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

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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 two subfamilies, Aleurodinae and Aleurodicinae, with the former being smaller and restricted mainly to the Neotropics (90). To date, more than 500 species of parasitoid in 23 genera within six 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 Proctotrupoidea (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 *Baeoentedon*, *Aphobetus*, and *Moranila* (Pteromalidae) are Australian; many *Cales* species originate in the Neotropics, with one known from Australia; and *Myiocnema comperei* (Aphelinidae) 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 described 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. bayati* 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 *Eretmocerus* (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 *Trialeurodes 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 bennetti*, the six most-studied *Encarsia*, and the five most-studied *Eretmocerus* 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 (*Eretmocerus*) 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*-*Trialeurodes 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, *Eretmocerus* 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 a cellular 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 (*Aleurotrixus 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 takabashi* (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. takabashi* 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. takabashi* at 35°C thrice as long as at 20°C (82). Oviposition lasts significantly longer on older, larger nymphs of *Encarsia* and *Eretmocerus* (47, 83).

COURTSHIP AND MATING BEHAVIOR

Observations on *Amitus*, *Encarsia*, and *Eretmocerus* 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 *Eretmocerus* 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 *Eretmocerus* 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 carbohydrate (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 *Delpbastus 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>Aleurotrixus floccosus</i>	Citrus	32
<i>Cales noacki</i>	<i>Aleurotrixus floccosus</i> <i>Tetraleurodes perseae</i>	Citrus Persea (avocado)	31
<i>Cales rosei</i>	<i>Aleurotrixus floccosus</i>	Citrus	97
<i>Encarsia dispersa</i>	<i>Aleurodicus dispersus</i>	Various	80
<i>Encarsia guadeloupae</i>	<i>Aleurodicus dispersus</i>	Various	89
<i>Encarsia baitiensis</i>	<i>Aleurodicus dispersus</i>	Various	77
<i>Encarsia bispida</i>	<i>Bemisia tabaci</i>	Various	109
<i>Encarsia inaron</i>	<i>Aleyrodes proletella</i> <i>Siphoninus phillyreae</i>	Brassica (cabbage) Various	1, 53
<i>Encarsia laborensis</i>	<i>Dialeurodes citri</i>	Citrus	115, 118
<i>Encarsia noysei</i>	<i>Aleurodicus pulvinatus</i> <i>Aleurodicus dugesii</i>	Cocos (coconut) Various	9, 75
<i>Encarsia perplexa</i>	<i>Aleurocanthus woglumi</i>	Citrus	58, 100
<i>Encarsia smithi</i>	<i>Aleurocanthus spiniferus</i>	Citrus	78
<i>Encarsia strenua</i>	<i>Singhiella citrifolii</i>	Citrus	9
<i>Encarsia tricolor</i>	<i>Aleyrodes proletella</i>	Brassica (cabbage)	117
<i>Entedononecremnus 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>Aleurotuberculatus takabashi</i>	Jasminum (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. phillyreae* (49)], whereas others used successive parasitoid species according to climatic and host abundance conditions [e.g., establishment of *En. smithi*, *En. clypealis*, *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 bispida</i>	<i>Bemisia tabaci</i>	109
<i>Encarsia sophia</i>	<i>Trialeurodes vaporariorum</i> <i>Bemisia tabaci</i>	140, 146
<i>Eretmocerus eremicus</i>	<i>Bemisia tabaci</i> <i>Trialeurodes vaporariorum</i>	124, 129
<i>Eretmocerus hayati</i>	<i>Bemisia tabaci</i>	53
<i>Eretmocerus melanoscuteus</i>	<i>Bemisia tabaci</i>	53
<i>Eretmocerus rui</i>	<i>Bemisia tabaci</i>	101
<i>Encarsia lutea</i>	<i>Bemisia tabaci</i>	109
<i>Amitus bennetti</i>	<i>Bemisia tabaci</i>	36, 72
<i>Encarsia bimaculata</i>	<i>Bemisia tabaci</i>	53
<i>Eretmocerus emiratus</i>	<i>Bemisia tabaci</i>	53

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 *Eretmocerus* 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 *Eretmocerus* 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 *Eretmocerus*, 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 *Eretmocerus* gained over native *Eretmocerus* 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 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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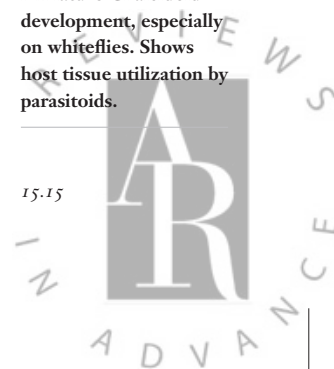
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