Review

Biology and ecology of trombidiid mites (Acari: Trombidioidea)

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ABSTRACT

Most mites of the family Trombidiidae are ectoparasites in the larval stage and free-living predators in the deutonymphal and adult stages on a variety of arthropods, among which are pests of many economic crops. This paper provides an updated review of their systematics, life history, reproduction, behaviour, predator–prey and parasite–host relationships, and population dynamics, with particular reference to their possible role in biological control.
Exp Appl Acarol 22: 139–155 © 1998 Chapman & Hall Ltd

INTRODUCTION

The mites of the family Trombidiidae and related groups are the large red velvet mites commonly found in soil, litter and other terrestrial habitats. These mites belong to the prostigmatid suborder Parasitengona, whose members have evolved a complex life cycle. With few exceptions, the larvae are parasitic on insects and other invertebrates and are morphologically different from the free-living post-larval stages, which are predators of small arthropods. Because their prey and hosts include insect and mite pests of economic importance, these mites are considered to have potential as biological control agents (Eickwort, 1983; Welbourn, 1983; Zhang, 1987, 1988). Previous reviews include those of Robaux (1974) for the general biology of the Trombidioidea, Welbourn (1983) for host–prey associations in the Trombidioidea and Zhang (1991a) for the biology of the Allothrombiinae. This paper provides an updated review of the biology and ecology of the Trombidiidae, with reference to their possible role in biological control.

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SYSTEMATICS AND CLASSIFICATION

The systematics of the Trombidiidae and related groups are in a state of flux, with the concepts of taxa and classification unsettled even at the family level (Table 1). Many of the subfamilies of Trombidiidae *sensu* Thor (1935) have been accorded family status in the Trombididoidea (Feider, 1955; Vercammen-Grandjean, 1973; Krantz, 1978; Kethley, 1982, 1990; Welbourn, 1983, 1984; Southcott, 1986b, 1987; Witte, 1991). The superfamily Trombidioidea was accorded even higher status (Trombidia) and further divided by Feider (1959). The classification of Feider (1979) recognized 22 families arranged in 11 superfamilies. A recent compromise was proposed by Welbourn (1991), who raised Trombidioidea *sensu lato* to the cohort Trombidina consisting of ten families in four superfamilies (Table 1); the restricted Trombidiidae (Trombidiinae, Podothrombiinae and Allothrombiinae) was placed in Trombidioidea *sensu stricto* along with the Microtrombidiidae, Eutrombidiidae and Neothrombiidae. This system was not followed by Southcott (1993, 1994). Welbourn's (1991) system was based on a phylogenetic analysis and is adopted by the present author. This paper concerns Trombidiidae *sensu stricto*; references to other related families are made to indicate general trends in trombidioid mites when the data on the Trombidiidae are few.

TABLE 1

Major classification systems of the Trombidina

Thor and Willmann (1947)	Vercammen-Grandjean (1973)	Feider (1979)	Welbourn (1991)
Trombidiidae	Trombidiodea	Trombidiina	Trombidiina
Trombellinae	Trombellidae	Tanaupodoidea	Tanaupodoidea
Tanaupodinae	Johnstonianidae	Johnstonianoidea	Tanaupodidae
Northrombiinae	Neotrombidiidae	Tanaupodastroidea	Chyzerioidea
Johnstonianiinae	Leeuwenhoekiidae	Trombiculoidea	Chyzeriidae
Trombiculinae	Trombiculidae	Anomalothromboidea	Trombiculoidea
Microtrombidiinae	Podothrombiidae	Trombelloidea	Johnstonianidae
Podothrombiinae	Trombidiidae	Calothromboidea	Trombiculidae
Trombidiinae	Trombidiinae	Notothromboidea	Leeuwenhoekiidae
Allothrombiinae	Allothrombiinae	Microtromboidea	Neotrombidiidae
	Feideriinae	Microtrombidiidae	Trombellidae
	Feideriinae	Eutrombidiidae	Audyanidae
	Microtrombidiinae	Neothrombiidae	Trombidoidea
	Georgiinae	Podothromboidea	Trombidiidae
	Stygothrombiidae	Trombidoidea	Neothrombiidae
		Trombidiidae	Eutrombidiidae
		Parathrombiidae	Microtrombidiidae
		Allothrombiidae	
Ten subfamilies	Eight families	Eleven superfamilies	Four superfamilies
		Twenty-two families	Twelve families

Hypotheses about the phylogenetic relationships have been proposed by Welbourn (1991) at the superfamily level, by Welbourn (1984) at the family level within the Trombidioidea and by Zhang (1994, 1995) at the generic level in the Trombidiidae and Neothrombiidae. These hypotheses are not conclusive and should all be tested in the future when more data (ontogenetic and molecular) are available.

The Trombidiidae and allied groups are poorly known taxonomically and their classifications are among the most difficult in the Prostigmata. Many species are known only from adults or deutonymphs, some species are known only from larvae and only a few species are known from both the larval and post-larval stages. Recently, studies have focused on the larval stage and correlations between the larval and post-larval stages (e.g. Welbourn, 1984, 1991; Southcott, 1986b, 1993, 1994; Zhang and Xin, 1992; Zhang, 1994, 1995). However, there are few taxonomic specialists on this group. Many species remain undescribed and many known species (in particular the post-larval stages) remain inadequately described. The accurate identification of species (in particular when only adult specimens are available) will remain very difficult until taxonomic revisions are published. The taxonomic difficulties of these mites are the main obstacles to studies on their biology and use in biological control.

DEVELOPMENT AND LIFE CYCLE

The sequence of life cycle stages is fairly constant in the Trombidiidae and related mites. The primitive pattern in the Prostigmata is retained: egg, pre-larva, larva, protonymph, deutonymph, tritonymph and adult males and females. Unlike other prostigmatid mites (except the Pterygosomatidae), their pre-larvae, protonymphs and tritonymphs are calyptostatic, whereas the larvae are ectoparasites and the deutonymphs and adults are free-living predators. Non-feeding larvae have been reported in one species (Smith, 1997).

The life cycle of the Trombidiidae in the field is usually univoltine (Henking, 1882; Howard, 1918; Miller, 1925; Hirst, 1926; Michener, 1946; Robaux, 1974; Aeschlimann and Vitou, 1986; Southcott, 1986b, 1994; Zhang, 1988; Zhang and Xin, 1989a,b; Zhang et al., 1995; Dong et al., 1996). In temperate regions, the eggs are laid in the soil during March–July and hatch after 1–2 months depending on the environmental conditions. The occurrence of the larvae is generally in synchrony with their hosts. The larvae are ectoparasitic on arthropod hosts and the attachment time is approximately 1 week or sometimes up to 2 weeks. They then detach from the host and move into the soil. Calyptostatic protonymphs develop within the cuticle of larvae. Deutonymphs emerge in the summer or autumn and forage on the soil surface and plants. Calyptostatic tritonymphs develop within the cuticle of deutonymphs in the soil and adults emerge in the autumn. Nymphs that appear late in summer or autumn may fail to mature in the same year and will complete their life cycle in the second or third year (Robaux, 1974). The adults usually hibernate

in the soil during the winter. Some species may lay eggs in autumn, e.g. *Allothrombium ovatum* Zhang & Xin (Dong *et al*., 1996) and *Johnstoniana parva* Wendt *et al*. (1994; Johnstonianidae). The adults of *Allothrombium pulvinum* Ewing and *A. ovatum* moult once more (Chen and Zhang, 1991; Dong *et al*., 1996). Michener (1946) and Southcott (1994) likewise observed post-imaginal moulting (one to several times) in the Microtrombiidae and called those that emerged from tritonymphs 'pre-adults'.

The development and survival of each life cycle stage is affected by the temperature, relative humidity (RH) and food availability/quality (Robaux, 1974). The eggs of *Allothrombium fuliginosum* (Hermann) need an RH of near 100% for optimal development and survival (Robaux, 1974). Exposure of *A. fuliginosum* pre-larvae to 85% RH for 4 days resulted in 80% mortality and the development of survivors was slower than that at 100% RH (Robaux, 1974). *Allothrombium pulvinum* eggs failed to develop normally at RHs lower than 80% (Zhang and Xin, 1989a; Saboori and Zhang, 1996). The larvae of *A. pulvinum* can survive in water for 10 days (Zhang and Xin, 1989a). The optimal temperatures for post-embryonic development for the Trombidiidae fall between 14 and 25°C and are slightly lower for the Trombidiinae and Microtrombidiidae than for *Allothrombium* (Robaux 1974).

The immature stages of *Allothrombium* species last for approximately 3 months in the laboratory (Table 2) and the rate of development depends very much on the temperature (Robaux, 1974). In the field, the development from egg to adult is a few months shorter in the Allothrombiinae (6–7 months) than the Trombidiinae and Microtrombiidae (approximately 10 months) (Robaux, 1974). In South Dakota, *Eutrombidium locustarum* (Walsh) [Eutrombidiidae] may complete one full and one partial generation within a year (Severin, 1944).

TABLE 2

Developmental times (in days) in *Allothrombium*

	Species			
	A. pulvinum	*A. ovatum*	*A. fuliginosum*	
Temperature (°C)	20–30	19	21	25
Egg	14–19	30–34[a]	13	10
Pre-larva	7–9	–	10	9
Larva	14–17	7–9	–	–
Protonymph	12–15	19–22	18	17
Deutonymph	18–22	16–29	49	–
Tritonymph	9–12	19–22	16–18	16–28
Location	China	China	France	
Reference	Zhang and Xin (1989a)	Dong *et al*. (1996)	Robaux (1974)	

[a] Egg and pre-larva.

HOST–PARASITE AND PREDATOR–PREY ASSOCIATIONS

The host and prey associations of Trombidoidea *sensu lato* were reviewed by Welbourn (1983) for records published before the early 1980s. An updated summary of the larval hosts is given in Table 3. The larval hosts of the majority of species are unknown at the present and any generalization about host range and specificity is likely to be premature. Trombidiid larvae have been found on many different orders of Insecta and Arachnida (Table 3). The host range of this family in terms of the different orders of arthropods they parasitize is nearly as wide as the combined host range of the rest of the Trombidina (excluding the Trombiculidae and Leeuwenhoekiidae). The larvae of *Podotrombium* and the monotypic *Monotrombium* are found exclusively on aphids, but those of other genera are found on several orders of insects. Within a trombidiid genus, some species are more or less restricted in host range (e.g. *A. pulvinum* on aphids) whereas others may be broadly polyphagous (e.g. *A. ovatum* on Homoptera, Lepidoptera and Coleoptera) (Zhang and Saboori, 1996).

TABLE 3

A summary of host associations of parasitic larvae of the Trombidina

Mites	Hosts
Tanaupodoidea	
Tanaupodidae	Homoptera and Diptera
Chyzerioidea	
Chyzeriidae	Orthoptera and Acari
Trombiculoidea	
Audyanidae	Scorpiones
Johnstonianidae	Diptera and Coleoptera
Neotrombidiidae	Coleoptera, Diptera and Lepidoptera
Trombellidae	Orthoptera and Diptera
Trombiculidae	Vertebrates (except fishes)
Leeuwenhokiidae	Vertebrates (except fishes)
Trombidioidea	
Eutrombidiidae	Orthoptera, Coleoptera, Arachnida, Chilopoda and Diplopoda
Microtrombidiidae	Diptera, Coleoptera and Lepidoptera
Neothrombiidae	Orthoptera, Diptera, Microcoryphia, Coleoptera and Chilopoda
Trombidiidae	
Allothrombium	Homoptera: Aphididae, Lepidoptera, Coleopteran, Opiliones and Acari
Clinotrombium	Araneae and Lepidoptera
Dinothrombium	Orthroptera, Coleoptera, Lepidoptera, Araneae and Solifugae
Monotrombium	Homoptera: Aphididae
Paratrombium	Hymenoptera, Hemiptera, Homoptera and Diptera
Podothrombium	Homoptera: Aphididae
Trombidium	Lepidoptera, Coleoptera, Diptera, Orthoptera, Hemiptera and Homoptera Hymenoptera, Araneae, Pseudoscorpiones and Opiliones

Data from an unpublished checklist by the author.

The adults of *Allothrombium* are generalized predators and can probably feed on most of the small arthropods that they can handle (Zhang, 1991a), whereas those of *Trombidium* feed exclusively on the eggs of collembolans (Robaux, 1974). However, few experimental tests on feeding ranges have been published.

HABITATS AND ACTIVITIES

During their parasitic phase, the larvae are found on arthropod hosts. When off the hosts, they are found in the soil as other life cycle stages. Trombidiid mites are common in soil, humus, moss and litter. Some species (e.g. *Dinothrombium* spp.) live in sandy soil or sands in semi-desert or desert areas. Their adults only become active on the sand surface after heavy rain (Newell and Tevis, 1960; Newell, 1979). Despite the fact that these mites forage for only a few hours each year, external gas exchange in *Dinothrombium magnificum* (Le Conte) is continuous, unlike the case in ticks and its locomotion energetics are typical of other small arthropods in spite of its unsegmented, flexible exoskeleton (Lighton and Duncan, 1995). *Allothrombium* adults are active on the soil surface and plants during the day, particularly in sunshine, but hide in the soil during the night and in winter (Robaux, 1974; Zhang and Xin, 1989a). *Trombidium* species spend most of their time in the soil and are only occasionally found on the surface. Their emergence to the surface depends on the amount of sunshine and, in some species, on rainfall as well (Robaux, 1974). The microtrombidiidae live mostly under the surface of soil, litter or humus.

MATING AND REPRODUCTION

Trombidiid mites are bisexual. The females must be inseminated before oviposition. Cytogenetic studies have shown that they are diploid; the chromosome number for *A. fuliginosum* males and females is $2n = 24$ (Sokolov, 1954).

Sex ratios in the Trombidiidae vary between species but males and females occur in more or less equal numbers in annual field samples (Robaux, 1974); the male : female ratio is 1 : 1 for *A. fuliginosum*, but varies from 1 : 0.75 for *Trombidium mediterraneum* (Berlese) to 1 : 1.75 for *Trombidium meyeri* (Krausse). Similar data were reported by Robaux (1974) for the Microtrombidiidae.

Sperm transfer is indirect (André, 1953; Moss, 1960; Robaux, 1974; Witte, 1991). Complex mating behaviours have been described for a few species and were reviewed by Robaux (1974) and Witte (1991). The males and females of trombidiid mites perform encircling dances, during which pair-dance signalling threads are deposited. In *Allothrombium*, the male and female tap the idiosomal dorsum of each other using their first legs during the dance. The male then deposits spermatophores on the substrate and the female comes along to capture them (Moss, 1960; Robaux, 1974).

The eggs are laid in masses in soil, humus, litter or sand. The females of *A. ovatum* prefer to lay eggs in wet soil with a water content of 12.5% (Zhang *et al.*, 1996). At 7–30°C, the oviposition period of *A. fuliginosum* lasts for approximately 1 month, but at 31°C it lasts for less than 2 weeks and fewer eggs are laid (Robaux, 1974). The oviposition period is shorter and fecundity lower when females are kept in the dark rather than in the light and when fasting rather than when feeding (Robaux, 1974).

Fecundity in the Trombidiidae varies between species and ranges from 60 eggs in *Podothrombium* (Robaux, 1974) to 100 000 eggs in *Dinothrombium tinctorium* (L.) (Newell, 1979). *Podothrombium* females lay fewer eggs (60–100) than those of *Allothrombium* (300–1250), the Trombidiinae (150–2000) and *Eutrombidium* (900–2500) (Robaux, 1974), but their egg size (265–365 µm) is larger than that of the other groups (140–220 µm). The fecundity of the Microtrombidiidae varies from 10 to 300 eggs (Robaux, 1974). Not surprisingly, fecundity is positively related to the size of the adult female (Robaux, 1974).

DISPERSAL AND DISTRIBUTION

When first hatched, the larvae of the Trombidiidae do not disperse immediately but congregate for a few days (and sometimes even weeks) near where the eggs were laid (Robaux, 1974). The larvae of *A. pulvinum* and *A. ovatum* congregate for 1 day before dispersing (Zhang and Xin, 1989ab; Dong *et al.*, 1996).

Like water mite larvae, larval trombidiid mites disperse via their hosts (Zhang, 1992a). Zhang and Li (1996) studied the dispersal of *A. ovatum* larvae into cotton using field experiments. The cotton plants in open plots had over ten times as many mites as plants in plots enclosed with plastic film to exclude migrating aphids. The larvae of *A. ovatum* emerge in spring when *Aphis gossypii* Glover alatae migrate to cotton. The factors affecting the migration of aphids also affect the dispersal of the mites. Zhang and Li (1996) showed that plastic film covers reflected light and reduced the migration of aphids into these fields. As a consequence, yellow sticky boards 100 cm above ground level caught fewer mites and aphids in film-covered fields than in open fields.

The dispersion of *A. pulvinum* larvae is highly aggregated on hosts (*A. gossypii*) and the pattern of distribution can be described well by Taylor's power law and negative binomial distribution (Zhang *et al.*, 1993). The distribution of *Allothrombium* larvae on cotton plants is also strongly aggregated and the degree of aggregation is similar to or slightly less than that of the aphids (Dong and Wang, 1992; Dong *et al.*, 1992; Zhang *et al.*, 1993; Zhang and Chen, 1994). Using fuzzy clustering methods, Dong and Wang (1992) showed that the dispersion pattern of *A. ovatum* larvae was similar to that of *A. gossypii* alatae during the first 2 weeks but became similar to that of apterous aphids during later periods, presumably due to

the fact that larval mites first dispersed via alate aphids but later moved onto apterae.

The distribution of *A. pulvinum* adults was highly aggregated in a peach orchard and the pattern fitted the negative binomial distribution (Zhang, 1992c). More mites were found on the ridges than in the furrow in the orchard.

ABUNDANCE AND DYNAMICS OF POPULATIONS

Because trombidiids spend most of their time in the soil, reported observations on their abundance and dynamics are in part reflections of their activities. In France, Robaux (1974) reported on extensive collections of various species and found that populations of *Allothrombium* peaked in March–April, with captures of nearly 200 individuals per month, whereas those of the Trombidiinae and Microtrombidiinae peaked in April and May, with captures of 30–80 individuals per month. Zhang (1992c) systematically sampled *A. pulvinum* adults in the field and estimated a mean density of six adults per square metre. *Allothrombium pulvinum* accounted for 57% of all natural enemies in orchards in Xingjiang, China (Zhou *et al*., 1989): 263 (148–384) mites per square metre were found at depths of up to 3 cm in the soil in apple orchards and 540 (268–1068) mites per square metre were found in pear orchards on 19 March 1988. *Allothrombium pulvinum* was also the most abundant natural enemy of *A. gossypii* and accounted for a mean of 80% of the natural enemies in cotton fields (Chen *et al*., 1994). The abundance of *A. pulvinum* was low in flooded fields and increased with the number of years since the field had been rotated from flooded to dry conditions. The latter trend was also found in *A. ovatum* in Shanxi, China (Zhang *et al*., 1996). *Allothrombium pulvinum* was also more abundant in monoculture cotton fields than in cotton–wheat intercropped fields (Chen *et al*., 1994); presumably this was due to the fact that intercropping reduced the migration of the aphids which carry mites into cotton fields.

Larval density is better estimated as the number of mites per host rather than per unit area, because they are parasitic on hosts. Peterson *et al*. (1992) reported mean densities of 1.88–2.88 *Trombidium* larvae per beetle, *Cerotoma trifurcata* (Forster), in Iowa, USA. Feider (1956) reported a mite load of eight larvae per *Phyllotreta* beetle. Large hosts such as Lepidoptera may carry up to 15 *T. mediterraneum* per moth (Robaux, 1974). A single housefly, *Musca domestica* L., could be parasitized by as many as 41 larvae of a microtrombidiid mite which occurred thoughout the year in India, with the maximum infestation occurring in July–September and the minimum infestation in November–February (Mittal and Dhiman, 1989). A female grasshopper, *Dissosteria carolina* (L.), was reported to be parasitized by 175 larvae of *E. locustarum* (Severin 1944). Dong *et al*. (1996) reported on the seasonal dynamics of *A. ovatum* larvae on cotton aphids; the mite densities were higher on alate hosts than on apterous hosts during the first half of May and decreased from an initial ten per alate host to zero in early June.

HOST–PARASITE AND PREDATOR–PREY INTERACTIONS

Host–prey–mate location
Larvae move negatively geotactic but positively phototactic (Henking, 1882; Severin, 1944; Robaux 1974; Zhang, 1992d). As larvae hatch in the soil, these mechanisms guide them out of the soil and increase their chances of finding hosts on the soil surface and plants. Movement on plants or habitat surfaces seems more or less arbitrary, at least for *A. pulvinum* (Zhang, 1991b). It is unknown whether they use chemical cues to locate hosts. The larvae of *M. fasciatum* (Koch) have modified third legs and can jump a distance of 25 times their body length (André, 1945). Robaux (1974) observed similar jumps in *Campylothrombium barbarum* (Lucas). It is unknown whether they aim at and can land on a targeted host. Robaux (1974) hypothesized that jumping in these mites is an adaptation to catch fast-moving hosts; larvae with less mobile hosts (e.g. *Allothrombium* parasitic on aphids) lack modified setae on legs III and do not jump.

   It was suggested that some species of Trombidina may use sound for host location (Southcott (1986a) and references therein). For example, the larvae of *Trombella alpha* Southcott were more frequent on male crickets than on females; Southcott (1986a) suggested that they used the singing of male crickets for host location. The tarsus III of this species has a dorsal row of unusual long setae, each with a pre-formed fracture line near the base. It was hypothesized that these setae have an auditory function (Southcott, 1986a).

   The searching behaviours of adults are virtually unknown. Recent studies on water mites showed that they can detect prey and sexual partners using chemical cues (Baker, 1996). Trombidiid mites, like their aquatic counterparts, have sensillae on the palpal tarsi. Whether they can locate prey by chemoreception is unknown. Robaux (1974) showed that males of *Paratrombium megalochirum* (Berlese) can follow the trail of females by detecting the pheromones associated with it. In *Allothrombium* and *Trombidium*, in the absence of females males deposit signal threads in a circular area for the females to detect and follow (Witte, 1991).

Host–prey selection
The larvae of trombidiids in general have broad host ranges, but some species are found on a particular group of hosts (Table 3). Less is known about host preference by trombidiid larvae than about host location. The only experimental work is that of Zhang (1996), who studied the selection of different aphid species by *A. pulvinum* in the laboratory; he showed a preference of the mites for certain aphid species.

   For a particular host species, the larvae of *A. pulvinum* prefer pea aphids that are already parasitized to unparasitized ones (Zhang, 1991b). Zhang (1991b) hypothesized that parasitized aphids might be weaker and, thus, more vulnerable to further attacks and that the interaction between mite and host might produce a chemical

(i.e. kairomone) which attracts other mites. Zhang (1991b, 1996) showed that this kind of preference may depend on the host species and size.

The larvae of *Allothrombium* generally prefer large to small aphids (Zhang, 1991b, 1996) and this could have adaptive significance by reducing the risk of having to change hosts during the larval stage. The alatae of *A. gossypii* are preferred by *A. ovatum* larvae in early spring (Dong and Wang, 1995), presumably because they use them as a means of transportation into cotton fields (Zhang and Li, 1996). Differential attack of two sexes of *C. trifurcata* (Forster) by *Trombidium* larvae was reported by Peterson *et al.* (1992).

When on aphids, trombidiid larvae prefer certain parts of the body. The larvae of *A. pulvinum* prefer the thorax of aphid hosts (Zhang, 1991b); the head is small and, thus, rarely attacked, while the abdomen is large but aphids can defend themselves by using their legs to push intruding mites off. The larvae of *Trombidium* were found under the elytra of *C. trifurcata* and were commoner on the first two abdominal segments (Peterson *et al.*, 1992). In the related Eutrombidiidae, larvae of *E. locustarum* were mainly found on the wings of grasshoppers (Severin, 1944). For *Eutrombidium australiense* Southcott, the main sites of attachment on 'short-horned' grasshoppers are at the insertion of leg III, followed by the prosternum, between them accounting for 80% of cases (Key, 1994).

Feeding on the host

Once an attachment site on the host is chosen, a larval mite inserts its chelicerae into the host and the mouth sucks fluid through the wound. Eutrombidiid and microtrombidiid larvae have oral rings which encircle the wound and anchor them on the hosts. Feeding tubes (stylostomes) were observed in hosts parasitized by *Allothrombium* and *Trombidium* larvae (Feider, 1956; Robaux, 1974). The nature of the stylostome is unknown, but it was hypothesized that it derives from the salivary secretion of the mites (Feider, 1956).

Rate of parasitism and effects of larvae on hosts

Rates of parasitism of hosts by trombidiid larvae have been reported for only a few species. The rate of parasitism of *C. trifurcata* by *Trombidium* larvae was 0.79–4.88% (Peterson *et al.*, 1992). In France, the larvae of *Allothrombium monspessulanum* Robaux & Aeschlimann parasitized up to 10% of lucerne aphids (Aeschlimann and Vitou, 1986). In China, the rates of parasitism of *A. gossypii* by *A. ovatum* larvae were much higher and could be as high as 100% (Dong *et al.*, 1996). In India, the larvae of an *Allothrombium* species parasitized 90% of the buzzing grasshoppers (*Sphingonotus savignyi* Sauss) in pitfall samples (Chandra, 1984). In Germany, the rate of parasitism of cereal leaf beetles (*Oulema* spp.) by the eutrombidiid mite, *Eutrombidium trigonum* (Hermann), was 0–3% (Heyer, 1992). In India, the rate of parasitism of green bottle flies, *Lucilia caesar* L., by larvae of a microtrombidiid species rose from 19.2% in May to 42.7% in August and fell back to 28.9% in October (Dhiman *et al.*, 1990).

Host survival and reproduction are affected by parasitism of trombidiid larvae and the degree of effect depends on the relative size of the parasite and host and the number of mites per host (mite load). The larvae of *A. pulvinum* can kill their host *Aphis fabae* Scopoli in 3 days when the mite load is two or more (Zhang and Xin, 1989a). They decrease the reproductive rate of adult aphids and arrest the development of nymphs when the mite load is one. For larger hosts such as the pea aphid, *Acyrthosiphon pisum* (Harris), five larvae of *A. pulvinum* kill only 50% of adult hosts in 4 days (Zhang, 1991b). In India, one to three larvae of a micro-trombidiid species had no marked influence on the host fly, but four or more mites per host influenced its body function and 10–16 mites weakened it so much that it was unable to take flight quickly (Dhiman *et al*., 1990). The larvae of *E. locustarum* apparently had little effect on the health of grasshopper hosts (Severin, 1944).

Prey consumption by deutonymphs and adults
Data on the prey consumption of trombidiid adults or deutonymphs are few. Each deutonymph and adult of *A. monspessulanum* can consume several aphids per day (Aeschlimann and Vitou, 1986) and an adult mite can consume 20 eggs per day of the curculionid beetle *Sitona discodeus* Gyllenhal. A deutonymph of *A. pulvinum* can consume a mean of 36 immature spider mites per day (Chen and Zhang, 1991). Deutonymphs of *A. pulvinum* showed a typical type II functional response and their predation capacity was higher than that of the phytoseiid mite *Phytoseiulus persimilis* Athias-Henriot (Zhang, 1992b). Zhang and Xin (1989b) observed that two hungry *A. pulvinum* adults could consume five aphids in 2 h, but they do not continue to feed when satiated. Zhou *et al*. (1989) found that *A. pulvinum* adults consumed seven newly hatched aphids per day. *Allothrombium pulvinum* nymphs and adults are predators of the poplar lace bug, *Hegesidemus habrus* Drake, in a poplar forest in Shandong, China (Zhao, 1992). Each nymph consumed 49–54 prey (mostly first and second instars) per day and each adult consumed 85 prey (mostly third and fourth instar nymphs) per day. Dong *et al*., (1996) found that the daily consumption rates of adult *A. ovatum* on various aphids were between 0.05 and 0.43 aphids. They also observed that these adults feed on alternate days.

NATURAL ENEMIES

Trombidiid mites may have few natural enemies. The adults cannibalize each other (e.g. Robaux, 1974) and are occasionally parasitized by larval trombidiids (Table 3). Sferra (1986) reported parasitism of a *Podothrombium* adult by a larva of the acrocerid fly *Pterodontia flavipes* Gray. Few entomophaga take trombidiids as prey, presumably because of the distastefulness of their body contents and their warning colour. Adults of a *Dinothrombium* species were offered as prey to many species of entomophagous animals but were rejected by most and spat out by those few that took them (J.O. Schmidt, personal communication).

ROLES IN BIOLOGICAL CONTROL

Although it has been suggested for a long time that trombidiid mites have potential in biocontrol (Howard, 1918; Welbourn, 1983), the actual demonstration of their effectiveness and use in pest control is recent. Most of the examples involve *Allothrombium* only.

Allothrombium larvae are important early-season natural enemies of *A. gossypii* in cotton fields (Anonymous, 1983; Dong, 1991; Chen *et al*., 1994). *Allothrombium pulvinum* has been shown to be a major limiting factor of *A. gossypii* population growth early in the growing season, when other natural enemies of *A. gossypii* are still rare in cotton fields (Chen *et al*., 1994). Other natural enemies, such as spiders and coccinellids, increase in abundance later in the season and complement *A. pulvinum* in providing successful control of early-season *A. gossypii* populations in unsprayed fields. Recent studies on another species, *A. ovatum*, in China showed similar results (Dong, 1991; Dong and Wang, 1992, 1993, 1995; Dong *et al*., 1996; Zhang and Li, 1996). However, in Germany, Bode (1980) noted that the incidence of *A. fuliginosum* larvae was low on *Metopolophium dirhodum* (Walk.) and its effects on the host were not strong.

Allothrombium deutonymphs are also important predators of spider mites (Zhang, 1992b) and can provide seasonal and/or partial control of summer populations of *Tetranychus urticae* Koch in cotton fields in Jiangsu, China (Chen and Zhang, 1991). In Xingjiang, China, *A. pulvinum* adults are predators of the spring cankerworm, *Paleacrita vernata* (Peck), in orchards and can significantly reduce prey numbers (Zhou *et al*., 1989). In Belgrade, the former Yugoslavia, *Allothrombium* adults attack 21–43% of the eggs of the cabbage moth, *Mamestra brassicae* L., in cabbage fields (Injac and Krnjajic, 1990). In northern Italy, *A. fuliginosum* adults and two insect predators attack the leafhopper *Rhytidodus decimusquartus* (Schrnk.) on poplars (Arzone *et al*., 1988). Their activity is occasional and is effective mainly in September–October; they can empty 5% of the overwintering eggs of the leafhopper. *Allothrombium fuliginosum* is also one of the natural enemies attacking the maize pest *Zyginidia pullula* (Boh.) in northern Italy (Vidano and Arzone, 1988). In Shandong, China, *A. pulvinum* adults are predators of the poplar lace bug, *H. habrus*, in a poplar forest and can reduce prey numbers by 70% in 20 days at predator–prey ratios of 1 : 40–50 (Zhao, 1992). Thus, *Allothrombium* may provide a variety of roles in pest control.

EPILOGUE

Due to limited space, this review has been restricted to the Trombidiidae, with only brief references to other trombidioid mites. Only recent information that is of most interest to the author is summarized. Hopefully this review will help to stimulate much-needed further research on the biology of these fascinating mites.

Progress on the systematics of this group is essential for any further studies on its biology (Eickwort, 1983; Welbourn, 1983). The heteromorphic larval and post-larval stages and complex life cycle offer challenging systems for studying the evolution of complex life histories (Wilbur, 1980; Istock, 1983). The applied importance of these mites is not restricted to use in biological control: extracts of the red velvet mite (*D. tinctorium*) have long been used for the treatment of male infertility in traditional eastern medicine and recently have been studied for chemical prospecting (Subhan *et al*., 1995).

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