

Whitefly Parasitoids: Distribution, Life History, Bionomics, and Utilization

Tong-Xian Liu,^{1,*} Philip A. Stansly,² and Dan Gerling³

¹State Key Laboratory of Crop Stress Biology for Arid Areas, Northwest A&F University, Yangling, Shaanxi 712100, China; email: txliu@nwsuaf.edu.cn

²Southwest Florida Research and Education Center, University of Florida, IFAS, Immokalee, Florida; email: pstansly@ufl.edu

³Department of Zoology, Tel Aviv University, Ramat Aviv, Israel 69978; email: dange@tauex.tau.ac.il

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*Corresponding author

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Abstract

Whiteflies are small hemipterans numbering more than 1,550 described species, of which about 50 are agricultural pests. Adults are free-living, whereas late first to fourth instars are sessile on the plant. All known species of whitefly parasitoids belong to Hymenoptera; two genera, *Encarsia* and *Eretmocerus*, occur worldwide, and others are mostly specific to different continents. All parasitoid eggs are laid in—or in *Eretmocerus*, under—the host. They develop within whitefly nymphs and emerge from the fourth instar, and in *Cales*, from either the third or fourth instar. Parasitized hosts are recognized by conspecifics, but super- and hyperparasitism occur. Dispersal flights are influenced by gender and mating status, but no long-range attraction to whitefly presence on leaves is known. Studies on *En. formosa* have laid the foundation for behavioral studies and biological control in general. We review past and ongoing studies of whitefly parasitoids worldwide, updating available information on species diversity, biology, behavior, tritrophic interactions, and utilization in pest management.

Monophagy: a type of specialized feeding habit in animals that only consume one kind of food

Polyphagy: a type of feeding habit in animals that consume many kinds of food

INTRODUCTION

Whiteflies (Hemiptera: Aleyrodidae) comprise about 1,550 species and occur worldwide, mostly in warm climates (37). The family comprises three subfamilies, Udamoselinae, Aleyrodinae and Aleurodicinae, with Aleyrodinae being smaller and restricted mainly to the Neotropics (90). To date, more than 500 species of parasitoids in 23 genera within eight families have been described for whiteflies (37, 102). Both basic and applied research on whitefly parasitoids have increased, due in part to the status of their hosts as major pests. We review research covering taxonomic status, distribution and host ranges, developmental history, reproduction, fecundity, dispersal, courtship, and mating of parasitoids. We also address current efforts to utilize whitefly parasitoids for biological control as a component of integrated pest management.

TAXONOMY, DISTRIBUTION, AND HOST RANGE

The six hymenopteran families of whitefly parasitoids are Aphelinidae, Encyrtidae, Eulophidae, Pteromalidae, and Signiphoridae, within the Chalcidoidea; and Platygasteridae, in the superfamily Platygastroidea (37, 102). We still lack biological information, including host identification, for several encyrtid, eulophid, and pteromalid species (56, 79, 102). Moreover, recent molecular studies have produced additional specific identities for which no host relationships or biological information is available (e.g., *Cales*; 95).

Reported host relationships range from monophagy, e.g., *Zarhopaloides anaxenor* (6), to polyphagy, e.g., *Encarsia formosa* (109). Co-evolution of host-parasitoid relationships is evident in some cases, such as the eulophid genera *Aleuroctonus*, *Dasyomphale*, and *Entedononecremnus*, which originate with their aleurodicine hosts in Central and South America (56). Nevertheless, the potential host range of a given parasitoid species may not be evident, as demonstrated by new host-parasitoid associations that often result from local species attacking introduced whiteflies (5, 7).

Females of most species are primary whitefly parasitoids except hyperparasitic species in the genera *Ablerus* and *Signiphora*. However, most species of *Encarsia* are heteronomous, with males and females attacking and developing in different hosts. Females generally develop as primary parasitoids, whereas males develop hyperparasitically on conspecific or heterospecific whitefly parasitoid larvae or pupae. In an unusual form of heteronomy, females of *En. porteri* develop as primary parasitoids of whiteflies, whereas males are obligate parasitoids of lepidopteran eggs (66). The nonheteronomous exceptions include *En. inaron* and *En. longicornis*, where both sexes develop as primary whitefly parasitoids. Additionally, *En. formosa* is uniparental, males being eliminated by symbiotic *Wolbachia* bacteria (64, 67, 147).

Although the distribution of some parasitoid genera has been widened during worldwide biological control efforts (5, 50, 52), original geographic distributions can be categorized as cosmopolitan (*Encarsia* and *Eretmocerus*) or geographically restricted. The latter category includes *Pomphale* and *Oomyzus* (Eulophidae) (India). The genera *Dirphys* (Aphelinidae); *Metaphycus* (Encyrtidae); *Aleuroctonus*, *Dasyomphale*, *Entedononecremnus*, and *Neopomphale* (Eulophidae); *Idioporus* (Pteromalidae); and *Signiphora* (Signiphoridae) are mostly in Central and South America (148). *Zarhopaloides* (Encyrtidae) and *Aphobetus*, and *Moranila* (Pteromalidae) are Australian; many *Cales* species originate in the Neotropics, with one known from Australia; and *Baeoentedon* (Eulophidae) and *Myiocnema comperei* (Eriaporidae) can be found in the Orient and Australia (37, 102).

OVIPOSITION AND DEVELOPMENTAL HISTORY

Developmental studies have been conducted on species of *Amitus* (38, 71), *Cales* (80, 85), *Encarsia* (2, 12, 32, 43, 44), *Eretmocerus* (44, 46), and *Euderomphale* (91). It is assumed that all whitefly species described from whiteflies develop within nymphs.

Oviposition

Eretmocerus species lay eggs between the whitefly nymph and the leaf surface; all others insert their eggs directly into the whitefly nymph. Often, all four nymphal host stages are acceptable for oviposition. Preferences for and suitability of different host instars vary among genera and species. Proovigenic *Amitus* species prefer first and second instars (34, 35, 71), whereas those *Encarsia* species that have been studied [*En. luteola* as *En. deserti* (50), *En. lutea* (46), *En. pergandiella* (84), *En. bimaculata* (111), *En. formosa* (63), and *En. sophia* (139)] prefer third and early fourth instars. Most studies on *Eretmocerus* indicate preference for second and third nymphal instars (22, 42, 70, 111). However, Yang & Wan (140) reported that *Er. hayati* prefers first instar nymphs for oviposition. The first host instar is avoided by *Cales noacki* (85), whereas the fourth instar is only utilized in its early stages, prior to pharate adult formation (42). In *En. inaron*, the lack of successful development in the fourth instar was attributed to incapability to arrest the development of hosts parasitized as fourth instars, resulting in a developmental race that ends in either a win for the parasitoid or a loss for both parasitoid and host (15).

Delayed development, presumably to allow for growth and maturation of the host, induces costs such as higher mortality and slower population growth (84, 89). These costs may be offset in the proovigenic species by the abundance of first and second instar hosts coupled with the demographic advantage conferred by early reproduction. In addition, ovicide is known in at least one species (*En. formosa*), which may first pierce competing eggs within the host before laying its own (99, 105).

Host Marking

Host marking is employed by many species, but the chemical nature of the marking pheromone has been best described in *Er. mundus*: The ovipositing female deposits methyl-branched cuticular hydrocarbons, C31 and C33 dimethylalkanes, on *Bemisia tabaci* nymphs (17). The mark is relatively nonvolatile and enables conspecific females to discriminate parasitized from unparasitized hosts. *Er. eremicus* also avoided these marked hosts, although *Er. mundus* did not respect hosts marked by *Er. eremicus* (3).

Immature Stages

Immature stages have been described for some species within only five genera. Eggs of *Amitus* are club shaped (71), those of *Cales*, *Encarsia*, and *Euderomphale* are hymenopteriform (32, 80, 91), and those of *Eretmocerus* are pear shaped (26). Egg provisioning may vary within the same genus, as observed for *En. formosa*, whose eggs have more yolk than those of *En. pergandiella*, enabling earlier hatching when parasitizing early whitefly instars (32).

First instar larvae of parasitoids tend to be elongate and mobile, whereas second and third instars are sessile and lack the elongate shape. For example, first instar *Amitus fuscipennis* are caudate, elongate, and agile, characteristics lost in later instars (92). Larvae of *C. noacki* have a hymenopteriform first instar that becomes globular in the second instar and is devoid of mandibles in the third instar (80). Larvae of female *Encarsia* are elongate and caudate in the first instar with stouter, more prominent tails than males (43), whereas second and third instars of both sexes are hymenopteriform. Larvae of *En. porteri* are sexually dimorphic and heteronomous, with the females being primary parasitoids of whiteflies and having the typical form of other *Encarsia* larvae, whereas unfertilized eggs are laid in lepidopteran eggs and the resulting early instar male larvae bear long spines along the venter and hornlike projections on the head capsule (66). First instar *Eretmocerus* spp. are pear shaped, becoming globular after penetrating the host.

Proovigenic species:

parasitoids that reach the adult stage with a complete complement of ripe eggs, which they deposit within a short period; no additional eggs are produced during the parasitoid's life

Bacteriome:

a specialized organ in some insects that hosts endosymbiotic bacteria (formerly termed mycetome)

The globular shape is retained by second and third instars with an indentation in the oral area (44, 51).

The developmental cycle of *Euderomphale chelidonii* includes a hymenopteriform egg and early first instar larva. Second and third instar larvae are globular and located in the center of the whitefly nymph (91). All aforementioned genera have apneustic larvae with no open spiracles except for the last (third) instar. Meconial pellets are deposited inside the mummified fourth instar host by pupating *Encarsia* species (e.g., 43) but are distinctly absent in *Cales* and *Eretmocer* (44, 80, 137). No reports regarding meconia exist for other species.

Development and Fecundity

Developmental data are mainly available for whitefly species causing economic damage; e.g., *Aleurocanthus woglumi*, *B. tabaci*, and *Trialetrodes vaporariorum* (5, 34, 60, 134). These data are circumstance dependent and difficult to generalize or characterize across genera or groups because key parameters are influenced by temperature, host, and plant. The range of developmental parameters among *B. tabaci* parasitoids was illustrated by Arnó et al. (5), who provided references and representative data for *Amitus bennettii*, the six most-studied *Encarsia*, and the five most-studied *Eretmocer* species. It is noteworthy that application of jasmonic acid on leaves of Chinese broccoli (*Brassica oleracea* var. *alboglabra*) significantly hastened the development of *En. formosa* while the parasitism rate remained unaffected (81).

HOST-PARASITOID INTERACTIONS

Whitefly parasitoid larvae utilize mainly the fourth instar, except *C. noacki*, which may emerge from third or fourth instars (80, 85). Developmental time is minimal following oviposition in (*Encarsia*) or under (*Eretmocer*) third or early fourth instar hosts (32, 111).

The nervous system, gut, bacteriomes (mycetomes), and gonads remain intact throughout parasitoid development (12, 44). Blackburn et al. (12) observed *En. formosa* eggs in the ventral ganglia of *T. vaporariorum*, although M.S. Hunter (personal communication) located eggs in the host hemolymph, indicating weak or absent immune responses. *En. formosa* larvae molt from second to third and final instar only after their host (*T. vaporariorum*) has molted to its fourth instar, the timing of which appears unaffected by parasitization. The unique phenomenon of the parasitized host's melanization is also synchronized with, and apparently results from, this molt. It is noteworthy that no such melanization occurs in *B. tabaci* parasitized by *En. formosa*.

Plant-induced *Encarsia*-whitefly synchronization was observed in the *En. scapeata*-*Trialetrodes lauri* system, where the host plant, *Arbutus andrachne*, induced both diapause and development of whitefly and parasitoid. No diapause was induced when *En. scapeata* was reared on *B. tabaci* (45).

In contrast to *Encarsia* species, *Eretmocer* species lay their eggs under the host, in contact with the leaf surface. *Er. mundus* eggs hatch three days after oviposition at 25°C, although penetration of the host by the first instar larva occurs only after onset of the whitefly's last molt (41). The first instar larva then induces development of a cellular, ectodermal structure that engulfs it and later forms an internal capsule within which the larva resides until pupation. The capsule is most prominent during the second larval instar, when an acellular space separates the larva from the capsule wall (44, 47, 51). No direct contact occurs between the larva and surrounding host cells until the third instar. Moreover, first and second instar larvae are equipped with needle-like mandibles that are unable to grasp or chew. In contrast, the third instar larvae have sickle-shaped mandibles and reside within a partial, broken capsule allowing access to host tissues.

Examination of ecdysteroid levels showed that the prepenetration of *Er. mundus* larvae usually induced permanent developmental arrest in its fourth instar whitefly host, presumably by reducing whole-body host ecdysteroid titers (41). Therefore, unless there is a local peak in molting hormone titer in the area of penetration, induction of capsule formation is apparently not due to an increase in ecdysteroid titer. *Er. mundus* does not completely devour its host's tissues, in contrast with other whitefly parasitoids. As a possible consequence, there is no correlation between host and parasitoid sizes in this species (44).

PARASITOID-PARASITOID INTERACTIONS

Er. mundus is able to recognize hosts parasitized by its own species through antennation (39, 70), although superparasitism is still observed (e.g., 44–46). *En. lutea* and *En. luteola* (as *En. deserti*) also recognize previously parasitized hosts but still superparasitize occasionally (46, 50). Ardeh (3) attributed superparasitism by *Er. mundus* and *Er. eremicus* to inexperience, as did Enkegaard (36), for *En. formosa*. Competitive elimination of supernumerary first instar *Er. mundus* larvae at the penetration stage has been reported by Lo Verde & van Lenteren (86). However, most eliminations of supernumerary larvae probably occur at the second instar phase, given that several second instar larvae can readily be seen in superparasitized whiteflies but only one adult usually emerges. A rare case of two adults emerging from the same *B. tabaci* host was recorded (44). Examination of parasitoid behavior and distribution of ovipositor probing holes revealed that *En. formosa* failed to distinguish, on the basis of antennal examination alone, between a host actually parasitized and one merely examined with the ovipositor.

Multiparasitism, the occurrence of two or more parasitoid species in a host (121), has been observed and examined in *Encarsia* and *Eretmocerus* species, which apparently often did not recognize the other's presence (3, 46, 94). According to Moretti & Calvitti (94), *Er. mundus* usually emerges from hosts later parasitized by *En. formosa*. Examination of field material demonstrated that superparasitism and multiparasitism occur under natural conditions. In the *En. lutea*–*Er. mundus* system, the overall percentage of hosts with more than one parasitoid was 21%. In half of these, *Er. mundus* had oviposited under a host already parasitized by *En. lutea*, whereas in 30% of them *En. lutea* had oviposited in a host parasitized by *Er. mundus* (3).

DISPERSAL AND FORAGING BEHAVIOR

Variation Among Species

Flight chamber observations and indirect trapping, mark-release-recapture techniques, and DNA analysis have been used to measure flight and dispersal distances (8, 13, 21, 74). Dispersal capacities among whitefly parasitoids differ significantly. *Amitus hesperidum*, a parasitoid of the citrus blackfly (*Aleurocanthus woglumi*), dispersed up to 3.7 km after only three generations from the release point (117). *C. noacki*, a parasitoid of the woolly whitefly (*Aleurotrix floccosus*), moved 12 m per week in a citrus orchard in France and colonized an area of 80 km² within 18 months after release (103). Indirect field studies include the observation that *En. opulenta* dispersed for 1 km in citrus orchards from the release point within three generations (117). Yellow sticky card counts indicated that *En. inaron* adults spread at least 45 m after release in trees infested by the ash whitefly, *Siphoninus phillyreae* (107). *Er. mundus* is permanently established in cotton (*Gossypium* spp.) fields in the San Joaquin Valley in California as far as 80 km from releases made over 10 years earlier, indicating long-distance dispersal (106, 108).

Er. hayati, a parasitoid of *B. tabaci*, was sampled at three spatial scales, local (tens of meters), field (hundreds of meters), and landscape (kilometers), around a release point in Australia for management of *B. tabaci*. The parasitoid showed a pattern of stratified dispersal, moving further, faster, and by a different dispersal mechanism than that revealed using a single local-scale sampling pattern (74). *Er. hayati* spread over several kilometers in a single generation and continued laying eggs for more than two weeks. Flight was in the same direction as the wind, and could have taken place at any time during the day when the wind speed was less than 2 m/s (73).

Effect of Gender and Mating Status

Flight duration of *Er. eremicus* is influenced by gender and mating status. Most *Er. eremicus* females responded to plant cues (a 550-nm filtered light) whereas males tended to fly toward a skylight cue from a mercury-vapor lamp (13). Moreover, 87% of *Er. eremicus* caught on traps at 3–10 m from a release point were males (8). Locally, males dispersed in a manner consistent with a simple diffusion model whereas females engaged in wind-assisted flight soon after leaving release sites. Females in flight chambers flew approximately tenfold longer distances than males, and unmated females flew 2.9-fold longer distances than mated females (8). The apparently greater dispersal tendencies of females may reflect the combined effect of resource- and mate-searching behaviors (104).

Chemical Cues

During host searching, parasitoid females use chemical cues in addition to host physical features (3). Whitefly parasitoids homed in on volatile semiochemicals from their hosts or host plants (11, 54, 58, 128), but olfactory responses varied significantly among parasite species and populations. *En. pergandiella* and *Er. mundus* responded positively to odors emitted from *B. tabaci*-infested foliage, whereas populations of *En. formosa*, *Er. staufferi*, and *Er. tejanus* did not (58). *En. formosa* was not attracted to or arrested by odors emanating from clean plant leaves, leaves infested with hosts and covered with honeydew, or honeydew alone (113). Host-searching behavior was random with respect to host presence even after the insect landed on a plant (135). Nevertheless, short-range search behavior was influenced by nonvolatile contact-kairomones contained in the host-produced honeydew (113), and volatile blends from *T. vaporariorum*-infested bean plants elicited a host-locating response (11). Similarly, *En. formosa* was not attracted to *T. vaporariorum* on gerbera, although more parasitoids were arrested after 24 h on plants with hosts (128). Moreover, contact with hosts or host-produced honeydew increased time spent on a particular leaf (135), thus increasing probability of finding suitable hosts.

Effect of Light

About 90% of *Er. eremicus* take off in response to a skylight cue rather than a green light plant cue (13). In contrast, *En. formosa* females showed a significant response to green light transmitted through a tobacco leaf (113). The importance of ultraviolet (UV) light has been demonstrated by the observation that *En. formosa* adults prefer to disperse into compartments covered with films that allow passage of UV light (33). Approximately 2.5-fold more parasitoids were found under standard UV-transmitting plastic film compared with UV-blocking plastic film (33). However, parasitoids land on plants shortly after release, suggesting that they would search for whitefly hosts even in an environment where UV light is blocked. Nevertheless, *Er. mundus* had difficulty finding host plants in the absence of UV light (25).

FUNCTIONAL RESPONSES AND HOST HANDLING

Functional response has been estimated for *En. formosa*–*T. vaporariorum*, *En. formosa*–*Trialeurodes ricini*, and *Er. longipes*–*Aleurotuberculatus takahashi* (36, 40, 82, 119, 135). All exhibited a Holling type II relationship (62), regardless of host instar (36, 40, 82, 119, 135). Although functional response curves remained type II functional response over a range of 20–35°C, the incidence of parasitism of *A. takahashi* by *Er. longipes* reached a maximum at 25°C (82).

Host searching by *En. formosa* is random on leaves, and encounters depend on host numbers and size (40). Host-related behavior, such as probing, inspecting, egg laying, host drumming, preening, and feeding, can vary substantially in frequency and duration among different host stages and parasitoid species (4). Likewise, handling time is affected by temperature; e.g., *Er. longipes* handled *A. takahashi* at 35°C thrice as long as at 20°C (82). Oviposition lasts significantly longer on older, larger nymphs of *Encarsia* and *Eretmocer* (47, 83).

COURTSHIP AND MATING BEHAVIOR

Observations on *Amitus*, *Encarsia*, and *Eretmocer* species demonstrated the following courtship sequence: antennal contact, mounting, postmount antennation, copulation, dismount, remount, postcopulatory guarding, and final dismount. Duration and individual features vary among species (3, 85, 137, 139). Males react to volatile pheromones by walking toward conspecific virgin females and displaying an arrestment response, wing and antennal vibrations, and wing fanning. Males react to nonvolatile pheromones by spending more time on and around patches on leaves that had been previously exposed to virgin females (3, 66).

Populations of different *Eretmocer* species display differences in mating behavior, especially among geographically isolated populations (3). A relatively long antennation period by *Er. eremicus* males is followed by rubbing the midlegs against the anterior edge of the female thorax three times. *Er. mundus* males, in contrast, engage in only one short bout of antennation followed by a few seconds of standing still on the female's back. These differences lead to premating isolation through rejection of *Er. eremicus* males by *Er. mundus* females (3). Two-day-old virgin females exposed to whitefly hosts mated when contacting a male, whereas mated females were not responsive to males (3).

HOST AND HONEYDEW FEEDING

Host Feeding

Females of all genera but *Amitus* and *Cales* perform destructive host feeding in which parasitoids feed on host body fluids to provide essential nutrients not available from honeydew feeding (19, 134, 142–144). Host feeding varies with parasitoid species, host age or size, and mating status (144). In a mixed host instar population, parasitoids generally prefer feeding on older hosts compared to younger hosts (142). Mated *Er. melanoscutus* and *En. sophia* fed on more hosts than unmated females under a range of host densities (146). Only mated *En. sophia* females host-fed, and host feeding resulted in killing more hosts than did oviposition. Moreover, host feeding occurred more frequently on younger whitefly nymphs than on older ones (146). *En. formosa* feeds on all stages of *T. vaporariorum*, although more frequently on second and late fourth instars than on first and third instars (98). Six-hour starvation of *En. sophia* stimulated host feeding, but long starvation may weaken searching ability (143). *Encarsia* females host-feed by penetrating the host cuticle using their pointed ovipositor, whereas *Eretmocer* females host-feed by penetrating the host's vasiform orifice with their spatulate ovipositor (48). Parasitoid females spend from a few seconds up to

Autoparasitoids: the male of the parasitoid species develops as a hyperparasitoid (sometimes of the female of the same species), and the female develops as a primary parasitoid

several minutes preparing the host for feeding, which often continues longer than oviposition (144).

Honeydew Feeding

En. formosa with access to honeydew had greater egg loads, matured more eggs, and increased longevity compared to parasitoids without access to honeydew. Host feeding alone did not increase egg load, maturity volume, or longevity (18, 19). However, parasitoids allowed to host-feed with honeydew present laid more eggs per hour of foraging per host-feeding attempt than parasitoids that were prevented from host feeding, indicating the value of additional carbohydrates (20).

INTRAGUILD AND PLANT INTERACTIONS

Intraguild Predation

Few subjects have elicited as much discussion in the biological control literature as intraguild predation. Interest stems from the possibility that effectiveness of biological control may be compromised by predation or other forms of intraguild competition. Although one recent study concluded that intraguild predation usually does not disrupt biological control (69), many others reached the opposite conclusion (110). The whitefly literature is no exception, particularly in regard to effects of autoparasitism among *Encarsia* species.

Interspecific Competition Among Parasitoids

Modeling, examination of competitive mechanisms, and field cage experiments have been used to evaluate competitive interactions among parasitoids. For the cotton-*B. tabaci* system, the combination of a primary parasitoid (*Eretmocerus* sp.) and an obligate autoparasitic species provided the greatest whitefly suppression, whereas addition of a facultative autoparasitoid disrupted control (93). Also, coexistence of a primary parasitoid with an autoparasitoid resulted in a more stable system, although with greater host density than a single species alone (16). Studies on competition between *Er. eremicus* and *En. sophia* for *T. vaporariorum* showed that either could suppress the other through multiparasitism, whereas *En. sophia* did more host feeding than its competitor. Nevertheless, autoparasitism was probably the dominant factor favoring *En. sophia* (27). In a recent examination of individual effects, it was found that both *En. formosa* and *Er. melanoscutus* were more suited to and preferred as secondary hosts for *En. sophia* than was *En. sophia* itself, rendering *En. sophia* especially disruptive (145). Furthermore, the oviposition period was longer and more hosts were parasitized by *En. sophia* females from heterospecific hosts compared to conspecific hosts. The authors concluded that even though *En. sophia* would likely interfere with a primary parasitoid such as *En. formosa*, it was still a better control agent for *B. tabaci*.

Field cage experiments have in general not corroborated modeling results that indicate negative effects of autoparasitoids on host suppression. Hunter et al. (65) released *B. tabaci* and then parasitoids onto caged cotton plants. Treatments were *En. eremicus* alone, *En. sophia* alone, a 0.5:0.5 mix of both, and a control with neither. Whereas the autoparasitoid *En. sophia* reduced density of the primary parasitoid *Er. eremicus* (though not the reverse), host suppression was unaffected. All combinations of *Er. eremicus*, *En. pergandiella*, and *En. formosa* were compared in another field cage study of a cotton-*B. tabaci* system (14). Most competitive interactions did not reduce host population suppression, with only releases of *En. formosa* + *En. pergandiella* resulting in lower levels of host mortality than expected from individual species. Likewise, accidental introduction of the

facultative autoparasitoid *En. smithi* did not change the typical outcome of eventual dominance by the presumably obligate autoparasitoid *En. perplexa* (misidentified as *En. opulenta*) in competition with *A. hesperidum* for the host *A. woglumi* (129).

Predator-Parasitoid Interactions

Predators and parasitoids of whiteflies coexist in natural and agricultural ecosystems. Field life table studies on *B. tabaci* in different cropping systems around the world revealed variable contributions to immature mortality from parasitism that in many cases was secondary to predation (97). Considerable effort evaluating intraguild predation has centered on determining whether or not key predators favor or disfavor parasitized prey, and not surprisingly laboratory results are mixed. All stages of the coccinellid *Delphastus catalinae* fed less on hosts containing parasitoid pupae, although adults did not discriminate in choice tests (141). Young coccinellid larvae also avoided hosts containing parasitoid larvae. Follow-up mesocosm studies in the greenhouse showed fewest whiteflies in treatments including *D. catalinae*, with or without *En. sophia*, 54 days after release of natural enemies.

In Arizona, the three principal predators of *B. tabaci* in cotton, *Geocoris punctipes*, *Orius insidiosus*, and *Hippodamia convergens*, showed a significant preference for larval and pupal stage *Er. sp. nr. emiratus* over early unparasitized fourth instar nymphs (96). Nevertheless, *G. punctipes* and *O. insidiosus* were nondiscriminating when the choice was between parasitized or unparasitized late fourth instar nymphs (96). However, field life table data revealed little intraguild predation, with estimated negative effects on whitefly generational mortalities of less than 2% (96). *G. punctipes* showed no preference for *T. vaporariorum* parasitized by *Er. eremicus*. Furthermore, oviposition by *Er. eremicus* was greater on hosts previously exposed to the predator, indicating a behavioral trait that tended to compensate for intraguild predation (136). Species-specific polymerase chain reaction (PCR)-primers were used to detect DNA fragments of *B. tabaci* and *T. vaporariorum* and their parasitoids *Er. mundus* and *En. pergandiella* in the predators, *Macrolophus pygmaeus* and *Nesidiocoris tenuis* (Hemiptera: Miridae), in tomato greenhouses in Spain. Parasitoid DNA was found to be abundant in the mirids but did not correlate with parasitoid abundance. This was in contrast to whitefly DNA and whitefly abundance, which were correlated. Thus, intraguild predation did not seem to be destabilizing in this system (96).

Entomopathogen-Parasitoid Interactions

There is little evidence of incompatibility between entomopathogens and whitefly parasitoids used for control of *B. tabaci* (5). Hamdi et al. (55) evaluated the combined use of *En. formosa* and one of three mycoinsecticides, *Lecanicillium muscarium*, *Beauveria bassiana*, or *Isaria fumosorosea*, for control of *T. vaporariorum* under laboratory and greenhouse conditions. The best treatment against second instar nymphs was *En. formosa* + *L. muscarium*, whereas this treatment was not different from *En. formosa* alone against third instars. In greenhouse experiments on tomato (*Solanum lycopersicum*), only *B. bassiana* increased whitefly mortality over that caused by *En. formosa* alone. Thus, some entomopathogens may have an additive effect on parasitism, depending on conditions, whereas others may not.

Parasitoid-Plant Interactions

Parasitoids may be attracted by visual cues and whitefly-induced plant volatiles but are generally deterred by leaf pubescence (68). In contrast, contact with leaf hairs may deform the nymph's body

Table 1 Introduced parasitoid species that achieved successful classical biological control of whiteflies

Parasitoid species	Whitefly species	Crops	References
<i>Amitus hesperidum</i>	<i>Aleurocanthus woglumi</i>	Citrus	57, 120
<i>Amitus spiniferus</i>	<i>Aleurothrixus floccosus</i>	Citrus	30
<i>Cales noacki</i>	<i>Aleurothrixus floccosus</i> <i>Tetraleurodes perseae</i>	Citrus <i>Persea</i> (avocado)	31
<i>Cales rosei</i>	<i>Aleurothrixus floccosus</i>	Citrus	95
<i>Encarsia dispersa</i>	<i>Aleurodicus dispersus</i>	Various	78
<i>Encarsia guadeloupae</i>	<i>Aleurodicus dispersus</i>	Various	88
<i>Encarsia bairiensis</i>	<i>Aleurodicus dispersus</i>	Various	75
<i>Encarsia hispida</i>	<i>Bemisia tabaci</i>	Various	109
<i>Encarsia inaron</i>	<i>Aleyrodes proletella</i> <i>Siphoninus phillyrae</i>	Brassica (cabbage) Various	1, 49
<i>Encarsia laborensis</i>	<i>Dialeurodes citri</i>	Citrus	115, 118
<i>Encarsia noyesi</i>	<i>Aleurodicus pulvinatus</i> <i>Aleurodicus dugesii</i>	Cocos (coconut) Various	10, 72
<i>Encarsia perplexa</i>	<i>Aleurocanthus woglumi</i>	Citrus	57, 101
<i>Encarsia smithi</i>	<i>Aleurocanthus spiniferus</i>	Citrus	76
<i>Encarsia strenua</i>	<i>Singhiella citrifolii</i>	Citrus	9
<i>Encarsia tricolor</i>	<i>Aleyrodes proletella</i>	Brassica (cabbage)	116
<i>Entedononecremmus krauteri</i>	<i>Aleurodicus dugesii</i>	Various	148
<i>Eretmocerus cocois</i>	<i>Aleurotrachelus atratus</i>	Cocos (coconut)	23
<i>Eretmocerus debachi</i>	<i>Parabemisia myricae</i>	Citrus	114
<i>Eretmocerus furubashii</i>	<i>Parabemisia myricae</i>	Citrus	114
<i>Eretmocerus longipes</i>	<i>Aleutotuberculatus takabashi</i>	<i>Jasminum</i> (jasmine)	118
<i>Idioporus affinis</i>	<i>Aleurodicus dispersus</i>	Various	10

margin, facilitating insertion of the *Eretmocerus* female's spatulate ovipositor between the nymph and leaf.

BIOLOGICAL CONTROL

Classical Biological Control

Classical biological control of whiteflies was first documented with Clausen & Berry's (26) introduction of *Er. serius* to control *A. woglumi* in Cuba. Classical biological control efforts have continued mainly against tropical or subtropical pests on perennials (Table 1). Some involved a single introduction [e.g., *En. inaron* against *S. phillyrae* (49)], whereas others used successive parasitoid species according to climatic and host abundance conditions [e.g., establishment of *En. smithi*, *En. chyealis*, *En. perplexa*, and *A. hesperidum* against *A. woglumi* in Mexico (38)].

Augmentation

Most augmentative biological control of whiteflies occurs in greenhouses, primarily in vegetable crops and against the two most polyphagous species, *T. vaporariorum* and *B. tabaci*. Greenhouses where the climate is controlled and pest influx can sometimes be limited are a conducive

Table 2 Parasitoids used in attempts at biological control of whiteflies leading to partial control or requiring continuous introduction

Parasitoid species	Whitefly species	References
<i>Encarsia formosa</i>	<i>Bemisia tabaci</i> <i>Trialeurodes vaporariorum</i>	60, 122, 123
<i>Encarsia hispida</i>	<i>Bemisia tabaci</i>	109
<i>Encarsia sophia</i>	<i>Trialeurodes vaporariorum</i> <i>Bemisia tabaci</i>	138, 146
<i>Eretmoceris eremicus</i>	<i>Bemisia tabaci</i> <i>Trialeurodes vaporariorum</i>	124, 127
<i>Eretmoceris bayati</i>	<i>Bemisia tabaci</i>	52
<i>Eretmoceris melanoscutus</i>	<i>Bemisia tabaci</i>	52
<i>Eretmoceris rui</i>	<i>Bemisia tabaci</i>	100
<i>Encarsia lutea</i>	<i>Bemisia tabaci</i>	109
<i>Amitus bennetti</i>	<i>Bemisia tabaci</i>	35, 71
<i>Encarsia bimaculata</i>	<i>Bemisia tabaci</i>	100
<i>Eretmoceris emiratus</i>	<i>Bemisia tabaci</i>	52
<i>Eretmoceris mundus</i>	<i>Bemisia tabaci</i>	124, 127

environment for biological control. At least 11 parasitoid species to date have been used for augmentative control of these two pest species (Table 2).

***Trialeurodes vaporariorum*.** Modern augmentative biological control could well be considered as originating with mass production and release of *En. formosa* for control of greenhouse whitefly (133). *En. formosa* is reported to attack at least 15 species in 8 whitefly genera (109) but is used mainly for control of *T. vaporariorum* followed by control of *B. tabaci*. Worldwide use of *En. formosa* as biological control for this pest in greenhouses was already estimated at about 5,000 ha in 1993 (133). Although *En. formosa* will attack *B. tabaci* (36), it is less effective against this host than some *Eretmoceris* spp. (44, 45, 48, 51). This may partly be due to temperature sensitivity of *En. formosa*, which is disadvantaged above 20°C (112).

***Bemisia tabaci*.** At least 115 parasitoid species of *B. tabaci* have been reported, but only 3 species have been widely used for augmentative biological control (126). The more proovigenic *Eretmoceris* spp. have higher reproductive rates than *En. formosa* (5, 112) and are also able to locate patches of *B. tabaci* more quickly (61). Therefore, interest has turned to *Eretmoceris*, in particular *Er. eremicus* and *Er. mundus* for control of *B. tabaci* (124, 125, 127).

Er. eremicus attacks both *B. tabaci* and *T. vaporariorum* with apparently equal facility (52, 53, 122). It is thus especially useful for controlling mixed infestations of the two whiteflies. It has been used to control pure infestations of *B. tabaci*, albeit with limited success (130). *Er. mundus* dominated in greenhouses in Spain where it and *Er. eremicus* were both released (124, 125, 127). Although immigration from outside the greenhouse partly explained this dominance, behavioral traits such as willingness to parasitize hosts parasitized by the other species (3, 4) may have assisted *Er. mundus* in competition with *Er. eremicus*. Similarly, introduced Old World species of *Eretmoceris* gained over native *Eretmoceris* spp. following invasion of exotic Old World *Bemisia* spp. in the southern United States and Australia (22, 28).

Successful management of *B. tabaci* using *Er. mundus* was demonstrated in large-scale commercial trials in protected pepper production facilities in Spain (124, 127). Control in tomato

was shown to be possible, although higher release rates were required to obtain the same level of control as in pepper (125).

Augmentation of parasitoids is used to control field and vegetable crop pests outdoors, although generally with less success than in greenhouses. *En. formosa* is used commercially worldwide to control *T. vaporariorum* in greenhouses but often does not control the same pest sufficiently outdoors (60). Moreover, *B. tabaci* is still considered a severe pest both in greenhouses and outdoors, although successful control with parasitoids was achieved in several cases (28). Correct matching of *B. tabaci* sibling species with the corresponding *Eretmocerus* species, as determined by molecular methods, may be the key to success (29).

Mass Rearing and Quality Control

Rearing of whitefly parasitoids requires a tritrophic system of plant, host, and wasp. A scheme for mass rearing *En. formosa* on *T. vaporariorum* using tobacco has been provided (132). Whitefly adults are released four to eight weeks after sowing the plants, and adult wasps are released two to three weeks later. Black pupae are brushed from the leaves after an additional one or two weeks, with the aid of recognition software, counted volumetrically, and glued to cards for shipment. Three generations of parasitoids can be reared on the same plant, in part due to vertical stratification of *T. vaporariorum*. The same system can be used for *Er. eremicus*, although the pupae are not black and therefore are less easily recognized. However, mass rearing of *Er. mundus* using *B. tabaci* as a host encountered a fatal obstacle when sterility of unknown etiology affecting both males and females spread throughout the industry (24). No known pathogens were identified, with the possible exception of *Rickettsia* spp., whose proliferation in *B. tabaci* is induced by *Er. mundus* (87).

Poor vigor or low numbers of natural enemies can lead to control failure and economic damage to crops. Viability, vigor, and fecundity can be compromised in storage and/or transport (78), and sex ratio, life span, fecundity, adult size, parasitism rate, and flight ability are also important (132).

Mass Release Rates and Methods

Both inundative and seasonal inoculative release methods have been utilized to control greenhouse whiteflies with *En. formosa* (133). For the former, *En. formosa* is released weekly as a biopesticide over a limited season, whereas for the latter, early-season releases are intended to control the pest directly but also to initiate a stable population of the parasitoid over a longer-term crop. Nevertheless, frequent inundative release may be necessary for satisfactory control on plants especially favorable to the whitefly, like cucumber and eggplant. Furthermore, parasitoid searching efficiency on cucumber is impaired by large leaf hairs, an encumbrance that can be somewhat remedied using less-hirsute cultivars (131). Hoddle et al. (59, 61) achieved better control of *B. tabaci* on poinsettia with a low inundative release rate of *En. formosa* (one compared to three wasps/plant/week). A similar study and similar results were obtained with *Er. eremicus*, although the outcome here was attributed to higher levels of parasitoid reproduction following low-rate releases (61).

Banker plants provide another method for introducing and maintaining parasitoid populations in the greenhouse. Papaya (*Carica papaya*) infested with *Trialeurodes variabilis* serving as a source of *En. sophia* dispersed at least 14.5 m to tomato (*Solanum lycopersicon*) and green bean (*Phaseolus vulgaris*) plants infested with *B. tabaci*, as well as to papaya control plants infested with *T. variabilis* (138). Parasitism rates in the two whitefly hosts on their respective plants were similar

(29–47%), whereas choice and no-choice tests confirmed preference of *T. variabilis* for papaya and nonsuitability of tomato, green bean, and cabbage (*Brassica oleracea*) (138).

Future of Whitefly Biological Control

Control of whiteflies with parasitoids on perennials has been a landmark in biological control and will probably continue to be greatly successful (9, 10, 23, 26, 30, 38, 76, 88). On annuals, whereas control of *T. vaporariorum* with *En. formosa* in greenhouses has generally been satisfactory, *B. tabaci* has been more problematic. The loss of *Er. mundus* was a setback partially averted by availability of *Er. eremicus*. However, Old World parasitoid species attacking *B. tabaci* tend to be more specialized and could provide better control (22), possibly without succumbing to contagious sterility.

Inoculation and conservation biological control, based primarily on parasitoids, have always been the foundation of whitefly management in perennial crops and ornamentals. Annual crops present a greater challenge, although biological control is becoming a cost-effective standard for greenhouse vegetable production, especially in Europe but also in Canada, the United States, and elsewhere. This is in response to increasing public sentiment against pesticides, which in turn is driving development of improved pest exclusion techniques, virus-resistant cultivars, more and cheaper natural enemy options, and better quality control. There remains a vast potential area of expansion in augmentative biological control of whiteflies in open-field crops. Parasitoids will always have their place in biological control, hopefully assisted in the future by a wider diversity of species, effective banker and/or refuge crops, and other technologies yet to be developed.

SUMMARY POINTS

1. Some 23 genera of whitefly parasitoids are known, all hymenopterans; only a minority have been studied. All but 2 genera include primary parasitoids; most *Encarsia* species have primary females and secondary males. All females are endoparasitoids of nymphs except for *Eretmocerus* spp., which lay eggs under the host. All but *C. noacki* emerge from fourth instar hosts only.
2. Parasitoid development is synchronized with host molting and developmental cycles. Both super- and hyperparasitism are observed in spite of intraspecific recognition.
3. Most parasitoids are weak flyers; flight is influenced by mating status and the chemical and physical features of the agroecosystems. Most parasitoid species exhibit a Holling type II functional response. The females of all genera but *Amitus* and *Cales* host-feed.
4. Field and field cage experiments do not demonstrate disruption of control through intraguild predation and parasitism, although autoparasitism may have some negative effects.
5. Parasitoids are important agents of biological control of whiteflies. Control of *T. vaporariorum* with *En. formosa* on annuals is economically successful in greenhouses, whereas control of *B. tabaci* with parasitoids is often insufficient. Biological control of whiteflies on annual crops in the open field remains a major challenge.

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LITERATURE CITED

5. A review listing who and what are known as parasitoids of *Bemisia*.

12. Showing the developmental interaction between parasitoids and hosts.

1. Abd-Rabou S. 2000. Role of *Encarsia inaron* (Walker) (Hymenoptera: Aphelinidae) in biological control of some whitefly species (Homoptera: Aleyrodidae) in Egypt. *Shashpa* 7:187–88
2. Antony B, Palaniswami MS, Kirk AA, Henneberry TJ. 2004. Development of *Encarsia bimaculata* (Heraty and Polaszek) (Hymenoptera: Aphelinidae) in *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) nymphs. *Biol. Control* 30:546–55
3. Ardeh MJ. 2004. *Whitefly control potential of Eretmocerus parasitoids with different reproductive modes*. PhD Thesis, Wageningen Univ., Wageningen, Netherlands
4. Ardeh MJ, Loomans AJM, van Lenteren JC. 2005. Selection of *Bemisia* nymphal stages for oviposition or feeding, and host-handling times of arrhenotokous and thelytokous *Eretmocerus mundus* and arrhenotokous *Er. eremicus*. *Biocontrol* 50:449–63
5. Arnó J, Gabarra R, Liu T-X, Simmons AM, Gerling D. 2010. Natural enemies of *Bemisia tabaci*: predators and parasitoids. In *Bemisia: Bionomics and Management of a Global Pest*, ed. PA Stansly, SE Naranjo, pp. 385–422. Dordrecht, Netherlands: Springer
6. Bailey PT, Martin JH, Noyes JS, Austin AD. 2001. Taxonomy and biology of a new species of *Zaphanera* (Hemiptera: Aleyrodidae) and its association with the widespread death of western myall trees, *Acacia papyrocarpa*, near Roxby Downs, South Australia. *Trans. R. Soc. South Australia* 125:83–96
7. Beitia F, Garrido A. 1985. Parasitism of *Cales noacki* (Hymenoptera, Aphelinidae) on *Trialeurodes vaporariorum* (Homoptera, Aleyrodidae). *Bol. Asoc. Española Entomol.* 9:119–22
8. Bellamy DE, Byrne DN. 2001. Effects of gender and mating status on self-directed dispersal by the whitefly parasitoid *Eretmocerus eremicus*. *Ecol. Entomol.* 26:571–77
9. Bellows TS Jr, Paine TD, Arakawa KY, Meisenbacher C, Leddy P, Kabashimo J. 1990. Biological control sought for ash whitefly. *Calif. Agric.* 44(1):4–6
10. Bellows TS, Meisenbacher C. 2000. Biological control of giant whitefly, *Aleurodicus dugesii*, in California. In *California Conference on Biological Control II*, ed. MS Hoddle, pp. 113–16. Riverside, CA: Univ. Calif. Riverside
11. Birkett MA, Chamberlain K, Guerrieri E, Pickett JA, Wadham LJ, Yasuda T. 2003. Volatiles from whitefly-infested plants elicit a host-locating response in the parasitoid, *Encarsia formosa*. *J. Chem. Ecol.* 29:1589–600
12. Blackburn MB, Gelman DB, Hu JS. 2002. Co-development of *Encarsia formosa* (Hymenoptera: Aphelinidae) and the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): a histological examination. *Arch. Insect Bioch. Physiol.* 51:13–26
13. Blackmer JL, Cross D. 2001. Response of *Eretmocerus eremicus* to skylight and plant cues in a vertical flight chamber. *Entomol. Exp. Appl.* 100:295–300
14. Bográn CE, Heinz KM, Ciomperlik MA. 2002. Interspecific competition among insect parasitoids: field experiments with whiteflies as hosts in cotton. *Ecology* 83:653–68
15. Brady CM, White JA. 2012. Everyone's a loser: Parasitism of late instar whiteflies by *Encarsia inaron* has negative consequences for both parasitoid and host. *Annu. Entomol. Soc. Am.* 105:840–45
16. Briggs CJ, Collier TR. 2001. Autoparasitism, interference, and parasitoid-pest population dynamics. *Theor. Popul. Biol.* 60:33–57
17. Buckner JS, Jones WA. 2005. Transfer of methyl-branched hydrocarbons from the parasitoid, *Eretmocerus mundus*, to silverleaf whitefly nymphs during oviposition. *Comp. Biochem. Physiol. A* 140:59–65

18. Burger JMS. 2002. *How to behave? Evolution of host-handling behaviour in the whitefly parasitoid Encarsia formosa*. PhD Thesis, Wageningen Univ., Wageningen, Netherlands
19. Burger JMS, Hemerik L, van Lenteren JC, Vet LEM. 2004. Reproduction now or later: optimal host-handling strategies in the whitefly parasitoid *Encarsia formosa*. *Oikos* 106:117–30
20. Burger JMS, Kormany A, van Lenteren JC, Vet LEM. 2005. Importance of host feeding for parasitoids that attack honeydew-producing hosts. *Entomol. Exp. Appl.* 117:147–54
21. Byrne DN. 1999. Migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. *Agric. Forest Meteorol.* 97:309–16
22. Castillo JA, Stansly PA. 2011. Biology of *Eretmoceris sudanensis* n. sp. Zolnerowich and Rose, parasitoid of *Bemisia tabaci* Gennadius. *Biocontrol* 56:843–50
23. Cave RD. 2008. Biocontrol of whitefly on coconut palms in the Comoros. *Biocontrol News Inf.* 29:1–18
24. Chiel E, Gerling D, Steinberg S, Klapwijk J, Bolckmans K, Zchori-Fein E. 2012. Contagious sterility in the parasitoid wasp *Eretmoceris mundus* (Hymenoptera: Aphelinidae). *Biocontrol Sci. Tech.* 22:61–66
25. Chiel E, Messika Y, Steinberg S, Antignus Y. 2006. The effect of UV-absorbing plastic sheet on the attraction and host location ability of three parasitoids: *Aphidius colemani*, *Diglyphus isaea* and *Eretmoceris mundus*. *Biocontrol* 51:65–78
26. Clausen CP, Berry PA. 1932. *The Citrus Blackfly In Asia, and the Importation of Its Natural Enemies into Tropical America*, Tech. Bull. 320, US Dep. Agric., Washington, DC
27. Collier TR, Hunter MS. 2001. **Interference competition between whitefly parasitoids, *Eretmoceris eremicus*, and *Encarsia transvena*. *Oecologia* 129:147–54**
28. De Barro PJ, Coombs MT. 2008. Post-release evaluation of *Eretmoceris hayati* Zolnerowich and Rose in Australia. *Bull. Entomol. Res.* 24:1–14
29. De Barro PJ, Liu SS, Boykin LM, Dinsdale AB. 2011. *Bemisia tabaci*: a statement of species status. *Annu. Rev. Entomol.* 56:1–19
30. DeBach P, Rose M. 1976. Biological control of woolly whitefly. *Calif. Agric.* 30(5):4–7
31. DeBach P, Warner SC. 1969. Research on biological control of whiteflies. *Citricraph* 54:301–3
32. Donnell DM, Hunter MS. 2002. Developmental rates of two congeneric parasitoids, *Encarsia formosa* and *E. pergandiella* (Hymenoptera: Aphelinidae), utilizing different egg provisioning strategies. *J. Insect Physiol.* 48:487–93
33. Doukas D, Payne CC. 2007. Effects of UV-blocking films on the dispersal behavior of *Encarsia formosa* (Hymenoptera: Aphelinidae). *J. Econ. Entomol.* 100:110–16
34. Dowell RV. 1979. Synchrony and impact of *Amitus hesperidum* [Hym.: Platygastridae] on its host, *Aleurocanthus woglumi* [Hym.: Aleyrodidae] in southern Florida. *Entomophaga* 24:221–27
35. Drost YC, Qiu YT, Postuma-Doodeman CJAM, van Lenteren JC. 1999. Life-history and oviposition behaviour of *Amitus bennetti*, a parasitoid of *Bemisia argentifolii*. *Entomol. Exp. Appl.* 90:183–89
36. Enkegaard A. 1994. Temperature dependent functional response of *Encarsia formosa* parasitizing the poinsettia-strain of the cotton whitefly, *Bemisia tabaci*, on poinsettia. *Entomol. Exp. Appl.* 73:19–29
37. Evans GA. 2007. *Parasitoids (Hymenoptera) Associated with Whiteflies (Aleyrodidae) of the World*. Beltsville, MD: US Dep. Agric. Version 070202. <http://www.sel.barc.usda.gov:8080/1WF/parasitoidcatalog.pdf>
38. Flanders SE. 1969. Herbert D. Smith's observations on citrus blackfly parasites in India and Mexico and the correlated circumstances. *Can. Entomol.* 101:467–80
39. Foltyn S, Gerling D. 1985. The parasitoids of the aleyrodid *Bemisia tabaci* in Israel: development, host preference and discrimination of the Aphelinid wasp *Eretmoceris mundus*. *Entomol. Exp. Appl.* 38:255–60
40. Fransen JJ, van Montfort MA. 1987. Functional response and host preference of *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae), a parasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae). *J. Appl. Entomol.* 103:55–69
41. Gelman DB, Gerling D, Blackburn MA. 2005. Host-parasitoid interactions relating to penetration of the whitefly, *Bemisia tabaci*, by the parasitoid wasp, *Eretmoceris mundus*. *J. Insect Sci.* 5:46
42. Gelman DB, Gerling D, Blackburn MB, Hu JS. 2005. Host-parasite interactions between whiteflies and their parasitoids. *Arch. Insect Biochem. Physiol.* 60:209–22
43. Gerling D. 1966. Studies with whitefly parasites of Southern California. I. *Encarsia pergandiella* Howard (Hymenoptera: Aphelinidae). *Can. Entomol.* 98:707–24

27. Parasitoid behavior and competition.

44. Gerling D, Blackburn MB. 2013. Immature development of *Eretmocerus mundus* (Hymenoptera: Aphelinidae). *Artrop. Struct. Dev.* 42:309–14
45. Gerling D, Erel E, Guershon M, Inbar M. 2009. Bionomics of *Encarsia scapeata* Rivnay (Hymenoptera: Aphelinidae), tritrophic relationships and host-induced diapause. *Biol. Control* 49:201–6
46. Gerling D, Foltyn S. 1987. Development and host preference of *Encarsia lutea* (Masi) and interspecific host discrimination with *Eretmocerus mundus* (Mercet) (Hymenoptera, Aphelinidae) parasitoids of *Bemisia tabaci* (Gennadius) (Homoptera, Aleyrodidae). *J. Appl. Entomol.* 103:425–33
47. Gerling D, Orion T, Delarea Y. 1990. *Eretmocerus* penetration and immature development: a novel approach to overcome host immunity. *Arch. Insect Biochem. Physiol.* 13:247–53
48. Gerling D, Quicke DLJ, Orion T. 1998. Oviposition mechanisms in the whitefly parasitoids *Encarsia transvena* and *Eretmocerus mundus*. *Biocontrol* 43:289–97
49. Gerling D, Rottenberg O, Bellows TS. 2004. Role of natural enemies and other factors in the dynamics of field populations of the whitefly *Siphoninus philyreae* (Haliday) in introduced and native environments. *Biol. Control* 31:199–209
50. Gerling D, Spivak D, Vinson SB. 1987. Life history and host discrimination of *Encarsia deserti* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Ann. Entomol. Soc. Am.* 80:224–29
51. Gerling D, Tremblay E, Orion T. 1991. Initial stages of the vital capsule formation in the *Eretmocerus-Bemisia tabaci* association. *Redia* 74:411–15
52. Gould J, Hoelmer K, Goolsby J, eds. 2008. *Classical Biological Control of Bemisia tabaci in the United States—A Review of Interagency Research and Implementation*. Dordrecht, Netherlands: Springer Sci. Business Media BV
53. Greenberg SM, Jones WA, Liu T-X. 2008. *Bemisia tabaci* (Homoptera: Aleyrodidae) instar effects on rate of parasitism by *Eretmocerus mundus* and *Encarsia pergandiella* (Hymenoptera: Aphelinidae). *Entomol. Sci.* 11:97–103
54. Guerrieri E. 1997. Flight behaviour of *Encarsia formosa* in response to plant and host stimuli. *Entomol. Exp. Appl.* 82:129–33
55. Hamdi F, Fargues J, Ridray G, Jeannequin B, Bonato O. 2011. Compatibility among entomopathogenic hyphocreales and two beneficial insects used to control *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae) in Mediterranean greenhouses. *J. Invertebr. Pathol.* 108:22–29
56. Hansson C, LaSalle J. 2003. Revision of the neotropical species on the tribe Euderomphalini (Hymenoptera: Eulophidae). *J. Nat. Hist.* 37:697–778
57. Hart WG, Selhime A, Harlan DP, Ingle SJ, Sanchez RM, et al. 1978. The introduction and establishment of parasites of citrus blackfly, *Aleurocanthus woglumi* in Florida (Homoptera: Aleyrodidae). *Entomophaga* 23:361–66
58. Heinz KM, Parrella MP. 1998. Host location and utilization by selected parasitoids of *Bemisia argentifolii* (Homoptera: Aleyrodidae): implications for augmentative biological control. *Environ. Entomol.* 27:773–84
59. Hoddle MS, van Driesche RG, Sanderson JP. 1997. Biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on poinsettia with inundative releases of *Encarsia formosa* (Hymenoptera: Aphelinidae): Are higher release rates necessarily better? *Biol. Control* 10:166–79
60. Hoddle MS, van Driesche RG, Sanderson JP. 1998. Biology and use of the whitefly parasitoid *Encarsia formosa*. *Annu. Rev. Entomol.* 43:645–69
61. Hoddle MS, van Driesche RG, Sanderson JP, Minkenberg OPJM. 1997. Biological control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on poinsettia with inundative releases of *Encarsia formosa* Beltville strain (Hymenoptera: Aphelinidae): Do release rates affect parasitism? *Bull. Entomol. Res.* 88:47–58
62. Holling CS. 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48:1–86
63. Hu JS, Gelman DB, Blackburn MB. 2002. Growth and development of *Encarsia formosa* (Hymenoptera: Aphelinidae) in the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): effect of host age. *Arch. Insect Biochem. Physiol.* 49:125–36
64. Hunter MS. 1999. The influence of parthenogenesis-inducing *Wolbachia* on the oviposition behaviour and sex-specific developmental requirements of autoparasitoid wasps. *J. Evol. Biol.* 12:735–41

65. Hunter MS, Collier TR, Kelly SE. 2002. Does an autoparasitoid disrupt host suppression provided by a primary parasitoid? *Ecology* 83:1459–69
66. Hunter MS, Rose M, Polaszek A. 1996. Divergent host relationships of males and females in the parasitoid *Encarsia porteri* (Hymenoptera: Aphelinidae). *Ann. Entomol. Soc. Am.* 89:667–75
67. Hunter MS, Woolley JB. 2001. Evolution and behavioral ecology of heteronomous aphelinid parasitoids. *Annu. Rev. Entomol.* 46:251–90
68. Inbar M, Gerling D. 2008. Plant-mediated interactions between whiteflies, herbivores, and natural enemies. *Annu. Rev. Entomol.* 53:431–48
69. Janssen A, Montserrat M, HilleRisLambers R, de Roos AM, Pallini A, Sabelis MW. 2006. Intraguild predation usually does not disrupt biological control. *Progr. Biol. Control* 3:21–44
70. Jones WA, Greenberg S. 1998. Suitability of *Bemisia argentifolii* (Homoptera: Aleyrodidae) instars for the parasitoid *Eretmocerus mundus* (Hymenoptera: Aphelinidae). *Environ. Entomol.* 27:1569–73
71. Joyce AL, Bellows TS Jr, Headrick DH. 1999. Reproductive biology and search behavior of *Amitus bennetti* (Hymenoptera: Platygasteridae), a parasitoid of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environ. Entomol.* 28:282–89
72. Kairo M, Vyjayanthi FL, Pollard GV, Hector R. 2001. Biological control of coconut whitefly, *Aleurodicus pulvinatus*, in Nevis. *Biocontrol News Inform.* 22(2):45N–50N
73. Kristensen NP, De Barro PJ, Schellhorn NA. 2013. The initial dispersal and spread of an intentional invader at three spatial scales. *PLOS One* 8(5):e62407
74. Kristensen NP, Schellhorn NA, Hulthen AD, Howie LJ, De Barro PJ. 2013. Wind-borne dispersal of a parasitoid: the process, the model, and its validation. *Environ. Entomol.* 42:1137–48
75. Kumashiro BR, Lai PY, Funasaki GY, Teramoto KK. 1983. Efficacy of *Nephaspis amnicola* and *Encarsia baitiensis* in controlling *Aleurodicus disperses* in Hawaii. *Proc. Hawaii. Entomol. Soc.* 24:261–69
76. Kuwana I, Ishii T. 1927. On *Prospaltella smithi* Silv., and *Cryptognatha* sp., the enemies of *Aleurocanthus spiniferus* Quaintance, imported from Canton, China. *J. Okitsu Horticult. Soc.* 22:77–80
77. Lacey LA, Millar L, Kirk AA, Perring TM. 1999. Effect of storage temperature and duration on survival of eggs and nymphs of *Bemisia argentifolii* (Homoptera: Aleyrodidae) and pupae of the whitefly parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). *Ann. Entomol. Soc. Am.* 92:430–34
78. Lambkin TA, Zalucki MP. 2010. Long-term efficacy of *Encarsia dispersa* Polaszek (Hymenoptera: Aphelinidae) for the biological control of *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae) in tropical monsoon Australia. *Aust. J. Entomol.* 49:190–98
79. LaSalle J, Schauff ME. 1994. Systematics of the Tribe Euderomphalini (Hymenoptera: Eulophidae) parasitoids of whiteflies. *System. Entomol.* 19:235–58
80. Laudonia S, Viggiani G. 1986. Osservazioni sugli stadi preimmaginali di *Cales nocaki* Howard (Hymenoptera Aphelinidae). *Boll. Lab. Entomol. Agrar. Filippo Silvestri Portici* 43:21–28
81. Li SJ, Xue X, Ren SX, Cuthbertson AGS, van Dam NM, Qiu BL. 2013. Root and shoot jasmonic acid induced plants differently affect the performance of *Bemisia tabaci* and its parasitoid *Encarsia formosa*. *Basic Appl. Ecol.* 14:670–79
82. Liu B, Şengonca Ç. 1998. Functional responses of the parasitoid, *Eretmocerus longipes* Compere (Hym., Aphelinidae) to densities of the whitefly, *Aleurotuberculatus takahashi* David et Subramaniam (Hom., Aleyrodidae) at different temperatures. *Anz. Schädlingskde Pflanzenschutz Umweltschutz* 71:53–56
83. Liu T-X. 2007. Life history of *Eretmocerus melanoscutus* (Hymenoptera: Aphelinidae) parasitizing nymphs of *Bemisia tabaci* Biotype B (Homoptera: Aleyrodidae). *Biol. Control* 42:77–85
84. Liu T-X, Stansly PA. 1996. Oviposition, development, and survivorship of *Encarsia pergandiella* (Hymenoptera: Aphelinidae) in four instars of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Ann. Entomol. Soc. Am.* 89:96–102
85. Lo Pinto M. 1989. Corteggiamento e accoppiamento di *Cales noacki* Howard (Hymenoptera: Aphelinidae). *Phytophaga* 3:93–114
86. Lo Verde V, van Lenteren JC. 2007. Battle for food: elimination of supernumerary larvae in the whitefly parasitoid *Eretmocerus mundus*. Presented at *X Eur. Workshop Insect Parasit.*, Sept. 17, Erice, Italy
87. Mahadav A, Gerling D, Gottlieb Y, Czosnek H, Ghanim M. 2008. Parasitization by the wasp *Eretmocerus mundus* induces transcription of genes related to immune response and symbiotic bacteria proliferation in the whitefly *Bemisia tabaci*. *BMC Genomics* 9:342–52

88. Mani M. 2010. Origin, introduction, distribution and management of the invasive spiraling whitefly *Aleurodicus dispersus* Russell in India. *Karnataka J. Agric. Sci.* 23:59–75
89. Manzano MR, van Lenteren JC, Cardona C. 2002. Searching and oviposition behaviour of *Amitus fuscipennis*, a parasitoid of the greenhouse whitefly. *J. Appl. Entomol.* 126:528–33
90. Martin JH. 1996. Neotropical whiteflies of the subfamily Aleurodicinae established in the western Palearctic (Homoptera: Aleyrodidae). *J. Nat. Hist.* 30:1849–59
91. Mazzone P. 1988. Osservazioni morfo-biologiche su *Euderomphale chelidonii* Erdös (Hym.: Eulophidae) parassitoide di *Aleyrodes lonceriae* Walker (Hom.: Aleyrodidae). *Atti XV Congr. Naz. Ital. Entomol.* 15:1013–18
92. Medina PS, Saldarianga AV, Perez LE. 1994. Biología del *Amitus fuscipennis* (MacGowen y Nebeker) bajo tres condiciones ecológicas en Rionegro (Antioquia). *Rev. Colombiana Entomol.* 20:143–48
93. Mills NJ, Gutierrez AP. 1996. Prospective modeling in biological control: an analysis of the dynamics of heteronomous hyperparasitism in a cotton-whitefly-parasitoids system. *J. Appl. Ecol.* 33:1379–94
94. Moretti RGM, Calvitti M. 2008. Intrinsic competition between the parasitoids *Eretmocerus mundus* and *Encarsia formosa* on *Bemisia tabaci*. *Entomol. Exp. Appl.* 129:44–53
95. Mottern JL, Heraty JM. 2014. Revision of the *Cales noacki* species complex (Hymenoptera, Chalcidoidea, Aphelinidae). *Syst. Entomol.* 39:354–79
96. Naranjo SE. 2007. Intraguild predation on *Eretmocerus* sp. nr. *emiratus*, a parasitoid of *Bemisia tabaci*, by three generalist predators with implications for estimating the level and impact of parasitism. *Biocontrol Sci. Tech.* 17:605–22
97. Naranjo SE, Castle SJ, De Barro PJ, Liu SS. 2010. Population dynamics, demography, dispersal and spread of *Bemisia tabaci*. In *Bemisia, Bionomics and Management of a Global Pest*, ed. PA Stansly, SE Naranjo, pp. 185–226. Dordrecht, Netherlands: Springer
98. Nell HW, Sevenster-van der Lelie LA, Woets J, van Lenteren JC. 1976. The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) II. Selection of host stages for oviposition and feeding by the parasite. *J. App. Entomol.* 81:372–76
99. Netting JF, Hunter MS. 2000. Ovicide in the whitefly parasitoid, *Encarsia formosa*. *Anim. Behav.* 60:217–26
100. Nguyen R, Bennett FD. 1995. Importation and field release of parasites against silverleaf whitefly, *Bemisia argentifolii* (Bellows and Perring) in Florida from 1990–1994. *Proc. Fla. State Hort. Soc.* 108:43–47
101. Nguyen R, Brazzel JR, Poucher C. 1983. Population density of the citrus blackfly, *Aleurocanthus woglumi* Ashby (Homoptera: Aleyrodidae), and its parasites in urban Florida in 1979–1981. *Environ. Entomol.* 12:878–84
102. Noyes JS. 2012. *Universal Chalcidoidea Database*. London: Nat. Hist. Mus. <http://www.nhm.ac.uk/chalcidoids>
103. Onillons JC. 1990. The use of natural enemies for the biological control of whiteflies. In *Whiteflies: Their Bionomics, Pest Status and Management*, ed. D Gerling, pp. 287–314. Andover, UK: Intercept
104. Papaj DR. 2000. Ovarian dynamics and host use. *Annu. Rev. Entomol.* 45:423–48
105. Pedata PA, Giorgini M, Guerrieri E. 2002. Interspecific host discrimination and within-host competition between *Encarsia formosa* and *E. pergandiella* (Hymenoptera: Aphelinidae), two endoparasitoids of whiteflies (Homoptera: Aleyrodidae). *Bull. Entomol. Res.* 92:521–28
106. Pickett CH, Keaveny D, Rose M. 2013. Spread and non-target effects of *Eretmocerus mundus* imported into California for control of *Bemisia tabaci*: 2002–2011. *Biol. Control* 65:6–13
107. Pickett CH, Pitcairn MJ. 1999. Classical biological control of ash whitefly: factors contributing to its success in California. *Biocontrol* 44:143–58
108. Pickett CH, Simmons GS, Goolsby JA. 2008. Releases of exotic parasitoids of *Bemisia tabaci* in San Joaquin Valley, California. See Ref. 52, pp. 225–41
109. Polaszek A, Evans GA, Bennett FD. 1992. *Encarsia* parasitoids of *Bemisia tabaci* (Hymenoptera: Aphelinidae, Homoptera: Aleyrodidae): a preliminary guide to identification. *Bull. Entomol. Res.* 2:375–92
110. Polis GA, Myers CA, Holt RD. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20:297–330

111. Qiu BL, de Barro PJ, He YR, Ren SX. 2007. Suitability of *Bemisia tabaci* (Hemiptera: Aleyrodidae) instars for the parasitization by *Encarsia bimaculata* and *Eretmocerus* sp. nr. *furubashii* (Hymenoptera: Aphelinidae) on glabrous and hirsute host plants. *Biocontrol Sci. Tech.* 17:823–39
112. Qiu YT, van Lenteren JC, Drost YC, Posthuma-Doodeman CJAM. 2004. Life-history parameters of *Encarsia formosa*, *Eretmocerus eremicus* and *E. mundus*, aphelinid parasitoids of *Bemisia argentifolii* (Hemiptera: Aleyrodidae). *Eur. J. Entomol.* 101:83–94
113. Romeis J, Zebitz CPW. 1997. Searching behaviour of *Encarsia formosa* as mediated by colour and honeydew. *Entomol. Exp. Appl.* 82:299–309
114. Rose M, DeBach P. 1992. Biological control of *Parabemisia myricae* (Kuwana) (Homoptera: Aleyrodidae) in California. *Israel J. Entomol.* 26:73–95
115. Sailer RI, Brown RE, Munir B, Nickerson JCE. 1984. Dissemination of the citrus whitefly (Homoptera: Aleyrodidae) parasite *Encarsia laborensis* (Howard) (Hymenoptera: Aphelinidae) and its effectiveness as a control agent in Florida. *Bull. Entomol. Soc. Am.* 30:36–39
116. Schmalstieg H, Katz P. 2008. Experiences of the use of *Encarsia tricolor* in biological control of *Aleyrodes proletella* on leaf cabbage. *Dtsch. Pflanzenschutz-Tag.* 56:417–37
117. Selhime AG, Hart WG, Harlan DP. 1982. Dispersal of *Amitus besperidum* and *Encarsia opulenta* released for the biological control of citrus blackfly in south Florida. *Fla. Entomol.* 65:165–68
118. Şengonca Ç, Liu B. 1998. Release of *Eretmocerus longipes* Compere (Hymenoptera: Aphelinidae) against *Aleurotuberculus takabashi* David & Subramaniam (Homoptera: Aleyrodidae) on jasmine plantations in the Fuzhou region of southeastern China. *Z. Pflanzenkrankh. Pflanzenschutz* 105:504–12
119. Shishehbor P, Brennan PA. 1996. Functional response of *Encarsia formosa* (Gahan) parasitizing castor whitefly, *Trialeurodes ricini* Misra (Hom., Aleyrodidae). *J. Appl. Entomol.* 120:297–99
120. Smith HD, Maltby HL, Jimenez EJ. 1964. *Biological control of the citrus blackfly in Mexico*. Tech. Bull. 1311, US Dept. Agric., Washington
121. Smith HS. 1929. Multiple parasitism: its relation to the biological control of insects. *Bull. Entomol. Res.* 20:141–49
122. Soler R, van Lenteren JC. 2004. Reproduction and development of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Proc. Neth. Entomol. Soc.* 15:111–17
123. Speyer ER. 1927. An important parasite of the greenhouse whitefly (*Trialeurodes vaporariorum* Westwood). *Bull. Entomol. Res.* 17:301–8
124. Stansly PA, Calvo J, Urbaneja A. 2005. Augmentative biological control of *Bemisia tabaci* biotype “Q” in greenhouse pepper using *Eretmocerus* spp. (Hym. Aphelinidae). *Crop. Prot.* 24:829–35
125. Stansly PA, Calvo J, Urbaneja A. 2005. Release rates for control of *Bemisia tabaci* (Homoptera: Aleyrodidae) Biotype “Q” with *Eretmocerus mundus* (Hymenoptera: Aphelinidae) in greenhouse tomato and pepper. *Biol. Control* 35:124–33
126. Stansly PA, Natwick ET. 2010. Integrated systems for managing *Bemisia tabaci* in protected and open field agriculture. In *Bemisia: Bionomics and Management of a Global Pest*, ed. PA Stansly, SE Naranjo, pp. 467–97. Dordrecht, Netherlands: Springer
127. Stansly PA, Sanchez PA, Rodriguez JM, Canizares F, Nieto A, et al. 2004. Prospects for biological control of *Bemisia tabaci* (Homoptera, Aleyrodidae) in greenhouse tomatoes of southern Spain. *Crop. Prot.* 23:701–12
128. Sütterlin S, van Lenteren JC. 2000. Pre- and post-landing response of the parasitoid *Encarsia formosa* to whitefly hosts on *Gerbera jamesonii*. *Entomol. Exp. Appl.* 96:299–307
129. Thompson CR, Cornell JA, Sailer RI. 1987. Interactions of parasites and a hyperparasite in biological control of citrus blackfly, *Alettracanthus woglumi* (Homoptera: Aleyrodidae), in Florida. *Environ. Entomol.* 16:140–44
130. van Driesche RG, Lyon S, Jacques K, Smith T, Lopes P. 2002. Comparative cost of chemical and biological whitefly control in poinsettia: Is there a gap? *Fla. Entomol.* 85:488–93
131. van Lenteren JC, Li ZH, Kamerman JW. 1995. Leaf hairs reduce the capacity of *Encarsia* to control greenhouse whitefly. *J. Appl. Entomol.* 119:553–59
132. van Lenteren JC, Tommasini MG. 2003. Mass production, storage, shipment and release of natural enemies. In *Quality Control and Production of Biological Control Agents: Theory and Testing Procedures*, ed. JC van Lenteren. Cambridge, MA: CABI

133. van Lenteren JC, van Roermund HJW, Sütterlin S. 1996. Biological control of greenhouse whitefly (*Trialeurodes vaporariorum*) with the parasitoid *Encarsia formosa*: How does it work? *Biol. Control* 6:1–10
134. van Lenteren JC, van Vianen A, Gast HF. 1987. The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae). XVI. Food effects on oogenesis, oviposition, life-span and fecundity of *Encarsia formosa* and other hymenopterous parasites. *J. Appl. Entomol.* 103:69–84
135. van Roermund HJW. 1995. *Understanding biological control of greenhouse whitefly with the parasitoid Encarsia formosa: from individual behaviour to population dynamics*. PhD Thesis, Wageningen Agric. Univ., Wageningen, Netherlands
136. Velasco-Hernández MC, Ramirez-Romero R, Cicero L, Michel-Rios C, Desneux N. 2013. Intraguild predation on the whitefly parasitoid *Eretmocerus eremicus* by the generalist predator *Geocoris punctipes*: a behavioral approach. *PLOS ONE* 8(11):e80679
137. Viggiani G, Battaglia D. 1983. Courtship and mating behavior of two species of *Amitus*, parasitoids of known whiteflies from the world. *Boll. Lab. Entomol. Agrar. Filippo Silvestri Portici* 40:115–18
138. Xiao YF, Chen J, Cantliffe D, McKenzie C, Houben K, Osborne LS. 2011. Establishment of papaya banker plant system for parasitoid, *Encarsia sophia* (Hymenoptera: Aphelinidae) against *Bemisia tabaci* (Hemiptera: Aleyrodidae) in greenhouse tomato production. *Biol. Control* 58:239–47
139. Yang NW, Ji LL, Lövei GL, Wan FH. 2012. Shifting preference between oviposition versus host-feeding under changing host densities in two aphelinid parasitoids. *PLOS ONE* 7(7):e41189
140. Yang NW, Wan F-H. 2011. Host suitability of different instars of *Bemisia tabaci* biotype B for the parasitoid *Eretmocerus hayati*. *Biol. Control* 59:313–17
141. Zang LS, Liu T-X. 2007. Intraguild interactions between an oligophagous predator, *Delphastus catalinae* (Coleoptera: Coccinellidae), and a parasitoid, *Encarsia sophia* (Hymenoptera: Aphelinidae), of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Biol. Control* 41:142–50
142. Zang LS, Liu T-X. 2008. Host-feeding of three parasitoid species on *Bemisia tabaci* biotype B and implications for whitefly biological control. *Entomol. Exp. Appl.* 127:55–63
143. Zang LS, Liu T-X. 2009. Food-deprived host-feeding parasitoids kill more pest insects. *Biocontrol Sci. Tech.* 19:573–83
144. Zang LS, Liu T-X. 2010. Effects of food deprivation on host feeding and parasitism of whitefly parasitoids. *Environ. Entomol.* 39:912–18
145. Zang LS, Liu T-X, Wan FH. 2011. Reevaluation of the value of autoparasitoids in biological control. *PLOS ONE* 6(5):e20324
146. Zang LS, Liu T-X, Zhang F, Shi SS, Wan FH. 2011. Mating and host density affect host feeding and parasitism in two species of whitefly parasitoids. *Insect Sci.* 18:78–83
147. Zchori-Fein E, Roush RT, Hunter MS. 1992. Male production induced by antibiotic treatment in *Encarsia formosa* (Hymenoptera: Aphelinidae), an asexual species. *Experimentia* 48:102–5
148. Zolnerowich G, Rose M. 1996. A new species of *Entedononecremnus* (Hymenoptera: Chalcidoidea: Eulophidae) parasitic on the giant whitefly, *Aleurodicus dugesii* Cockerell (Homoptera: Aleyrodidae). *Proc. Entomol. Soc. Wash.* 98:369–73