorded it as part of a *Megaphragma* complex originating from *Megalurothrips sjostedti* infesting leguminose wild plants and cultivated crops in Benin. Other species are known from a particular subfamily only: *M. ghesquièrei* was collected from eggs of *Panchaetothrips noxius* infesting coffee (Ghesquière, 1939) and *M. priesneri* was found within colonies of *Retithrips syriacus* on vine leaves (Kryger, 1932). There are also a number of records from thrips species belonging to the Thripinae: *M. deflectum* and two other yet unidentified species from *Scirtothrips dorsalis* and a *Megaphragma* sp. from *Pseudodendrothrips mori* in Japan (Takagi, 1988). Hirose (1989) and Hirose et al. (1993) collected a *Megaphragma* sp. from eggplants infested with *T. palmi* in Thailand. *M. longiciliatum* attacks the eggs of *Frankliniella lilivora* on *Polyantes tuberosa* around Bangalore, India (Subba Rao, 1969). Although in the laboratory a single adult was reared from one of several eggs of *T. tabaci* exposed to *M. longiciliatum*, it was never found attacking eggs of *T. tabaci* in the field (Narayanan, 1971). The only other host record except thrips has been reported by Lin (1981) who reared an undescribed species from the eggs of a cicadellid, *Empoasca formosana* Paoli, on tea in Taiwan.

Biology

Most of the biology, behaviour and ecology of *Megaphragma* is known by the observations of Hessein & McMurtry (1988) of *M. mymaripenne* attacking *H. haemorrhoidalis* and Tamò (1991) and Tamò et al. (1993) for *Megaphragma* spp. attacking *M. sjostedti*. Although Ghesquière (1939) announced publication of studies on the ethology and ecology of *M. ghesquièrei*, these have not been found. Quantitative data about *Megaphragma* are lacking.

Egg parasitoids belong to the smallest of all insect parasitoids. Most of the collected *Megaphragma* species measure 0.20-0.36 mm in length. *M. caribea* from Guadeloupe however measures only 0.17 mm (Delvare, 1993). Some specimens of *M. mymaripenne* originating from California have measured 0.18 mm in length (Doutt & Viggiani, 1968) and some from Haiti only 0.17-0.20 mm (Dozier, 1932). Specimens of *M. priesneri*, reared from *R. syriacus* in Egypt are the largest in size: 0.50 mm (Kryger, 1932). The size can partly be explained by the size of the eggs of the thrips host from which they have been reared, e.g. *Leucothrips* (Dozier, 1932) vs. *H. haemorrhoidalis* (Doutt & Viggiani, 1968). Dimensions of the eggs of *R. syriacus* are relatively large: sizes vary from 0.28-0.31 mm in length and 0.125-0.15 mm in width (Rivnay, 1939), those of *R. cruentatus* (Rahman & Bhardway, 1937) are 0.26 mm long and 0.12 mm wide; those of *H. haemorrhoidalis* 0.325 x 0.105 (Rivnay, 1935), those of *T. tabaci* measure 0.28 x 0.10 mm and *F. occidentalis* 0.30 x 0.11 mm (Loomans, pers. comm.).

It is not known however, how *Megaphragma* females actually lay there eggs: through the oviposition hole made by the egg laying thrips female or drilling through the leaf tissue. Adults of *M. mymaripenne* started to search for hosts about 40-60 minutes after emergence from the thrips egg blister (Hessein & McMurtry, 1988). While searching, the female walks around an egg blister locating the softer parts with her antennae. There stinging usually occurs, during oviposition the female puts her weight on the hind legs and the wings, curving her abdomen forward and inserting her ovipositor into the side or sometimes middle of the egg blister. The same egg blister can be stung more than once. After ovipositing in several egg blisters, which can range from 30-120 minutes, with intervals of drinking and cleaning, the adult female cleaned her body and then walked or flew to another part of the leaf, where she resumed searching (Hessein & McMurtry, 1988). Oviposition time ranged from 0.5-7.5 minutes, but no parasitoids emerged when oviposition time was less than 2.5 minutes. Eggs that were completely covered with thrips faecal material were also stung, but a longer time was needed.

Thrips eggs are laid in the leaf tissue superficially. Most panchaetothripine species infest their host plant leaves when these have become mature (Ananthakrishnan, 1984). Eggs may be laid on both sides of the leaf, texture controls the locality (Rivnay, 1939). The place where the egg is laid is considerably elevated for most panchaetothripine species, and may be easily recognized visually (so called 'egg blisters': *H. haemorrhoidalis* – Ebeling, 1959; McMurtry, 1961; *R. syriacus* – Rivnay, 1939), especially just before hatching of the larvae. Thripine species belonging to the genera *Frankliniella*, *Thrips*, etc. prefer young plant parts for oviposition. The place of the egg can only be recognized by the eye occasionally, depending on the host plant, e.g. sweet pepper. Other species like *Scirtothrips citri*, whose eggs are embedded deeply in the plant, the incision closes almost completely after the ovipositor is withdrawn (Lewis, 1973). Differences in egg laying strategy of the panchaetothripine and thripine host species may play a role in the searching efficiency of the parasitoid. Parasitoids of such a small body size like *Megaphragma*, the length of the ovipositor is extremely small too: 12.5% (Ghesquière, 1939), 30% (Doutt & Viggiani, 1968) or to 50% maximum of the total length (Lin, 1992), i.c. 0.065 mm – 0.130 mm. The ability to parasitize hosts of different species, might be mechanically determined: the ability to reach the egg or not.

If semiochemicals are involved in host searching by *Megaphragma* spp. is not clear. The faecal material of the *H. haemorrhoidalis* seems to be one of the main factors for the female *M. mymaripenne* for eliciting probing and oviposition responses. Dried faecal material sometimes induces a brief response and egg blisters without faecal material were stung sometimes stung too (Hessein & McMurtry, 1988). Oviposition deterrent substances, acting as kairomone for a wide range of egg parasitoids, have not been identified yet for any thrips species. However, e.g. Lewis (1973) observed that *H. haemorrhoidalis* deposits a drop of excrement on the exposed tip of the egg, presumably to seal the cavity. Also Rivnay (1939) states that the female *R. syriacus* covers as a rule, but not always, the site of the egg with an opaque fluid, which perhaps is her faeces. The red-banded thrips *S. rubrocintus* seals the point of insertion on the underside of leaves with a drop of liquid excrement which dries on the leaf as a dark flat scale so that the egg pocket is concealed (Entwistle, 1972). The imperfectly circular exit holes, characteristic for the emergence of the parasitoids (avocado: Ebeling, 1959; McMurtry, 1961; eggplant: Hirose, 1989), are minute: 0.08-0.09 mm in diameter (Pemberton, 1931) and are found mostly on the underside of the leaves.

Most species exhibit deuterotoky: both ♀ and ♂ have been found. From *M. longiciliatum* only the ♀ is known and *M. mymaripenne* reproduces parthenogenetically in the laboratory, although occasionally a male was collected in the field (Hessein & McMurtry, 1988). Parthenogenetic reproduction is normal for *Megaphragma* (*deflectum*, AL) occurring in tea plantations in Japan (Takagi, 1988), males occurring very rarely. Developmental time from egg to adult at 22-23 °C and 10-42% RH, ranged from 36-46 days, with an average of 41.4 days for *M. mymaripenne* attacking *H. haemorrhoidalis* (Hessein & McMurtry, 1988). Compared to the parasitoid, the greenhouse thrips has a shorter developmental time: under similar conditions it ranged from 24-58 days, average 31 days (ibid.). Total developmental time of the single adult that emerged from one of the eggs of *T. tabaci* exposed to *M. longiciliatum* was 20 days (Narayanan, 1971, conditions unknown). Longevity of adult parasitoids is about 2 days, its egg-laying capacity is unknown. Adult greenhouse thrips lived 40.6 days on average, ranging from 24-36 days (Hessein & McMurtry, 1988), laying 1-2 eggs per day, or an average of 38.3 per female (Ebeling, 1959), producing 5-6 generations in a year in California (Ebeling, 1959).

Most records concerning *Megaphragma* species are descriptive, quantitative studies are scarce. In his survey of avocado groves in southern California, McMurtry (1961) found that *M. mymaripenne* was distributed throughout most of the avocado growing area, appearing quite abundant in some thrips-infested groves, but scarce or absent in others. The same was valid within a single grove: sampling in the fall of 1960, 22-27% of the eggs had been parasitized, on some leaves as high as 75% of the egg blisters contained exit holes. Taking monthly samples during a two year period, Hessein & McMurtry (1988) found parasitization ranged from 21.7-41.1% and 3.2-51.0% in Santa Barbara and Orange county orchards, highest parasitization occurring in November and January.

Assessing the importance of parasitism by *Megaphragma* spp. as a mortality factor affecting *M. sjostedti* field populations in cowpea in Benin, Tamò (1991) and Tamò et al. (1993) found that parasitization differed according to the locality. The parasitization level generally was very low in the centre (<2%), and reaching levels up to 30% in the south. The highest parasitization was recorded on wild Leguminosae host plants like *Pueraria phaseoloides* (53%) and *Centrosema pubescens* (47%) and *Cajanus cajan* (20%), in the south the major host plants of *M. sjostedti* during the dry season (November-February). As opposed to cowpea where eggs are deposited in organs susceptible to wilt or drop (leaf petioles and reproductive structures), in *P. phaseoloides* thrips eggs are embedded in the stem, which stays alive until the whole plant dies, thus allowing a higher survival and parasitization rate of *Megaphragma*. In citrus plantations in Japan, adults of *Megaphragma* occur from the middle of May onwards until October, reaching highest levels (but <10%) during August and September (Takagi, 1988) in non-sprayed fields or prior to spraying chemicals. Takagi (op. cit.) also noted a difference in parasitization level for different leaf levels (table 16).

Although thrips populations are attacked in the egg-stage, before the actual feeding damage is done, and application of egg parasitoids has been recommended in the past (Balachowsky & Mesnil, 1936), controlled releases for the control of thrips pests in greenhouses seems difficult. McLeod (1962) reported on a transport of *M. mymaripenne* from California to Ontario, Canada and 205 adults were released for the control of *H. haemorrhoidalis* in two greenhouses, but if it became established is un-

Table 16. Parasitization of *S. dorsalis* eggs by *Megaphragma* in different leaf levels in an unsprayed tea field at Toyosato, september 1985, total on 10 autumnshoots (Takagi, 1988).

Leaf level	1	2	3	4	5	6	7	8	9	10
Total number eggs	2	10	32	38	48	49	45	40	16	0
% parasitized	0	30	37.5	60.5	12.5	18.3	2.2	2.5	0	0

known. In spite of the sometimes high parasitization levels, Hessein & McMurtry (1988) and Tamò (1991) consider it doubtful that *Megaphragma*, by itself, is a regulating factor of thrips populations. Its relative short longevity of about 2 days and the long developmental time of the parasitoid compared to that of its host, might limit its ability to suppress increasing populations of thrips. Massrearing of egg parasitoids might be another serious constraint. Up till now, only Tamò et al. (1993) and Hessein & McMurtry (1988) managed to rear *Megaphragma* in the laboratory on a small scale. They reared a new generation of egg parasitoids, using infestation cages tied upon cowpea inflorescences infested with *M. sjostedti* and avocado leaves on water-soaked foam pads, infested with *H. haemorrhoidalis*. Their small size and short life as an adult, makes them very vulnerable to transport and difficult to apply as well.

3.3.2 Mymaridae

3.3.2.1 Polynema indica Narayanan & Subba Rao 1961

Taxonomy

Polynema (Polynema) indica Narayanan & Subba Rao belongs to the family Mymaridae. A key to genera allied to the genus *Polynema* Haliday, to the subgenera of *Polynema* and to the Indian species of the subgenus *Polynema* is provided by Narayanan & Subba Rao (1961). The same authors first described females of *P. indica*. The female measures 0.94 mm, head and thorax are dark brown, the abdomen is brown and the extremities golden yellow. The antennae have 9 segments and are relatively large (see figure 10), the slender wings are characterized by its long marginal fringes. Daniel (1986) first described *P. indica* attacking thrips eggs and mentioned the presence of males as well.

Distribution, hosts, host plant associations

P. indica has only been found in India: Narayanan & Subba Rao (1961) collected it in Delhi during May and June 1960. Host, host plants and ways of collection were not mentioned. Later Daniel (1986) collected it again near Madras from September 1982 till February 1983. Together with *G. shakespearei*, it occurred in relative large quantities in 1982-1983 on groundnut (*Arachis hypogea*) as well as an annual weed (*Achyranthes aspera*) present in the crop field, both infested with *Caliothrips indicus* (Thripidae: Panchaetothripinae).

Biology

All biological data available, including reproduction, sex-ratio, behaviour, efficiency of parasitization, interaction with the thrips host as well as its seasonal occurrence and population fluctuations in the field, have been described solely by Daniel (1986). The quantitative information provided however is sometimes missing (temperature, declines from 24-33 °C October 1st to 18-24 °C January 1st, outdoors) or incomplete (reproduction capacity, host data).

P. indica is a solitary endoparasitoid of *Caliothrips* eggs. Once parasitized, the eggs were not attacked for a second time. The parasitoid searched the leaf surface of both host plants (*A. hypogea, A. aspera*) with its antennae especially close to the veins where the host, *C. indicus*, normally laid her eggs. It located the place where the host egg was embedded by probing the leaf surface. Then it moved around the host egg area for 30-45 seconds, assessed the suitability of the egg for oviposition and inserted its ovipositor and laid a single egg into it. Unparasitized eggs of *C. indicus* normally hatch after 6-8 days incubation and completes its life-cycle in 11-14 days (Ananthakrishnan, 1984). The life-cycle of *P. indica* is similar: within 12-15 days a single adult emerged from each parasitized host by making a hole in the egg blister. Sex-ratio was constant 3♀:2♂, mating occurred frequently, lasting 20-30 seconds. On average 18 ± 3.2 adults emerged from the egg mass of a single *C. indicus*, 12-17% of which was parasitized on the weed and up to 9% on the crop. Although the host *C. indicus* was present on the weed almost all year, the incidence of *P. indica* was only seasonal. Two months after the appearance of the pest on groundnut in July, parasitization occurred in low levels during 2-3 months (September-November). When thrips populations declined, end of September, both host and parasitoid switched over to fresh *A. aspera* weeds, which appeared after the rains. *P. indica* was present during a 5-6 months period (October-February), parasitization reaching moderate levels in December-January. The presence of *P. indica* coincided with that of *G. shakespearei*, attacking the larval stages of *C. indicus*. Both populations followed a similar trend. The impact of *G. shakespearei* was however considered much larger than that of the egg parasitoid.

3.4 Erroneous records

In earlier reviews and publications, some records on hymenopterous parasitoids have been included, which are doubtful as being parasitoids of thrips or are even erroneously mentioned as such, because they had just been found in association with thrips. None of these records either state that these species actually parasitize thrips or that they have been reared from thrips. E.g. Crawford (1913) found *Thriposoma grafi* Crawford (recently synonymized to *Baryscapus grafi* (Walker) by LaSalle & Graham, 1990) (Eulophidae: Tetrastichinae) in sunflower with aphids and thrips and Girault (1917) obtained *Camptoptera pulla* Girault (Mymaridae) from leaves with *Aleyrodes* species and *Caliothrips fasciatus*, but both are definitively not thrips parasitoids (LaSalle pers. comm.), as has been mentioned by Ananthakrishnan (1984) and Lewis (1973) in their lists of thrips parasitoids. As already has been mentioned in 3.2.1.5, Risbec (1958) associated *Pediobius dipterae* (males) with thrips in Madagascar, but earlier records from Senegal made by the same author (Risbec, 1951) were from dipterous and lepidopterous hosts, so this reference at least needs confirmation. *Entedonastichus (Thripoctenoides) thione* has been reidentified to *Asecodes coronis* after remounting by Boucek & Graham (1978) (see 3.2.1.4).

Mani (1942) found a male(!) *Mymar indica* Mani (= *Mymar taprobanicum* Ward) (Mymaridae) along with thrips collected by Mani (1942) in dandelion flowers, but they actually are parasitoids of Delphacidae (Krombein et al., 1979). Also *Pezomachus thripites* (Ichneumonidae) has been associated with thrips on wheat ('these parasitoids were observed emerging from thrips larvae in some numbers; they copulated a short time after which the female deposited her eggs in the larvae of thrips': Russell (1912b) referring to Taylor (1860)) and has been later been referred to as such by Bagnall (1914) and Sakimura (1937a), but its description was very meagre (Russell, 1912b) and according to Muesebeck et al. (1951) the single female of it was unrecognizable.

Lewis (1973), included *Tetrastichus atratulus* (Nees) in his list of thrips parasitoids, parasitizing *Liothrips setinodis*, but many species have been described under this name and it remains unclear which one it is, as the type is lost (Domenichini, 1965). As cited by Callan (1943), Bondar (1922) erroneously reported a *Baryconus* sp. (Scelionidae; parasitoids of katydids (Orthoptera), Krombein et al., 1979) as an egg-parasite of *Selenothrips rubrocinctus*. A number of other erroneous records are due to wrong identification or reclassification of parasitoid species. They have already been discussed in the respective sections above.

3.5 Miscellaneous Hymenoptera records

3.5.1 Ceraphronidae (Ceraphronidea)

A single ♀ of *Aphanogmus fumipennis* (Thomson), which had previously been known to attack only Cecidomyiidae larvae (larvae are predators of thrips: Lewis, 1973), was reared in 1970 from an immature individual of *T. tabaci*, (Dessart & Bournier, 1971). It was collected on onion at Montpellier, France; conditions of the collection suggest that the egg of the parasitoid was laid in the 2nd instar or even the 1st instar of *T. tabaci*. Developmental time of the prepupa and pupa (see figures in Dessart & Bournier, 1971) was 6 and 15 days respectively. It is not known if this parasitoid normally develops on this host.

3.5.2 Eucharitidae (Chalcidoidea)

Chalcidoid planidia (first instar larvae, 0.13-0.18 mm), usually parasitic on mature larvae and pupae of ants (for a survey see Clausen, 1940ab; Johnson, 1988; for its morphology see Heraty & Darling, 1984), have occasionally been found as ectoparasitoids on larvae of thrips (table 17) in the USA, Malaysia and India. Planidia hatch from eggs laid in or on plant tissue and attach themselves usually to foraging ants (Hymenoptera: Formicidae). The ants phoretically transport the planidia to the nest, where the planidia drop off and attach to larval ants. Clausen (1940ab) studying the oviposition habits of Eucharidae observed that females of *Psilogaster antennatus* Gahan deposited their eggs only in close association with the eggs of *Selenothrips rubrocinctus*, commonly found on mango and *Erythrina* foliage in Malaysia. The eggs were placed vertically, regular spaced, in clusters of 50 to 100 or more, surrounding a freshly laid thrips egg. The female parasitoid was attracted to the egg itself rather than to the mass of excrements covering the egg. The egg hatched simultaneously with those of the thrips and the planidia attached themselves to the young thrips larva as soon as it emerged from the egg and was carried about until the first moult of the latter (Clausen, 1940).

All other host records are from thripine species. Wilson & Cooley (1972) recorded a planidium ectoparasitic on larvae of *F. occidentalis* in Texas. The planidia were found attached to the abdominal integument of first stage larvae, but were embedded in the abdomen and thorax of the larger 2nd-stage larvae (Wilson and Cooley, 1972; Johnson, 1988). Burks (in Wilson & Cooley, 1972) reported on similar planidia on *Frankliniella* spp. from Arizona and California. Beshear (1974) discovered planidia of *Orasema* sp. attached to 41 larvae of *Microcephalothrips abdominalis* and *Frankliniella* sp., (probably *tritici*) in Georgia. First and second stage larvae collected from flowers of *T. helianthoides*, had on average 3.4 (1-18) planidia attached to their body.

A phoretic relationship has been suggested with thrips too (Clausen, 1940a; Das, 1963), the chalcidoid planidium being transferred to the ant host eventually. Priesner (1960) states that probably all smaller ants, primarily these visiting inflorescences, must be considered as predators of thrips. In most cases (table 17) of *Orasema* and *Psilogaster* species however, host plants and thrips were not attended by any ants, or carried into their nests. On the other hand it is interesting to note that e.g. the highly aggressive ant *Wasmannia auropunctata* (Roger), found in association with *Orasema* spp. in the USA and Cuba (Johnson, 1988), has been re-

Table 17. Survey of thrips parasitoid species belonging to the Eucharitidae. Distribution, host species and host plant associations.

Distribution	host species	host plant	date	reference
Psilogaster antennatus **Gahan**[1]				
Malaysia	*Selenothrips rubrocinctus*	mango *Erythrina* sp.	1930.i	Clausen 1940ab
Unknown [1]				
Arizona	*Frankliniella* sp.	?	1964	Burks, *in*:
California	*Frankliniella* sp.	?	1966	
Texas	*Frankliniella occidentalis*	*Xanthocephalum microcephalum*	1970.x	Wilson & Cooley 1972
Orasema **sp.** [1]				
Georgia	*Frankliniella* sp, (*tritici*) *Microcephalothrips abdominalis*	*Tetragonotheca helianthoides*	1970.v	Beshear, 1974
Florida	unid. thrips	?	?	Johnson, 1988
Orasema assectator Kerrich [2]				
India, Assam	*Scirtothrips dorsalis*	*Thea sinensis*	1960	Das, 1963 [No]
Orasema coloradensis Gahan [3]				
Idaho	*Sericothrips* sp.	*Chrysothamnus nauseosus* *Chrysothamnus vicidiflorus*	1984.x	Johnson et al., 1986
Orasema viridis Ashmead [1]				
Arizona	unid. thrips	*Haplopappus* sp.	1984.viii	Johnson et al., 1986

Ant hosts: [1]: no direct relation to ant hosts observed; [2]: *Pheidole* sp. not foraging on tea ; [3]: *Formica subnitens* .
Thrips hosts: [No]: not observed

Table 18. Attempts for biological control of thrips pests with thrips parasitoids.

Target species	country target	crop	parasite species released	country origin	year	st	control achieved	reference
Selenothrips rubrocinctus	Trinidad	cacao	*G. shakespearei*	Ghana	1935-	1	recoveries, no control	Adamson 1936,
		cashew			1942	1	established, no control	Callan 1943
Selenothrips rubrocinctus	Trinidad	gr.house	*G. shakespearei*	Trinidad	1942/3	3	established, complete control	Callan 1943
Selenothrips rubrocinctus	Grenada	cacao	*G. shakespearei*	Trinidad	1936/7	0	no recoveries	Pickles 1938
Selenothrips rubrocinctus	Jamaica	mango	*G. shakespearei*	Trinidad	1937	1	repeated recoveries	Edwards 1938,
					1970	1	recoveries	Bennett 1970
Selenothrips rubrocinctus	P. Rico	cacao	*G. shakespearei*	Trinidad	1936-	1	recoveries	Dohanian 1937ab,
					1938	1	1st gen. recoveries	Bartlett 1939
Heliothrips haemorrhoidalis	Maryland	gr.house	*G. shakespearei*	P. Rico	1936	0	laboratory tests	Bartlett 1939
Heliothrips haemorrhoidalis	California	orange	*G. shakespearei*	Trinidad	1962	0	recoveries, no establ.	McMurtry et al. 1963
Heliothrips haemorrhoidalis	California	avocado	*G. shakespearei*	Bermuda	1982	0	recoveries, no establ.	Hessein et al. 1989
Heliothrips haemorrhoidalis	California	avocado	*T. semiluteus*	Australia	1986/9	3	adequate control	McMurtry et al. 1991
Heliothrips haemorrhoidalis	Hawaii[1]	croton	*T. semiluteus*	?	1988	1	recoveries	Early 1990pc
Heliothrips haemorrhoidalis	Israel	avocado	*T. semiluteus*	USA, Ca	1991	2	recoveries, establishment	Wysocki 1993pc
thrips	Germany	gr.house	*T. semiluteus*	?	1992	?	?	Albert et al. 1993
Heliothrips haemorrhoidalis	Canada	gr.house	*M. mymaripenne*	USA, Ca	1942	0	?	McLeod 1962
Hercinothrips femoralis	Florida	?	*G. shakespearei*	P. Rico	1939	?	?	Watson et al. 1939
Gynaikothrips ficorum	Bermuda	ficus	*G. shakespearei*	Jamaica	1960	0	no recoveries	Cock 1985
Gynaikothrips ficorum	Bermuda	ficus	*T. gentilei*	Brazil	1963	0	no recoveries	Bennett 1965
Thrips tabaci?	Hawaii	?	*G. shakespearei*	Trinidad	1936	0	no recoveries	Clausen 1978
Thrips tabaci	P.Rico	onion	*G. shakespearei*	Trinidad	1936/7	1	1st gen. recoveries	Bartlett 1939
Thrips tabaci	Bermuda	onion	*G. shakespearei*	Trinidad	1938	0	recoveries 1938, no establ.	Bennett & Hughes 1959
Thrips tabaci	Egypt	?	*G. shakespearei*	Ghana	1938/9	-	shipment failed	Kamal 1951
Thrips tabaci	Barbados	onion	*G. shakespearei*	Jamaica		-	no survival, no releases	Cock 1985
Thrips tabaci	Hawaii	onion	*C. russelli*	USA, Ca	1930/1	0	no establishment	Swezey et al. 1939
			C. vinctus	Philip.	1931	0	rearing failed	Fullaway et al. 1934
			C. menes	Japan	1932/4	1	recoveries, no control	Sakimura 1937c
	Barbados	onion	*C. menes*	India	1970	0	no recoveries	Narayanan 1971
	Britain	onion	*C. menes*	India	1970	0	lab. test, no release	Carl 1971
Thrips palmi	Florida		*C. menes*	Thailand	1992	1	recoveries	Baranowski 1993 pc
Frankliniella schultzei	Netherlands.[1]	cactaceae	*C. menes*	Brazil	1990	1	recoveries	Loomans 1991
Frankliniella occidentalis	Netherlands	gr.house	*C. menes*	Japan	1992	0	lab. tests, no release	Loomans pc
			C. menes	USA	1993	0	lab. tests, no release	Loomans pc
			C. americensis	USA	1993	0	lab. tests, no release	Loomans pc

[1]: accidentally introduced. st, state: - = shipment failed, no release, 0 = no recoveries, 1 = recoveries, 2 = partial control, 3 = substantial control, ? = unknown

ported on few occasions to carry larvae of *S. rubrocinctus* in its jaws in Trinidad (Callan, 1943) and that in Brazil the ant *Azteca chartifex* Forel is used to control cacao thrips (Entwistle, 1972). Other thrips species, like *G. ficorum* infesting Cuban laurel in Florida, discharge anal exudates that act as an effective defensive allomone for *W. auropunctata*, commonly disabling workers to subdue their potential prey (Howard et al., 1987), attacks being rare.

Although feeding has sometimes been observed on larvae of *Sericothrips* sp. by planidia of *Orasema* sp. (Johnson et al., 1986), no eucharitids are able to complete their development on their thrips host. At this time thrips is not considered an alternate host, but carriers or accidental hosts, but the exact role of thrips in the life cycle of eucharitids remains unclear (Johnson, 1988).

3.5.3 Sphecidae (Sphaecoidea)

Sphecids are not known as parasitoids of thrips, but because they belong to the Hymenoptera, they are briefly discussed here as well. Species in the genera *Spilomena*, *Ammoplanus* and *Xysma* (Pemphredoninae), nesting in pre-formed cavities, have been recorded being predators of thrips larvae (Muesebeck et al. 1951, Krombein, 1958b). In the USA, *Xysma ceanothae* and *Spilomena barbari* Krombein are known to carry second instar larvae of *Frankliniella*/*Thrips* and *Sericothrips* as prey to their nests (Krombein, 1958b). A female of *Spilomena pusilla* (Say) was intercepted (Krombein, 1958a) holding a paralyzed second stage larva of *Sericothrips* (*variabilis*) in her mandibles. In Europe, *Spilomena troglodytes* Lind. was seen making collections of thrips larvae (probably *Frankliniella* sp.) in stems of *Rubus*, as food for their brood and in Egypt, *Ammoplanus* spp., the smallest indigenous Sphecidae, are greatly suspected to be specialized in thrips (Priesner, 1960). Riek (1970) mentions that Australian species belonging to the Pemphredoninae which often nest in holes in wood, are regular visitors of flowers and except with Collembola or Homoptera, provision their nests also with Thysanoptera. In the Costa Rican rainforest, cells of two nests of *Microstigmus thripoctenus* Richards suspended on a straight pedicel from the underside of leaves, were mass provisioned with immature Thripidae, loosely piled as food for their offspring. Some of the thrips prey were identified as *Leucothrips* sp. and *Bradinothrips* sp., minute, solitary leaf feeders (Matthews, 1970).

4. Discussion

With the recent increase of the impact of thrips pests like *F. occidentalis* and *T. palmi* on agricultural and horticultural ecosystems, hymenopterous parasitoids have gained interest as potential biological control agents. Efforts to implement thrips parasitoids in greenhouse IPM programmes for the control of thrips pests have not been made before. Most attention has been paid to predatory insects like *Amblyseius* and *Orius* spp. (see Riudavets, this volume), but since control of thrips pests like *F. occidentalis*, is only partly successful in a number of important crops, the option of using parasitoids is worthwhile to consider.

Relatively little is known about most parasitoids attacking thrips in general, and those parasitizing *F. occidentalis* in particular. Up till now 26 larval parasitoid species and 12 egg parasitoid species have been described, parasitizing 70 species of Thysanoptera, many of which are known as pests. For most parasitoid species all what is known, however, are their collection data. Their biology and ecology is poorly studied. Their taxonomic status has been poorly described from a few specimens only in several cases, thus urging for a revision and reclassification of genera and species. A number of species have not been described yet.

The effectiveness of a number of parasitoids as natural enemies of thrips pests is therefore difficult to predict. Rates of parasitism found in the field are sometimes quite high, 40% or more, mostly during pest outbreaks (*G. shakespearei*: Cotterell, 1927; Daniel, 1986; Takagi, 1988; *C. menes*: Bühl, 1937; Hirose, 1989; *C. pacuvius* Kütter, 1936b; unknown: Hukkinen, 1936; *M. mymaripenne*: Hessein & McMurtry, 1988), but this is not always a good indicator for parasitoid impact (see Van Driesche, 1983) and natural control. In almost all records, the influence of parasitoids on thrips populations has been made after their occurrence in the field or after introduction. Up till now this has mainly been done empirically: most studies on thrips parasitoids have focused on assessing the seasonal occurrence and level of parasitism of indigenous pests in the field, sometimes complemented with additional studies on the behaviour and biology of thrips-parasitoid combinations in the laboratory (e.g. Russell 1912b; Sakimura, 1937ab; Bühl, 1937; Daniel, 1986; Murai, 1988a). Most attention was paid to a few common species, like *C. menes* and *G. shakespearei*. Except for the avocado-greenhouse thrips system (McMurtry & Johnson, 1963; Hessein & McMurtry, 1988, 1989; McMurtry et al., 1993), a proper evaluation of parasitoid characteristics before release, has only been performed partly and monitoring after releases was not performed systematically. Ecological studies on parasitoids of thrips species which are not considered as pests are very rare (Dyadechko, 1964).

Classical biological control of thrips pests, by releasing parasitoids in an inoculative way, restoring old and establishing new combinations (cf. Carl, 1982) of pest and parasitoid species has been tried in the past by trial and error (1930's: *T. tabaci*

Table 19. Criteria for the evaluation and selection of thrips parasitoids for seasonal inoculative control. Negative side effects excluded. Climate: t = temperate, m – M = mediterranean, T = tropical. Host: T = Thripinae; P = Panchaetothripinae. Target host in first column: + = develops on *F. occidentalis* (underlined) or related thripine host species; – other species. Original host, all other columns: + = good; – = not or lower than that of host; ? = unknown.

Species parasitoid	Criterion synchronization internal target host	seasonal original host	climatic adaptation	culture possible	reproduction rate	searching capacity	host
Ceranisus							
menes	+	+/–	tMT +/–	+/–	–	?	T
pacuvius	–	+	t +	–	–	+/–	T
russelli	+	–	M +/–	+/–	+/–	+/–	PT
americensis	+	–	tM +	+/–	+	?	T
vinctus	+	+/–	T –	+/–	?	?	T
maculatus	–	+	T –	?	+	?	P
lepidotus	+	?	tM +	?	?	?	T
planitianus	?	?	M +	–	?	?	?
javae	–	?	T –	?	?	?	?
Goetheana							
shakespearei	+	+/–	Tm +/–	+	?	?	PT
Thripobius							
semiluteus	–	+	Tm +/–	+	+	?	P
hirticornis	–	–	Tm –	?	?	?	P
Megaphragma							
mymaripenne	–	+/–	Tm +/–	–	?	+/–	PT
longiciliatum	+	?	T –	–	?	?	T
sp. (Benin)	+	+/–	T –	+/–	+/–	?	T

in Hawaii; 1930's *S. rubrocinctus* and in 1960's *T. tabaci* in the Caribbean; *H. haemorrhoidalis* in California) without great success, but is reconsidered again recently (*T. palmi* in Japan and Florida) (see table 18). Although *F. occidentalis* has been accidentally introduced into Europe, application of classical inoculative biological control programmes has never been considered a serious option: *F. occidentalis* and other thrips pests are mainly key pests in insolated greenhouses and only a pest in outdoor crops in the Mediterranean Area and Central Europe. Application by seasonal inoculation and/or inundation or conservation and augmentation in the respective areas are considered as useful strategies for control.

Techniques and criteria for the evaluation of the potential of and pre-selection as biocontrol agents have been formulated and reviewed elsewhere (Van Lenteren, 1986; Hokkanen, 1989; Mackauer et al., 1990), and depend on the type of biological control programme considered: for classical biological control programmes (Hokkanen & Pimentel, 1984; Waage, 1990; Waage & Mills, 1992), either for introduced or native pests (Pimentel, 1963; Carl, 1982) or for conservation and augmentation of indigenous natural enemies (Luck, 1992; Luck et al., 1988). Although applicable for a number of thrips-parasitoid combinations and thrips pest situations, these programmes will not be discussed here. In greenhouse systems, the procedure is followed as described in by Van Lenteren & Loomans (introduction, this volume), and is based on its proven value in the past either for seasonal inoculative (Minkenberg, 1990) or inundative (Pak & Van Lenteren, 1988) biological control. For the selection of candidate thrips parasitoids for application in greenhouse systems, criteria and characteristics as formulated by e.g. Van Lenteren (1986), Van Lenteren & Woets (1988), Minkenberg & Van Lenteren (1986) and Minkenberg (1990), will be used below as tools to discuss their potential, following a sequence as suggested by Van Lenteren (1986) and Van Lenteren & Woets (1988).

A number of species, like *C. nigrifemora*, *C. femoratus*, *C. margiscutum* and *G. incerta* and *Megaphragma* spp., will not be discussed below, because nothing is known about them, except their place and date of collection; they could be useful, but a proper evaluation is difficult, based on the present literature information. For others their biology will be related to the set of criteria and to the type of biological control programme (table 19).

4.1 Negative side-effects

Negative side-effects like hyperparasitism, attacking beneficials or non-target hosts in the area of introduction should not occur. Hyperparasitism of thrips parasitoids by secondary parasitoids is not known. Attack of beneficials has been recorded rarely: *C. menes* has been collected in association with predatory thrips, e.g. *Aeolothrips intermedius* in Argentina (DeSantis, 1961) and Europe (Loomans, pers. obs.), but no direct parasitization has been observed. However, *T. gentilei* is known to parasitize the plaeothripid predator *Androthrips flavipes* Schmutz, one of the controlling factors of gall inhabiting thrips in India, both in the laboratory and in the field (Ananthakrishnan & Swaminathan, 1977; Varadarasan & Ananthakrishnan, 1981). The same species is able to parasitize beneficials like *Liothrips* (*urichi*, *mikania*) used as biological control agents of weeds (Cock, 1982b).

4.2 Good culture methods

Good mass production methods for natural enemies are the basis for successful greenhouse biological control programmes. Production methods have been developed for a few larval parasitoid species only, mainly for laboratory purposes: *Megaphragma* spp. have been reared for a single generation by Hessein & McMurtry (1988) and Tamò et al. (1993), but because of its minute size are very difficult to rear, making a proper evaluation difficult. *C. menes* has been reared on bean pods (Loomans, 1991) and artificially on pollen and honey solution (Murai, 1990), methods which were also used for *C. americensis* (Loomans, unpubl. data). For release purposes, *C. menes* was reared on *T. tabaci* on onion (Sakimura, 1937b) and *C. vinctus* on *M. usitatus* on bean stems (Fullaway & Dobroscky, 1934). Using *S. rubrocinctus* (Panchaetothripinae) as a host, *G. shakespearei* has been reared for a number of generations on leaves of cashew (Adamson, 1936) and tropical almond (Bartlett, 1939). Numbers reached, however, were never higher than 10,000 per month. Only for *T. semiluteus* a real mass production method has been developed, using *H. haemorrhoidalis* on citrus fruits (Newberger & McMurtry, 1992), which makes it commercially available. Good culture conditions are closely intertwined with quality control measures, to ensure minimum field performance. The right choice of a thrips host to rear e.g. *C. menes*, might not only influence production per unit of time, but it size (and thus its quality) is positively correlated to the host is has been reared from (Murai, 1988a; Bühl, 1937).

4.3 Host selection

The capacity to attack and successfully develop on the target thrips pest, or what is called internal synchronization with development of the host, is an important prerequisite for selection. Here, it involves host acceptance, host specificity and host suitability. Thrips parasitoids often are specific to genera within the same family or even subfamily. As can be seen from appendix 2, only a few thrips species have been recorded as hosts for each parasitoid species; in some cases only a single thrips species is known as a host, but quantitative checks on host preference and host suitability are scarce (e.g. Sakimura 1937a). A high degree of specificity, regarded as a very desirable attribute in classical biological control (Huffaker & Rosen, 1990), but is not considered an important criterion for seasonal inoculative control or inundative control in greenhouses, because usually one or two related thrips species are present only. An indication of the host range of thrips parasitoids is known of a small number of species (e.g. *C. menes, C. russelli, G. parvipennis*) only. Many species can already be discarded as a potential control agent when *F. occidentalis* or *T. tabaci* are the target host (see appendix 2). *Thripastichus gentilei, Pediobius thysanopterous* and likely *Entedonastichus* spp., *Ceranisus bicoloratus* and *Ceranisus nubilipennis* can be discarded because they prefer phlaeothripids as hosts.

Records of thrips parasitoids found on *F. occidentalis* or closely related species, are scarce. Only *C. menes* and *C. americensis* are known to attack and develop on *F. occidentalis* and *T. tabaci* and *C. lepidotus* was found in association with *F. occidentalis* in Spain (Lacasa, pers. comm.), but has never been reared from it. Only few larval parasitoid species have been recorded from other *Frankliniella* species: *C. menes* parasitizes *F. intonsa* (Murai, 1988a) and *F. schultzei* (Loomans, 1991), *C. russelli* was reared from *F. tritici* (Fitch) by Russell (1912b) in California, the egg parasitoid *M. longiciliatum* has been recorded from *F. lilivora* in India (Subba Rao, 1969). *G. shakespearei* is known to complete its development on *T. tabaci* but attempts to control *T. tabaci* with *G. shakespearei* failed. Also a number of other species is known to attack and develop on species within the thripine subfamily. However, of most species the full host range and degree of host specificity is unknown. How parasitoids act when several thrips species occur simoultaneously (cf. Loomans, 1991), is poorly understood. On *Ricinus communis* a mixture of 7 species occur (Ananthakrishnan, 1984); *C. menes* parasitized three of them, but levels on *R. syriacus* increased only after the other two had disappeared (Daniel et al., 1983, 1986; Daniel, 1986).

Which host larval stage is preferred or accepted depends on the thrips-parasitoid combination. In the case of *F. occidentalis*, parasitization by *C. menes* is related to host age (Loomans et al., 1992) and host size (Loomans et al., 1993) and its success ratio related to larvae's vigourous defense measures, excretion of anal droplets and successful attempts to escape. Also for other thripine species larva-parasitoid interactions were unsuccessful due to larval defense reactions (e.g. Kutter, 1936b; Russell, 1912b; Billes, 1941). Protective glands are not known in Thysanoptera, and rarely one observes thrips with antennae and legs in cataleptic immobility: stuck flat to the leaf, difficult to remove. This habit is practised by some species of turf and bark thrips (Priesner, 1960) and has occasionally been observed for *H. haemorrhoidalis* and *F. occidentalis* (Loomans pers. obs.).

4.4 Environmental adaptation

Environmental adaptation to the greenhouse system encompasses habitat adaptation, host-plant adaptation and climatic adaptation. After the occurrence of a certain multivoltine thrips pest, evaluation of natural enemies usually starts by reviewing its distribution and biological characteristics (Tommasini & Maini (this volume)). Habitat characteristics determine the conditions and restrictions at which a parasitoid should do its work. Therefore influenced by (1) biotic factors like the type of crop and host-plant condition, multi-cropping systems, presence of weeds, etc., (2) abiotic factors like climatic conditions and (3) culturing practices like application of pesticides or cropping system (open field, greenhouse or screenhouse). Within this set-up, parasitoid characteristics determine the rate of parasitism and thus the success of a biological control programme. Because the greenhouse habitat is relatively constant compared to outdoor habitats, parasitoids do not necessarily need to adapt to a broad range of environmental conditions. To some extent adaptation is related to the geographical conditions, e.g. in Northwest Europe vs. South of Europe, where temperature ranges are quite different.

Climatic requirements can directly interfere with the parasitoids activity. Most parasitoid species reviewed above, thrive best under temperature conditions between 20 and 30°C. Rainfall can influence parasitoid activity directly, or indirectly for those species which pupate in the soil. Thrips parasitoids show a moderate tolerance to climatic extremes and their natural incidence is highly seasonal due to temperature limitations. Parasitoid activity is largely dependent on temperature. In Japan, *C. menes* is absent in onion fields during months with an average temperature less than 20°C (Sakimura, 1937b) and is absent during the rainy season with extreme temperatures higher than 35°C during the summer months in India (Daniel, 1986; Saxena, 1981). It seems to be absent in dry areas (figure 3) and dry periods (Loomans, 1991), but humidity requirements are not well understood. For parasitoid species, coming from tropical climates like *T. semiluteus*, *G. shakespearei* or *Megaphragma* spp., high temperatures are necessary for the development (Daniel, 1986; Hessein & McMurtry, 1989), making them of less value in the control of thrips attacking temperate-climate crops like cucumber or even warm-temperature crops like sweet pepper. They could, however, be useful in subtropical climates which prevail in the Mediterranean Area. At 20°C or lower development stops for a number of tropical species, whereas developmental time of *C. menes* shows a great variation and long duration (Murai, 1988a), related to its geographic origin, but this seems more a state of quiescence than real diapause. Whether diapause or quiescence of parasitoids hamper possible use for biocontrol in temperate zones has not been studied.

Whether parasitoids are able to adapt to different host plants is not clear. *Thripobius*, *Goetheana* and *Megaphragma* spp. have been collected mainly from evergreen shrubs and trees, *Entedonastichus* seems to be confined to grassy areas, and *Ceranisus* and some *Megaphragma* species occur in a variety of annual and flowering perennial host-plants. *T. gentilei*, *P. thysanopterous*, often are part of the complex interrelationships between gall-forming phlaeothripid thrips species and harmless, predatory and parasitic inquilines. There is no strict relationship to a single host plant species, but host plant architecture and structure influences searching efficiency. Within a certain host plant the physiological condition regulates thrips reproductive capacity and preferences for feeding sites: e.g. mature leaves are preferred by panchaetothripine thrips species and their parasitoids like *Thripobius*, *Goetheana*, *Megaphragma*. The rate of parasitism by *G. shakespearei* on tea plants in Japan varied with the leaf level (Takagi, 1988). In India it was much lower on the crop than on weeds (Daniel, 1986). *C. menes* has been collected from a large variety of host plants (table 4), both vegetative (onion: Sakimura 1937b; eggplant: Hirose et al., 1993) as well as flowering parts (Loomans, 1991). Thripine host species prefer young plant parts, open leaf structures, buds and flowers. *C. menes* can be found to search in such places, but parasitization was much lower when hosts were concealed than in the open (Sakimura, 1937ab), and searching efficiency of *C. menes* and *C. russelli* was lower on hairy leaves. Whether they are adapted well enough to maintain itself on *F. occidentalis* or other thripine pest species in European greenhouses is not clear.

4.5 Seasonal synchronization

Developmental time for almost all thrips parasitoid species, is relatively long and their longevity rather short compared to their thrips host (see tables 5, 9, 12). Developmental data available for thrips parasitoid species are often based on field observations with fluctuating temperatures, and have sometimes not been specified. For example developmental times for *F. occidentalis* and *T. tabaci* varies from 14-21 days between 20-25°C, whereas *C. menes* takes at least two weeks more to complete its life-cycle. Their longevity is about equal. Only *T. semiluteus* and *G. shakespearei* are known to complete their life-cycle in a shorter period than its target pest, *H. haemorrhoidalis*. That of *C. russelli* was about equal to that of *C. fasciatus*: about 3 weeks in the insectary at 22.5°C. Seasonal synchronization is not considered very important in the case of thrips pest infestations in greenhouses: because generations are overlapping soon after an infestation, the suitable host stages will be present continuously. Well timed releases could synchronize populations at the start. A large variation in developmental time as prevails in yellow strains of *C.*

menes, could spread the occurrence of adults over time, thus being present also during low larval density periods. Differences in life-history indicate that possibly different biotypes or geographical races of *C. menes* are involved. Records (Sakimura 1937a; Hirose 1989; Carl 1971; Daniel, 1986; Murai, 1990) on the biology of *C. menes* on different thrips hosts show similarities as well as differences compared to *F. occidentalis*, which might be explained by differences in origin of the parasite and in host species. Different degrees of parasitism and life-history parameters on different geographical host strains have not been evaluated properly (cf. Sakimura, 1937a).

4.6 Reproductive capacity

A high intrinsic rate of increase (r_m) or net reproductive potential (fecundity, R_0) and short generation time (T_g), relative to that of the thrips pest is one of the main criteria in the pre-introductory evaluation. It is a compilation of different separate characteristics of the parasitoid like fecundity, longevity and parasitoid activity, including host feeding and/or mutilation. Only for *C. menes* these parameters have been determined, in relation to *F. intonsa* (Murai, 1988a, 1990), but a proper life-table analysis (Bellows et al., 1992) has never been performed. The net reproduction (R_o) and the intrinsic rate of increase (r_m) varied largely with temperature, mainly due to a large variation in developmental period. The r_m values, 0.047 and 0.098 at 20°C and 25°C respectively, for a Japanese strain of *C. menes*, were much lower than that of its host *F. intonsa* (Murai, 1988a, 1990). The intrinsic rate of *F. intonsa* was 0.158 at 25°C (Murai, 1990) and that of *F. occidentalis* 0.095 at 20°C on chrysanthemum and 0.171 at 25°C (Robb 1989). Preliminary results on other *C. menes* strains (host *F. occidentalis*) are analogous (Loomans & Murai, unpubl. data). Based on its relative r_m value alone, *C. menes* cannot be considered as a suitable candidate for seasonal inoculative biological control of *F. occidentalis*, but could be used in inundative programmes. For other trips-parasitoid combinations, data on fecundity and longevity indicate that values for their hosts are higher. Below 20°C, the reproductive capacity of most thrips parasitoids is very low, most parasitoids entering a state of quiescence, whereas thrips species still are able to reproduce. Pest kill rates usually are determined under optimal laboratory conditions for both pest and parasitoid, where parasitoids are provided with a surplus of the suitable host stage. In the field or greenhouse, parasitoids must be able to locate their host at much lower densities and where preferred larval sizes of *F. occidentalis* are mostly concealed.

4.7 Foraging behaviour

The ability to locate and reduce thrips populations in a greenhouse will largely influence the overall rate of parasitism. Searching efficiency of thrips parasitoids is largely unknown. A series of search characteristics have been mentioned, like travel speed, ability to spread, preference for certain hosts or developmental stages, handling time, interference, high intrinsic searching capacity, etc. Although difficult to perform, studies on functional and aggregative response (cf. Minkenberg & Parrella, 1990; Hughes et al., 1992) combine a number of these aspects, but their value has been a subject of much debate (op. cit.).

Field parasitism by *C. menes* when attacking *T. tabaci* on onion in Japan (Sakimura, 1937b) showed a clear positive density-dependent relationship. But the percentage parasitism was not specified per age-classes sampled. Whether this increase in parasitism with host density was due to a numerical response (aggregative or reproductive) or to a functional response was not clear. The percentage parasitism for *Ceranisus* sp. attacking *R. cruentatus* in wax apple fields in Taiwan (Chiu, 1984) showed a clear negative density-dependent relationship.

It is also unknown whether semiochemicals are involved in host searching. Preference for a certain larval stage or age has been reported for a most thrips-parasitoid combinations (see chapter 3), but explanations for preference lack. Panchaetothripine species cover the egg after oviposition. The faecal material of the *H. haemorrhoidalis* seems to be one of the main factors for the female *M. mymaripenne* for eliciting probing and oviposition responses (Hessein & McMurtry, 1988). Oviposition deterrent substances, acting as kairomone for a wide range of egg parasitoids in e.g. Lepidoptera, have not been identified yet for any thrips species. Larvae of a number of Panchaetothripinae (*Retithrips*, *Caliothrips*, *Selenothrips*, *Heliothrips*, *Rhipiphorothrips*) constantly keep their abdomen in an uplifted position bearing a droplet of intestinal liquid, enclosed by the whorl of anal bristles (Rivnay, 1935, 1939; Entwistle, 1972; Chiu, 1984) and *Hercothrips fasciatus* larvae cover almost half of their body with liquid excrements. *F. occidentalis* produces an alarm pheromone (Teerling et al., 1993a) that acts as a kairomone for polyphagous predators (*Amblyseius cucumeris* and *Orius tristicolor*) (Teerling et al., 1993b). Whether these substances are used by parasitoid species is yet unknown.

4.8 Conclusion

Very few parasitoid species show some potential for the control of *F. occidentalis* in a greenhouse system (table 19). *T. semiluteus* fits our selection criteria best, but is a specific natural enemy of *H. haemorrhoidalis*. *C. americensis*, *C. menes*, *C. russelli*, *G. shakespearei* and maybe *C. lepidotus* are specific for thripine hosts, in particular for *F. occidentalis* or related species, and can be reared in the laboratory. All mentioned species have a generation time equal to or more than that of their host. Thrips parasitoids have gained little interest up till now. A thorough and systematic exploration of *F. occidentalis* populations for natural enemies in newly invaded areas and in its country of origin has never been undertaken and has been reently initiated in the South of Europe (Loomans, 1991) and Western USA (Loomans, unpubl. 1993). In addition, the existence of biotypes (geographical or host races) has to be properly evaluated. Assessing the efficiency of new parasitoids as natural enemies of thrips, always has been initiated and performed from a pest, i.e. growers, point of view, not from that of the parasitoid perspective. For a good evaluation of its potential and its biotic and abiotic requirements, it should not only be considered why the biology and ecology of a parasitoid makes it an effective candidate, but also what makes it ineffective and to be able to obtain essential insight in characteristics of successful natural enemies.

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Appendix

Appendix 1a. Current names and synonyms of species in the genus *Ceranisus* (Hymenoptera: Eulophidae) associated with thrips (Thysanoptera).

Current name	Synonyms/identification name
1. Genus *Ceranisus* Walker 1840	*Ceranisus* Walker 1840 [7, 9, 1]
	Thripoctenus Crawford 1911 [9]
	Epomphale Girault 1915 [5, 3]
	Entedonomphale Girault 1915 [3]
	Cryptomphale Girault 1917 [11]
1. *Ceranisus americensis* (Girault)	1. *Thripoctenus americensis* Girault 1917 [9]
2. *Ceranisus bicoloratus* (Ishii)	1. *Thripoctenus bicoloratus* Ishii 1933 [9]
3. *Ceranisus femoratus* (Gahan)	1. *Thripoctenus femoratus* Gahan 1932 [9]
4. *Ceranisus javae* (Girault)	1. *Epomphale javae* Girault 1917 [3]
5. *Ceranisus lepidotus* Graham 1963	
6. *Ceranisus maculatus* (Waterston)	1. *Thripoctenus maculatus* Waterston 1930 [9]
7. *Ceranisus margiscutum* (Girault)	1. *Entedonomphale margiscutum* Girault 1915 [3]
	2. *Entedonomphale stalini* Girault 1934 [3]
8. *Ceranisus menes* (Walker)	1. *Pteroptrix menes* Walker 1939 [9]
	2. *Diglyphus aculeo* Walker 1848 [10a]
	3. *Asecodes aculeo* (Walker) [6]
	4. *Thripoctenus brui* Vuillet 1914 [1]
	5. *Epomphale auriventris* Girault 1915 [3]
	6. *Epomphale rubensteina* Girault 1934 [3]
	7. *Ceranisus rosilloi* De Santis 1961 [12]
	8. *Ceranisus brui* (Vuillet)[*]
9. *Ceranisus nigrifemora* DeSantis 1961	
10. *Ceranisus nubilipennis* (Williams)	1. *Thripoctenus nubilipennis* Williams 1916 [9]
	2. *Cryptomphale nubilipennis* Girault 1917 [3]
11. *Ceranisus pacuvius* Walker 1842	1. *Cirrospilus pacuvius* Walker 1838
	2. *Entedon acestor* Walker 1839 [10a]
	3. *Derostenus clavicornis* Thomson 1878 [4]
	4. *Ganahlia clavicornis* (Thomson) [1]
	5. *Thripoctenus kutteri* Ferrière 1936 [2]
12. *Ceranisus planitianus* Erdös 1966	1. *Thripoctenus kutteri* Erdös (nec Ferr.) [8a]
13. *Ceranisus russelli* (Crawford)	1. *Thripoctenus russelli* Crawford 1911 [9]
14. *Ceranisus vinctus* (Gahan)	1. *Thripoctenus vinctus* Gahan 1932 [9]

1: Boucek 1959, 2: Boucek 1961, 3: Boucek 1988, 4: Boucek & Graham 1978, 5: Burks 1971, 6: Dalla Torre 1898, 7: Erdös 1954, 8: Erdös 1956, a: Erdös 1966, 9: Graham 1959, 10: Graham 1963, 10a: Graham in Boucek & Graham 1968, 11: Peck 1963, 12: DeSantis & Fidalgo in prep., *: wrong combination

DeSantis (1979) erroneously mentioned *Euderomphale menes* (Walker) (= *E. flavimedia* Howard 1881) and *Euderomphale clavicornis* (Thomson) (= *Ceranisus pacuvius*) as synonyms of *Ceranisus menes*; see Graham, 1963, Erdös, 1966.

Appendix 1b. Current names and synonyms of parasitoids species in the genera *Thripobius*, *Goetheana*, *Entedonastichus*, *Pediobius* and *Thripastichus* (Hymenoptera: Eulophidae) associated with thrips (Thysanoptera).

Current name	Synonyms/identification name
2. Genus *Thripobius* Ferrière 1938	
1. *Thripobius semiluteus* Boucek 1976	
2. *Thripobius hirticornis* Ferrière 1938	
3. Genus *Goetheana* Girault 1920	*Dasyscapus* Gahan 1927 [3]
1. *Goetheana shakespearei* Girault 1920	*Dasyscapus parvipennis* Gaham 1927 [1] *Dasyscapus thripsivorous* Narayanan et al. 1960[1] *Goetheana parvipennis* (Girault)
2. *Goetheana incerta* Annecke 1962	
4. Genus *Entedonastichus* Girault 1920	*Pirenoidea* Girault 1922 [1] *Thripoctenoides* Erdös 1954 [1]
1. *Entedonastichus albicoxis* (Szelényi)	1. *Thripoctenoides albicoxis* Szelenyi 1982
2. *Entedonastichus carbonarius* (Erdös)	1. *Thripoctenoides carbonarius* Erdös 1954 [1]
3. *Entedonastichus dei* (Girault)	1. *Pirenoidea dei* Girault 1922 [1]
4. *Entedonastichus gaussi* (Ferrière)	1. *Thripoctenoides gaussi* Ferrière 1958
5. *Entedonastichus mirus* Girault 1920	
6. *Entedonastichus kaulbarsi* (Yoshimoto)	1. *Thripoctenoides kaulbarsi* Yoshimoto 1981
5. Genus *Thripastichus* Graham	*Tetrastichus* Haliday (Graham 1987)
1. *Thripastichus gentilei* (Del Guercio)[2]	1. *Eulophus gentilei* (n.n.) Del Guercio 1910 2. *Tetrastichus gentilei* Del Guercio 1911 3. *Tetrastichus tatei* Dozier 1937 4. *Tetrastichus thripophonus* Waterston 1923 5. *Tetrastichus rhipiphorothripscidis* N.R.R 1960
6. Genus ***Pediobius* Walker 1846**	*Pleurotropis* Förster 1856
1. *Pediobius thysanopterous* (Burks)	1. *Pleurotropis thysanopterous* Burks 1971
2. *Pediobius dipterae* (Risbec)	1. *Pleurotropis dipterae* Risbec 1951

1: Boucek 1988, 2: Graham 1987, 3: Girault 1930

Appendix 2. Host list of hymenopterous parasitoids attacking Thysanoptera, including synonyms of host references. Synomyms according to reference list of Jacot-Guillarmod (1970, 1971, 1974, 1975, 1978, 1979), Jacot-Guillarmod & Brothers (1986) (*: not in this catalogue) and Umeya et al., 1988.

TEREBRANTIA

THRIPIDAE

PANCHAETOTHRIPINAE	parasitoid	country	reference
Monilothripini			
Zaniothrips ricini Bhatti	*C. menes*	India	Daniel et al., 1983
Panchaetothripini			
Brachyurothrips anomalus Bagnall	*T. semiluteus*	Sao Tomé	Boucek, 1976
Caliothrips fasciatus (Pergande)	*C. russelli*	California	Russell, 1912ab
Heliothrips fasciatus Pergande			
Hercothrips fasciatus (Pergande)			
Caliothrips indicus (Bagnall)	*G. shakespearei*	India	Narayanan et al., 1960
Caliothrips insularis (Hood)	*G. shakespearei*	Trinidad	Callan, 1943
Hercothrips insularis Hood			
Dinurothrips hookeri Hood	*G. shakespearei*	lab	Callan, 1943
Heliothrips haemorrhoidalis (Bouché)	*T. semiluteus*	Australia	Boucek, 1988
		South Africa	Steyn et al., 1993
	M. mymaripenne	Hawaii	Pemberton, 1931
		California	Boyce & Mabry, 1937
		Chili	DeSantis, 1965
		Guadeloupe	Delvare, 1993
	Megaphragma sp.	India	Narayanan, 1971
Heliothrips spp.	*T. semiluteus*	Brazil	LaSalle & McM., 1989
	G. shakespearei	Trinidad	Callan, 1943
Hercinothrips femoralis (O.M.Reuter)	*T. semiluteus*	Hawaii	Early, 1990 pc
Heliothrips femoralis (Reuter)	*G. shakespearei*	Benin	Tamò, pc
Hercothrips femoralis (Reuter)			
Panchaetothrips indicus Bagnall	*T. semiluteus*	India	Boucek, 1976
Panchaetothrips noxius Priesner	*M. ghesquièrei*	Zaire	Ghesquière, 1939
Retithrips syriacus (Mayet)	*T. hirticornis*	Tanzania	Ferrière, 1938
Retithrips aegyptiacus Marchal		Ghana	
		Kenya	BMNH, pc
		Zimbabawe	
	C. menes	India	Daniel, 1986
	M. mymaripenne	Egypt	Kryger, 1932
		Israel	Rivnay, 1939
Rhipiphorothrips cruentatus Hood	*C. maculatus*	India	Waterston, 1930
Rhipophorathrips cruentatus Hood	*Ceranisus* sp.	Taiwan	Chiu, 1984
	C. menes	Taiwan	Chang, 1991
	T. gentilei	India	Narayanan et al., 1960
Selenothrips rubrocinctus (Giard)	*G. shakespearei*	Ghana	Cotterell, 1927
Heliothrips rubrocinctus Giard		Venezuela	Annecke, 1962
		Bahamas	Bennett & B., 1982
	M. mymaripenne	Guadeloupe	Delvare, 1993
	M. caribea	Guadeloupe	Delvare, 1993
Thrips (spec. indet.)	*C. javae*	Indonesia	Girault, 1917b

Appendix 2 continued, host list Thripinae

THRIPINAE	parasitoid	country	reference
Dendrothripini			
Pseudodendrothrips mori (Niwa)	*G. shakespearei*	Japan	Takagi, 1988[1]
	*Megaphragma*sp.	Japan	Takagi, 1988
Leucothrips (cf. *piercei*) O.M. Reuter	*M. mymaripenne*	Haiti	Dozier, 1932
Microthrips sp.			
Sericothripini			
Scirtothrips dorsalis Hood	*G. shakespearei*	Japan	Murai, pc
	M. deflectum	Japan	Polaszek, pc
	Megaphragma sp.		Takagi, 1988[1]
Thripini			
Ceratothrips ericae (Haliday)	*Ceranisus* sp.	UK[1]	Bagnall, 1914[2]
Taeniothrips ericae (Haliday)			
Oxythrips parviceps Uzel			
Physothrips ericae (Haliday)			
Chirothrips hamatus Trybom	unid.	Finland	Hukkinen, 1936
Frankliniella intonsa (Trybom)	*C. menes*	Japan	Murai, 1988ab
Frankliniella formosa Moulton			
Frankliniella lilivora Takahashi *	*M. longiciliatum*	India	Subba Rao, 1969
Frankliniella occidentalis (Pergande)	*C. menes*	California	Loomans, 1993 pc
Euthrips occidentalis Pergande		Europe	Loomans, 1991
		Israel	Rubin & K., 1992
	C. americensis	Canada[1]	Seamans, 1923
		California	Loomans, 1993 pc
		Arizona	
Frankliniella schultzei (Trybom)	*C. menes*	Netherlands	Loomans, 1991
Frankliniella dampfi Priesner			
Frankliniella tritici (Fitch)	*C. russelli*	California	Russell, 1912ab
Euthrips tritici Fitch			
Kakothrips pisivorus (Westwood)	*C. menes*	France	Vuillet, 1914
Kakothrips robustus Uzel		Germany	Bühl, 1937
Frankliniella robusta Uzel		Russia	Antsiferova & T., 1974
Kakothrips pisivora (Westwood)		Switzerland[1]	Teulon et al., 1992
	C. pacuvius	Switzerland	Kütter, 1936ab
		Netherlands	Franssen, 1960
		Hungary	Jenser, 1993 pc
Limothrips cerealium (Haliday)	*C. lepidotus*	Spain	Lacasa, 1990 pc
Megalurothrips usitatus (Bagnall)	*C. vinctus*	Philippines	Gahan, 1932
Taeniothrips longistylus Karny	*C. femoratus*	Philippines	Gahan, 1932
Taeniothrips nigricornis (Schmutz)	*C. menes*	Philippines	Tamò, 1991 pc
Megalurothrips sjostedti Trybom	*C. menes*	Benin	Tamò et al., 1993
	Ceranisus sp.	Zambia	Tamò, 1992 pc
	M. mymaripenne	Benin	Tamo et al., 1993
	Megaphragma sp.	Benin	Polaszek, pc
Microcephalothrips abdominalis			
(Crawford)*C. menes*		Japan	Sakimura, 1937a
Thrips abdominalis Crawford		Korea	Paik et al., 1981
Neurisothrips fullawayi (Moulton)	*C. menes*	Hawaii Isl.	Yoshimoto, 1965
Isoneurothrips fullawayi Moulton			
Odonthothrips ulicis (Haliday)	*C. pacuvius*	UK	BMNH, 1977 pc

Appendix 2 continued, host list Thripinae

Ramaswamiahiella subnudula (Karny)	*C. menes*	India	Narayanan, 1971
Thrips subnudula Karny			
Taeniothrips alliorum Priesner	*C. menes*	Japan	Sakimura, 1937a
Taeniothripsx sp.			Kurosawa, 1931
Taeniothrips atratus (Haliday)	*Ceranisus* sp.	UK[1]	Bagnall, 1914
Physothrips atratus (Haliday)			
Taeniothrips inconsequens (Uzel)	unknown	Germany	Carl et al., 1989
Taeniothrips laricivorous Kr. & Farsk	unknown	Czechia	Kratochvíl & F., 1942
Taeniothrips picipes (Zetterstedt)	*Ceranisus* sp.	UK[1]	Bagnall, 1914
Taeniothrips primulae (Haliday)			
Thrips coloratus Schmutz	*C. menes*	Japan	Murai, 1988a
Thrips flavus Schrank	*C. menes*	lab	Bühl, 1937
Thrips hawaiiensis (Morgan)	*C. menes*	Japan	Murai, 1988a
Thrips palmi Karny	*C. menes*	Thailand	Hirose et al., 1993
		Japan	Hirose et al., 1992
Thrips paluster O.M.Reuter	*Ceranisus* sp.	UK[1]	Bagnall, 1914
Thrips palustris O.M.Reuter			
Thrips setosus Moulton	*C. menes*	Japan	Murai, 1988a
Thrips tabaci Lindeman	*C. menes*	Indonesia	Van Heurn, 1923
		Japan, Korea	Sakimura, 1937a
		Philippines	Ishii, 1933
		India	Narayanan, 1971
		Argentina	DeSantis, 1961
	C. russelli	USA - Ca	Russell, 1912b
	G. shakespearei	Indonesia	Van Heurn, 1923
		Trinidad	Clausen, 1978
Thrips simplex (Morison)	*C. russelli*	USA -Ca	McKenzie, 1935
Taeniothrips gladioli Moulton			
Toxothrips ricinus Bhatti	*C. menes*	India	Daniel et al., 1986
thrips (spec. indet.)	*C. pacuvius*	Scotland	Teulon et al., 1992
	G. shakespearei	Bulgaria	Pelov, 1990 pc

[1]: found in association with

TUBULIFERA

PHLAEOTHRIPIDAE

IDOLOTHRIPINAE	parasitoid	country	reference
Pygothripini			
Cryptothrips nigripes (O.M.Reuter)	*E. gaussi*	Ukraine	Dyadechko, 1964
Cryptothrips rectangularis Hood	*C. nubilipennis*	USA - Mass.	Williams, 1916
Megalothrips spinosus Hood	*C. nubilipennis*	USA - Mass.	Williams, 1916
PHLAEOTHRIPINAE			
Acanthothrips nodicornis O.M.Reuter	*E. gaussi*	Ukraine	Dyadechko, 1964
Androthrips flavipes (Schmutz) pred.	*T. gentilei*	India	Varadarasan et al., 1981
Arrhenothrips ramakrishna Hood	*T. gentilei*	India	Varadarasan et al., 1981
Crotonothrips dantahasta Ananth. *	*T. gentilei*	India, lab	Varadarasan et al., 1981
Gynaikothrips flaviantennatus Moulton	*T. gentilei*	India, lab	Varadarasan et al., 1981
Gynaikothrips ficorum (Marchal)	*T. gentilei*	Puerto Rico	Dozier, 1936
Gynaikothrips uzeli (Zimmermann)		Bermuda	Bennett, 1963
		Brazil	Bennett, 1965
		France	Bournier, 1967
Hoplothrips pedicularius Haliday *	*T. gentilei*	Germany	Domenichini, 1965
Liothrips laureli (Mason) *	*T. gentilei*	USA - FLa	Mason, 1922
Cryptothrips laureli Mason			
Liothrips mikaniae (Priesner) *	*T. gentilei*	Costa Rica	Cock, 1982b
		Trinidad	
Liothrips oleae (Costa) *	*T. gentilei*	Italy	Del Guercio, 1911
Phloeothrips oleae Costa		Croatia	Tominic, 1950
		Greece	Alexandrakis, 1986
Liothrips setinodis O.M.Reuter *	*E. gaussi*	Ukraine	Dyadechko, 1964
Liothrips hradecensis Uzel		Germany	Ferrière, 1958
Liothrips urichi Karny *	*T. gentilei*	Trinidad	Simmonds, 1930
Liothrips varicornis Hood *	*T. gentilei*	Trinidad	Cock, 1982b
Liothrips wasabiae Haga et Okajima *	*C. bicoloratus*	Japan	Murai, 1992 pc
Mallothrips indicus Ramakrishna *	*T. gentilei*	India	Sharma et al., 1965
Manothrips floridensis (Watson) *	*T. gentilei*	Florida	Yothers & Mason, 1924
Cryptothrips floridensis Watson			
Phlaeothrips coriaceus Haliday *	*E. gaussi*	Ukraine	Dyadechko, 1964
Phlaeothrips pillichianus Priesner *	*E. gaussi*	Ukraine	Dyadechko, 1964
Hoplandrothrips pillichianus (Pr.) *			
Schedothrips orientalis Ananthakrishnan *	*T. gentilei*	India	Varadarasan et al., 1981
Teuchothrips longus (Schmutz) *	*T. gentilei*	India, lab	Varadarasan et al., 1981
Thilakothrips babuli Ramakrishna *	*T. gentilei*	India	Varadarasan et al., 1981
thrips (spec. indet.)	*C. bicoloratus*	Japan	Murai, 1992 pc
	E. gaussi	Ukraine	Dyadechko, 1967