Chapter 4
Systematics and Biology of *Encarsia*

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Abstract The genus *Encarsia* includes 343 described species and numerous undescribed species. Immatures are parasitoids of various whiteflies, armored scales, aphids, Lepidoptera or even the opposite sex of the same species. Several species are known to attack *Bemisia*, but so far, none have proved effective in the control of the pest species in this genus. The taxonomy and classification of *Encarsia* species is undergoing rapid changes using both morphological and molecular techniques. *Wolbachia* and newly discovered bacteria are associated with sex ratio distortion in species of *Encarsia*. Whiteflies appear to be the basal host associated with members of this genus, with only a few species potentially host specific for *Bemisia* whiteflies.

4.1 Introduction

Species of *Encarsia* Förster (Hymenoptera: Aphelinidae) are minute, solitary, endoparasitic wasps found worldwide. *Encarsia* is the largest genus within Aphelinidae, with a total of 343 described species (Noyes 2001; Heraty et al. 2007). However, a large number of species are undescribed and often even the named species of *Encarsia* are difficult to identify. Adults are known to attack the sessile stages of whiteflies, armored scale insects, aphids and lepidopteran eggs (Viggiani 1984; Polaszek 1991; Williams and Polaszek 1996). Most species are autoparasitic with females developing as primary endoparasitoids and males as hyperparasitic endoparasitoids of the same or other species (Williams and Polaszek 1996; Hunter and Woolley 2001). Males of only two species, *Enc. inaron* (Walker) and *Enc. longicornis* Mercet, have been shown to develop as primary parasitoids of their

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whitefly host (Mazzone 1983; Viggiani 1988). In some species, males are rare or absent, with these aberrant sex ratios associated with either a specialized group of bacteria or with *Wolbachia* (Zchori-Fein et al. 2001). *Encarsia* is one of the most important parasitic groups exploited for biological control (Noyes and Hayat 1994). Several species have demonstrated their importance in the control of citrus blackfly (*Enc. clypealis* (Silvestri)), *Enc. perplexa* Huang and Polaszek [as *Enc. opulenta* (Silvestri)] and *Enc. smithi* (Silvestri)) (Clausen 1978), spiny blackfly (*Enc. smithi*) (Kuwana 1934), San Jose scale (*Enc. perniciosi* (Tower)) (Clausen 1978), greenhouse whitefly (*Enc. formosa* Gahan) (Clausen 1978; van Lenteren and Woets 1988; Hoddle et al. 1998), and ash whitefly (*Enc. inaron* (Walker)) (Bellows et al. 1992).

Many whitefly species in the genus *Bemisia* (Aleyrodidae) are severe pests of agricultural crops in North America (McAuslane et al. 1993; Toscano et al. 1998) and elsewhere. *Encarsia* species may be important native parasitoids of *Bemisia*, but the species imported as biological control agents have yet to demonstrate their ability to establish and suppress these whiteflies (Goolsby et al. 1998). Even with an extensive worldwide search for parasitoids of *Bemisia*, relatively few of the 41 described species that are known to attack *Bemisia* have been used in these biological control programs. The parasitoids that were successfully recovered and released may simply be the most common species in agricultural situations, but given that many species are cryptic and either difficult or impossible to identify without refined behavioral or genetic data, many possibilities for new control agents exist. In this chapter we review the changes in our knowledge of *Encarsia* from a taxonomic and phylogenetic perspective, and how this may ultimately affect our ability to use these species as biological control agents of whiteflies or armored scales.

4.2 Taxonomy

The majority of species now placed in *Encarsia* were previously assigned to one of three genera: *Encarsia* Förster 1878, *Prospaltella* Ashmead 1904, and *Aspidiotiphagus* Howard 1894. Other generic names applied to these species include *Doloresia* Mercet 1912, *Mimatomus* Cockerell 1911, *Paraspidiotiphagus* Alam 1956, *Prospaltoides* Brèthes 1914 and *Trichaporus* Mercet 1930, but all have been synonymized. Until recently, biological characteristics were used to separate genera with *Encarsia* species parasitic on whiteflies and *Aspidiotiphagus* and *Prospaltella* attacking armored scales. Viggiani and Mazzone (1979) synonymized all these under *Encarsia*. DeBach and Rose (1981) argued that a set of morphologically distinct species with a narrowed fore wing having an asetose patch that were parasitic on scales should remain as the distinct genus *Aspidiotiphagus,* and they erected *Aleurodiphilus* to contain species having a similar fore wing and parasitizing whiteflies. Hayat (1983) treated all these genera as *Encarsia* and we follow that convention here.

The number of described species of *Encarsia* is increasing at a rapid rate. Just since 1995, 127 species (37.0% of the total number of 343) have been described (Evans et al. 1995; Jasnosh 1995; Chou et al. 1996; Krishnan and Vasantharaj David 1996; Evans and Angulo 1996; Evans 1997; Evans and Polaszek 1997; Evans and Castillo 1998; Hayat 1998; Evans and Polaszek 1998; Huang and Polaszek 1998; Polaszek et al. 1999; Gomez and Garcia 2000; Heraty and Polaszek 2000; Myartseva 2001; Schmidt et al. 2001; Manzari et al. 2002; Pedata and Polaszek 2003; Hernández-Suárez et al. 2003; Polaszek et al. 2004; Schmidt and Polaszek 2007a, b). However, these may represent only a small proportion of the total number of species that are in existence today. Most *Encarsia* species are described from material that is reared, which generally means a focus on species of agricultural importance. However, it is interesting that given the intense focus on species of *Bemisia* over the past several years, only nine of these 127 new species are known to attack this host. As we move from agricultural to natural ecosystems, we can expect the number of species to increase dramatically. For example, in one canopy fogging sample in Sulawesi, Indonesia, more than 156 species of *Encarsia* were recognized, which is more than half of the known species (Noyes 1989). Current descriptions are based on morphological characters that are relatively easy to recognize, but these do not take into account differences in behavior and reproductive incompatibility that distinguish cryptic or sibling species (Heraty and Polaszek 2000).

Molecular sequence data are being used to help establish the identity of species. Differences in the 28S-D2 rDNA transcript gene regions were used to differentiate two closely related species, *Encarsia formosa* Gahan and *Enc. luteola* Howard (Babcock and Heraty 2000). The nature of these species has been debated, and these data provide evidence to support the use of very minor morphological characters to recognize these species (antennal sensillum, number of cells across the axilla and degree of scutellar sculpture) (Polaszek et al. 1992; Schauff et al. 1996). A similar approach was taken using the same gene region to establish the identity of *Encarsia estrellae* Manzari and Polaszek, *Enc. dichroa* Mercet and *Enc. inaron* (Walker) and also for species within the *meritoria*-complex (Manzari et al. 2002; Polaszek et al. 2004). More species are likely to be discovered as they are analyzed at the molecular level. Closely related species are more readily distinguished by their ITS2, COI or COII sequence divergence than by their morphological differences (Stouthamer et al. 1999; Giorgini and Monti 2003; R. Stouthamer, personal communication). Within *Encarsia*, morphologically similar but genetically distinct and geographically isolated populations of *Enc. smithi* (Babcock et al. 2001) would suggest that they are different species. On the other hand, some species exhibit considerable behavioral divergence that is not demonstrated by a corresponding genetic divergence. *Encarsia sophia* (Girault) has varying levels of reproductive isolation and host choice that are not reflected in either their morphological or genetic differences for the 28S gene region (Heraty and Polaszek 2000; Babcock et al. 2001; Hernández-Suárez et al. 2003), although they may be reflected in COI (Giorgini and Monti 2003). Mating and host choice differences in populations of *Enc. formosa* attacking *Bemisia* on *Poinsettia* are neither reflected in 28S-D2 or ITS2 sequences, nor in a more extensive survey of AFLP (amplified fragment-length

polymorphism) differences (Nemec and Stary 1984; Y. Gai and R. Stouthamer, personal communication). Clearly, we are only just beginning to understand the true diversity of the genus using molecular parameters.

Unfortunately, much of the current descriptive effort is focused on the redescription and illustration of species already described. Even recently described species such as *Enc. protransvena* Viggiani have been subsequently redescribed and illustrated as many as six different times. *Encarsia sophia* (Girault and Dodd) (=*Enc. transvena* Timberlake) has been redescribed nine times, and *Enc. formosa* Gahan at least 10 times. Often these redescriptions are produced as part of regional treatments, and as such are necessary, because unfortunately most *Encarsia* are recognized by an overall combination of characters, and not a set of unique characters. Thus any diagnosis requires a fairly complete treatment of the overall character set pertaining to each species. As identification keys and species group placement are better developed, perhaps this redundant aspect of *Encarsia* taxonomy can be overcome. Morphometrics has been an aid in delimiting species boundaries in closely related species (Heraty and Polaszek 2000; Manzari et al. 2002; Polaszek et al. 2004). High resolution digital photography is a significant breakthrough that may simplify future descriptions and allow for better recognition of described species. The digital illustrations of the body, antenna and wings of *Encarsia* species by Manzari et al. (2002), Pedata and Polaszek (2003) and Polaszek et al. (2004) are superb examples of how imaging technology can enhance our means of describing features of a species.

4.3 Identification Keys to Species

Progress is being made toward providing reliable keys to the species of *Encarsia*. Hayat (1989) provided the first reliable key to the species of India. While regionally limited in scope, the key includes many of the species found elsewhere. Comprehensive regional keys in the traditional couplet format have been developed for species in China (Huang 1994; Huang and Polaszek 1998), India (Hayat 1989, 1998), Egypt (Polaszek et al. 1999), and Russia (Jasnosh 1989). More user-friendly pictorial-format keys were developed for *Encarsia* parasitic on whiteflies in North America (Schauff et al. 1996), and Australia and the Polynesian islands (Schmidt et al. 2001). These regional keys are useful, but they always fall short of a satisfactory identification tool because they are not comprehensive on a worldwide level; and with the consistent importation, natural spread and discovery of species, it is difficult to name species with confidence unless representative material is available. Several recent studies have focused instead on worldwide reviews of species within a species group, which include the *cubensis* group (Evans and Polaszek 1998), the *flavoscutellum* group (Evans et al. 1995), part of the *strenua* group (Heraty and Polaszek 2000), the *longifasciata* group (Pedata and Polaszek 2003) and part of the *luteola* group (Polaszek et al. 2004). Polaszek et al. (1992) focused on a comprehensive review of the *Encarsia* attacking *Bemisia*, but this addressed only 19 of the 41 species now known to attack *Bemisia*, although it did address the species most

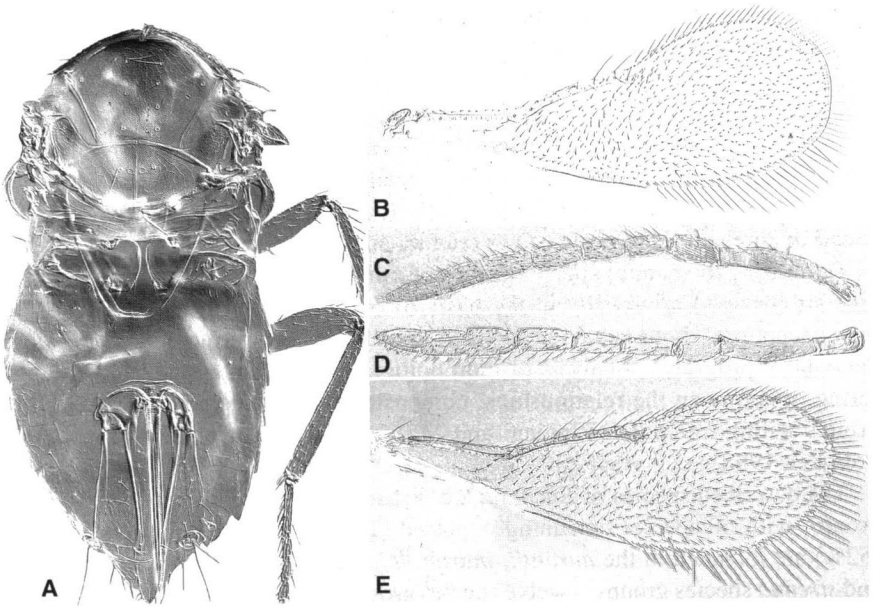

Fig. 4.1 Digital images of *Encarsia*. (**A–C**) *Encarsia bimaculata*; (**D–E**) *Encarsia protransvena.*

commonly encountered. Nobody has yet tried to produce a digital identification key using some of the standard packages now available (i.e., Lucid; www.lucidcentral.com). With the availability of digital imaging technology (Fig. 4.1), this may be the next logical step.

4.4 Species Relationships

A goal of systematics is to group species into evolutionary units that are presumed to share a common ancestor. Many species of *Encarsia* are undescribed, but we still must be able to accurately recognize species with the greatest potential for biological control. A common assumption is that closely related species may share similar habits and host preferences to known species, and are therefore desirable candidates for biological control. Species of the *citrina* group attack armored scale insects and species in the *flavoscutellum* group attack Hormaphididae. Because of their shared evolutionary history, closely related species are expected to have similar insect or plant host relationships, courtship patterns, environmental preferences or other behavioral attributes. If we can readily characterize these groups, and they have an evolutionary basis, then hopefully we can make accurate predictions of their host associations and other behavioral characteristics of interest. These relationships are

most commonly determined by the presence of shared derived morphological characters (synapomorphies). Unfortunately, species groups of *Encarsia*, which are our first approximation of related species, are often defined by combinations of characters, many of which are characteristic of one or more species placed in other species groups. Even obvious group characteristics are found in clearly unrelated groups of species; for example, the close placement of scutellar sensillae, which are considered diagnostic of the *strenua* group, are now known to be convergent and found in unrelated groups of species (Heraty and Polaszek 2000).

Delimiting the natural species groups of *Encarsia* is important. Currently, species are grouped arbitrarily on the basis of overall similarity. This can lead to misconceptions about behavior and host associations that are crucial for biological control programs. Analysis of morphological characters alone has led to differing opinions on the relationships, composition and placement of species into groups within *Encarsia* (Viggiani and Mazzone 1979; Hayat 1998; Huang and Polaszek 1998).

The described species of *Encarsia* are distributed among 25 recognized species groups, with 60 species remaining unplaced (Table 4.1). The majority of species (52%) are included in the *aurantii*, *inaron*, *lahorensis*, *luteola*, *opulenta*, *parvella* and *strenua* species groups. Twelve species groups were first suggested by Viggiani and Mazzone (1979), and 32 species group names have been proposed by various authors. Seventeen species groups were recognized by Hayat (1998), who chose not to recognize four groups (*elegans*, *inquirenda*, *luteola* and *perflava*), which have been recognized by subsequent authors (Huang and Polaszek 1998; Polaszek et al. 1999; Babcock et al. 2001), and other groups were either proposed but not addressed (*scapeata*, *singularis*, *tremblayi*) or proposed after Hayat's review (*citrella*, *cubensis*, *divergens*). Over the last 20 years there has been an effort to accurately define and place species into these groups (Evans et al. 1995; Hayat 1998; Huang and Polaszek 1998; Evans and Polaszek 1998; Heraty and Polaszek 2000; Babcock et al. 2001; Manzari et al. 2002; Pedata and Polaszek 2003; Polaszek et al. 2004), but there is a need for a more comprehensive review of groups beyond that of Hayat (1998).

Many species can be allocated into morphologically and behaviorally distinct groups. For instance, species in the *citrina* group (previously *Aspidiotiphagus*) are all armored scale parasites and can be readily distinguished by a narrowed fore wing with a concave posterior margin, asetose patch on the fore wing, and the propodeum with reticulate sculpture (DeBach and Rose 1981). The *strenua* group can be recognized by having one or more setae on the margin of the wing at the apex of the costal cell, a bare area just anterior to the stigmal vein, and closely spaced placoid sensillae on the scutellum (Heraty and Polaszek 2000). Not all of these characters are unique. A distinct asetose wing spot also is found in members of the *cubensis* and *parvella* (previously *Aleurodiphilus*) groups, but a vague bare spot is also found in some species in the *perflava* group. Certain characters may or may not indicate relationships. For example, *Enc. quercicola* has close sensilla on the scutellum, but not the wing characteristics of the *strenua* group. In an opposite pattern, some characteristics, perhaps mistakenly identified, may artificially group taxa.

Table 4.1 Attributes of species groups of *Encarsia*. (Adapted from an earlier version of Heraty et al. 2007).

Attacked group	No. spp.	Scale	White-Fly	*Bemisia*	*Trial.*	OtWh	OtHo	No. of host genera 1	2	3	4	5+
Unplaced	60	10	8	1	1	5	1a?	16	1	1	–	–
aurantii	43	19	11	2	0	11	2a?, 2b	18	5	3	–	–4
citrella	4	0	4	3	0	4	0	1	1	2	–	–
citrina	9	7	0	–	–	–	0	4	–	1	–	2
cubensis	7	0	5	3	1	5	0	2	1	1	–	1
divergens	2	1	0	–	–	–	0	1	–	–	–	–
duorunga	3	0	2	2	0	0	0	2	–	–	–	–
elegans	4	0	2	0	0	2	0	1	–	1	–	–
flavoscutellum	4	0	0	–	–	–	3c	2	1	–	–	–
inaron	19	0	14	7	2	13	1b, 1d?, 1e	7	2	2	1	2
inquirenda	4	3	0	–	–	–	0	2	1	–	–	–
lahorensis	13	0	10	2	2	9	1a?, 1b, 1e	6	–	2	1	1
longifasciata	5	0	3	1	0	2	0	1	1	–	–	1
lutea	9	0	9	2	1	9	1a?, 1b	6	1	–	–	2
luteola	11	0	10	6	5	7	0	6	–	–	1	3
merceti	3	0	4	0	0	4	0	3	1	–	–	–
opulenta	16	0	15	0	1	14	1a?, 1b	11	3	1	–	–
parvella	14	0	13	4	2	13	1b	7	2	3	–	1
perflava	6	0	4	1	1	4	0	1	–	1	–	2
scapeata	2	0	1	0	0	1	0	1	–	–	–	–
septentrionalis	1	0	1	0	0	1	1a?	–	–	1	–	–
singularis	3	3	0	–	–	–	0	3	–	–	–	–
strenua	27	1	24	8	6	21	1a?, 1f, 1g?	16	3	3	–	3
tremblayi	1	0	1	0	0	1	0	1	–	–	–	–
tricolor	6	0	4	0	1	4	1b	2	2	–	–	–
tristis	1	0	1	0	0	1	0	–	1	–	–	–
Total	277	44	146	42	23	133	25	120	26	22	3	22

Abbreviations: *Trial.* = *Trialeurodes* spp., OtWh = other whiteflies, OtHo = other hosts (a = Coccidae or Pseudococcidae, b = Hymenoptera, c = Hormaphididae, d = Thysanoptera, e = Lepidoptera, f = Psyllidae, g = Aphididae). Numbers of host genera attacked do not include questionable records.

For example, 26 of the species in the *strenua* group attack whiteflies, but *Enc. titilliata* (Girault), which possesses all three of the *strenua*-group characters, attacks armored scale (Heraty and Polaszek 2000). Other characteristics such as sculpture of the thorax, shape of the scutellar sensilla, and coloration, suggest that *Enc. titilliata* may actually belong elsewhere, but without a larger scale analysis this cannot be verified. Because *Encarsia* are small, many of their characteristics appear to be simple reductions and possibly not valuable for assessing phylogenetic relationships. The *luteola* group all have a 4-segmented mid tarsus, but this also occurs in the *cubensis* group. Because this character represents a simple reduction from 5 to 4 segmented tarsi, Hayat (1998) presumed that this would not be a good character for assessing group relationships and placed the included species into other species groups.

To properly evaluate which features can accurately assess the relationships of species, morphological characters need to be identified and assessed in a phylogenetic analysis. In an analysis of relationships between *Encarsia* and two closely related sister taxa, Polaszek and Hayat (1992) were able to find only 24 characters to assess relationships between genera, of which only eight were variable within *Encarsia*. Babcock et al. (2001) used a morphological matrix of 14 characters to assess the relationships of 24 species in 10 species groups. The results were not very satisfactory, with resolution of only the *luteola* and *strenua* species groups, and little resolution of relationships within these species groups (Fig. 4.2). Identifying and evaluating phylogenetically significant morphological characters for more than 200 species is likely impossible.

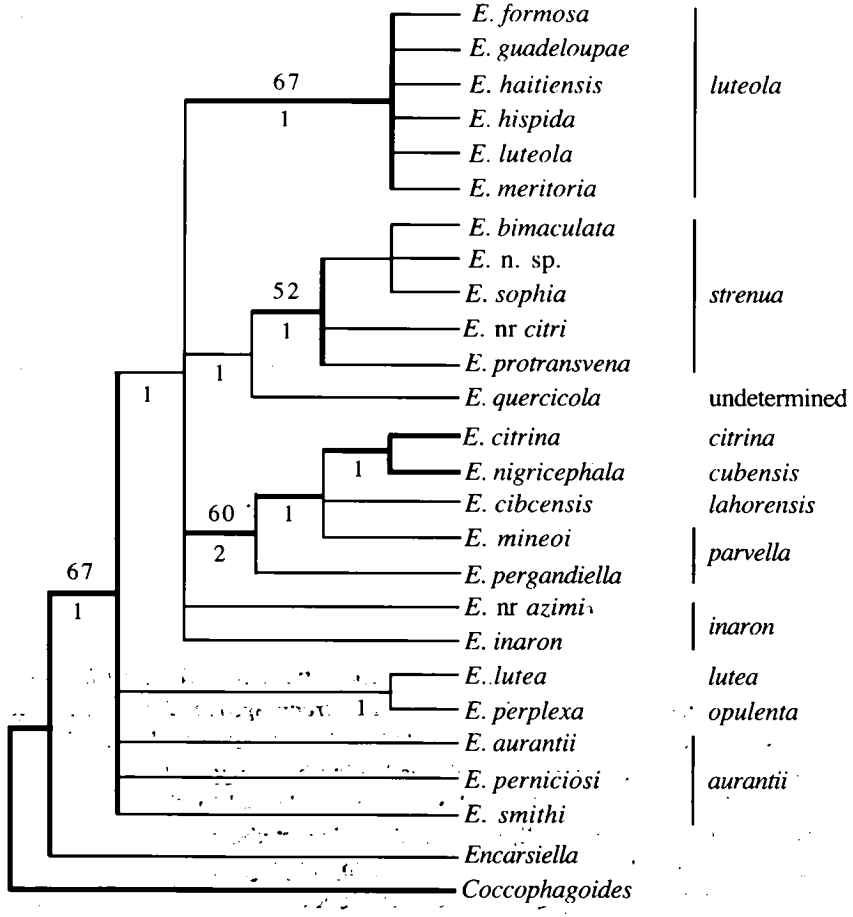

Fig. 4.2 Strict consensus of four trees from a morphological analysis of 14 characters after Successive Approximations Character Weighting of 50 most parsimonious (MP) trees (Adapted from Babcock et al. 2001). Thin lines collapse in the consensus of 50 MP trees.

The analysis of nucleotide sequence data provides an opportunity to assess relationships and test the validity of morphological features currently used for placing species of *Encarsia* into groups (Heraty 2003). To evaluate the species of *Encarsia* on a large scale, only sequence data will be useful. Protein or RAPD (randomly amplified polymorphic DNA) comparisons may be useful for identification of populations or limited to comparisons of a few closely related species (Kirk et al. 2000), but they cannot address large numbers of taxa, and there are inherent problems associated with phylogenetic comparisons using these techniques (Blackeljau et al. 1995). Babcock and Heraty (2000) used sequences of the D2 expansion region of 28S rDNA to evaluate the relationships of four species in the *luteola* group. These not only indicated the expected sister group relationship between *Enc. luteola* and *Enc. formosa*, but also contained conserved marker sites for two restriction enzyme sites that could distinguish these two species. Expanding on this analysis, Babcock et al. (2001) used the same sequences to evaluate the relationships of the same 26 species discussed above. The results were similar for an analysis of 70 populations or a subset of 26 representative populations (species) and two outgroup taxa (*Coccophagoides* and *Encarsiella*). The resulting hypothesis of relationships was almost completely resolved and supported monophyly of the *luteola*, *inaron* and *strenua* groups, with strong resolution of the species included within these groups. Importantly, the results established that 4-segmented tarsi, male antennal complexes, and closely spaced scutellar sensillae were homologous, phylogenetically informative characters. Manzari et al. (2002) built upon this data set by adding four different species (*Enc. dichroa, Enc. estrellae, Enc. tricolor* and *Enc.* nr *azimi*). The results were similar and again supported the monophyly of the expanded *inaron* group.

We reanalyzed a new data set for *Encarsia* that combined the species of three papers (Babcock et al. 2001; Manzari et al. 2002 [but without *Eretmocerus*], Pedata and Polaszek 2003). Together with *Dirphys*, *Encarsiella* was proposed as the monophyletic sister group to *Encarsia* (Polaszek and Hayat 1992). The sequence alignment was used from Babcock et al. (2001), and only one additional insertion event was needed to accommodate an extra base found in all populations of *Enc. estrellae*. A strict consensus of the three resulting trees is presented in Fig. 4.3, which conflicted only in the relationships of species within the *inaron* group. This tree is identical to a similar analysis from Heraty (2003), but with the addition of *Enc. arabica* Pedata and Polaszek. Other than the *parvella* group, species in groups represented by more than one species are all supported as monophyletic. The results of five analyses (Babcock et al. 2001; Manzari et al. 2002; Heraty 2003; Pedata and Polaszek 2003; and current analysis) are generally the same, but with different placement of *Enc. nigricephala*, *Enc. aurantii* and in some of the between group relationships. In all of the results, *Encarsiella* falls within *Encarsia*. To constrain *Encarsia* as monophyletic, with *Encarsiella* as a sister taxon, an additional 32 steps are required to explain the difference for both of the new analyses (34 and 82 taxa). As reported in Babcock et al. (2001), the relationships within species groups do not change under the constraint hypothesis.

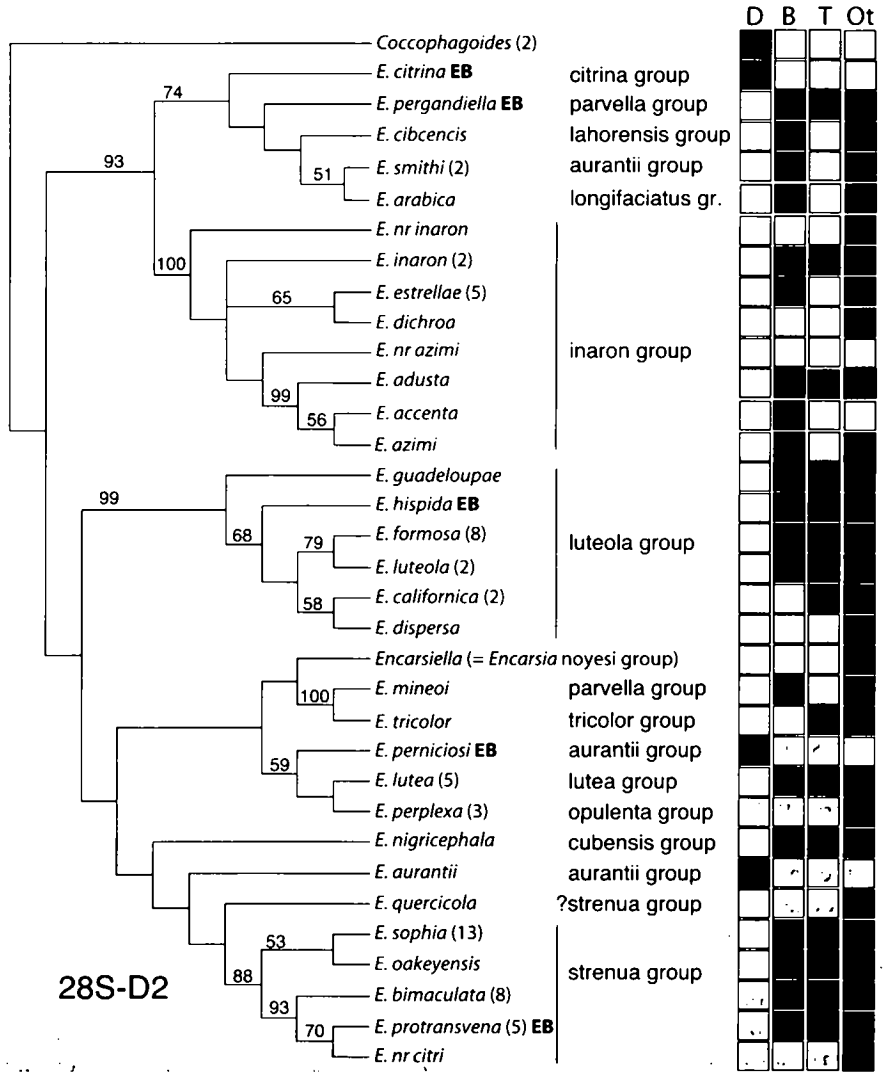

Fig. 4.3 Strict consensus of three trees of 856 steps (c.i. 0.41, r.i. 0.62) recovered from a parsimony analysis of 28S-D2 rDNA from 32 species of *Encarsia* and two closely related genera (*Coccophagoides* and *Encarsiella*). Data were analyzed using PAUP 4.0*b9 (Swofford 2002) using 100 random addition sequences and TBR branch swapping. Only the 28S-D2 transcript region without the first 134 bases (highly conserved region not sequenced for the Manzari et al. 2002 species) was used. Bootstrap proportions greater than 50% are shown above branches. The same results were obtained when additional populations, identified by the numbers in parentheses, were added for a total of 82 terminal taxa (sequences from Babcock et al. 2001; and Manzari et al. 2002; some names corrected from Schmidt et al. 2001), but with 17 trees of 905 steps. These were identical to the 3 trees after pruning out the extra populations. Behavioral attributes indicated: D = Diaspididae host; B = *Bemisia* host; T = *Trialeurodes vaporariorum* host; O = other whitefly host. Species with bacterial associate marked with EB.

At this point it is difficult to interpret these results. Either *Encarsiella* is not a valid genus but simply an aberrant group within *Encarsia*, *Encarsia* are not a monophyletic group (potentially many genera), or we have simply not sampled enough species or gene regions to develop a satisfactory result. Based on similar information, *Encarsiella* was recently transferred and placed as the *Encarsia noyesi* species group (Schmidt and Polaszek 2007b). As only one gene region has currently been sampled in 32 of 343 species, the latter is probably true for now. However, the amount of genetic divergence within *Encarsia* may suggest an old divergence. For both the D2 and D3 expansion regions of 28S rDNA, the level of divergence found between species groups is equivalent to the variation between subfamilies or families of other Chalcidoidea (Heraty 2003). Adding more species of *Encarsia*, as well as other genera of Coccophaginae, will be necessary to resolve the phylogeny of the group, but at least an initial framework has been developed.

4.5 Biological Attributes of *Encarsia*

It is difficult to assess biological changes within a phylogenetic perspective when most of the specialized aspects of behavior are known for only a few species or appear to be unique characteristics within *Encarsia*. Behavioral traits associated with mating and reproduction are very clearly elucidated in Hunter and Woolley (2001) and we do not plan to review these biologies here.

4.5.1 Sex Ratio Distortion in Encarsia

Wolbachia is recognized as a sex-ratio determining Proteobacteria, but within *Encarsia* has been found only in *Enc. formosa*, which is parthenogenetic (Zchori-Fein et al. 2001). The recognized sister group, *Enc. luteola*, is bisexual, and of the other species of *Encarsia* assayed none has *Wolbachia* (Fig. 4.3; marked by EB). A new bacterial associate belonging to the Cytophaga-Flexibacter-Bacteriod group of bacteria (EB) was, however, identified in six species of *Encarsia* that are dispersed across the genus (Fig. 4.3; Zchori-Fein et al. 2001). In all species, but excluding one population of *Enc. pergandiella*, the bacterium was associated with parthenogenesis. A phylogeny of the EB bacteria using 16S rDNA placed the bacteria within *Encarsia* as monophyletic with a divergence between the sequence of EB in *Enc. hispida* versus that of *Enc. berlesei*, *Enc. citrina* and *Enc. pergandiella* that had bootstrap support of 88% (Zchori-Fein et al. 2001). This divergence may correspond to the phylogenetic divergence between *Enc. hispida* and both *Enc. citrina* and *Enc. pergandiella* in Fig. 4.3. As more sequences of the EB bacteria and associated *Encarsia* become known, it will be interesting to note if the two phylogenies are concordant.

4.5.2 Host Relationships of Encarsia

Encarsia species are endoparasitoids, with one potential case of ectoparasitism known for both sexes of *Enc. ectophaga* (Silvestri) on armored scale (Hunter and Woolley 2001). Most species of *Encarsia* are autoparasitoids, with female eggs deposited on a primary host and male eggs deposited as parasitoids of the same or other species of *Encarsia* (Walter 1983a, b; Viggiani 1984; Polaszek 1991; Williams and Polaszek 1996; Hunter and Woolley 2001); however, males and females of *Enc. inaron* and *Enc. longicornis* Mercet are both primary parasitoids of whiteflies and in some species males develop as primary parasitoids of lepidopteran eggs (Hunter and Woolley 2001).

Whiteflies are the recorded host for 146 species of *Encarsia* (Table 4.1). The *aurantii* group, as defined by Heraty et al. (2007), includes 11 species attacking whiteflies and 19 species parasitic on armored scale. Three species groups comprised of 15 species are parasitic only on armored scale, and another 10 unplaced species of *Encarsia* have been reared from scales (Table 4.1). Only the *flavoscutellum* group is exclusively parasitic on another group of Hemiptera, the Hormaphididae (Evans et al. 1995). Hosts in the Coccidae, Pseudococcidae, Psyllidae and Thysanoptera are all considered as doubtful records (Polaszek 1991; Williams and Polaszek 1996). Lepidopteran eggs are parasitized by two species, in different species groups. *Encarsia porteri* (Mercet) is heterotrophic with females developing in whiteflies and males only in lepidopteran eggs (Polaszek 1991), and an undescribed species closely related to *Enc. inaron* has both males and females developing only in eggs of Lepidoptera (Williams and Polaszek 1996).

The outgroup used in the phylogenetic analysis, *Coccophagoides*, is a parasite of armored scale, whereas the two proposed sister taxa of *Encarsia, Encarsiella* and *Dirphys*, are whitefly parasitoids (Noyes 2001). A shift to scale parasitism is not a unique event within *Encarsia* (Babcock et al. 2001, Fig. 4.3). Given the distribution of armored scale parasitism for the taxa in Fig. 4.3, it is more parsimonious to assume that parasitism of whiteflies is ancestral, and that armored scale parasitism occurred independently at least three times.

A total of 42 species distributed across 12 species groups (and unplaced species) have been reared from *Bemisia* (Table 4.1). The *inaron, luteola, parvella* and *strenua* groups have the largest number of species known to attack *Bemisia*. These groups also have among the largest numbers of *Encarsia* species, although the *aurantii* group (43 species) has only two *Bemisia* parasitoids and the *opulenta* group (16 species) has no species attacking *Bemisia*. Only eight species of *Encarsia* have been reared exclusively from *Bemisia* (*Enc. accenta* Schmidt, *Enc. desantisi* Viggiani, *Enc. duorunga* Hayat, *Enc. mohyuddini* Shafee and Rizvi, *Enc. polaszeki* Evans, *Enc. reticulata* Rivnay and *Enc. silvestrii* Viggiani and Mazzone) (Heraty et al. 2007). In some cases, this apparent host specificity at the generic level may be simply due to not having encountered enough specimens to record them from different hosts. For example, *Enc. polaszeki* has been encountered and reared only once (Evans 1997). Most species of *Encarsia* that attack *Bemisia* also parasitize at least one other genus of whiteflies,

with six of the most common species (*Enc. lutea, Enc. formosa, Enc. nigricephala, Enc. pergandiella, Enc. protransvena* and *Enc. sophia*) attacking more than five host genera (Noyes 2001; Heraty et al. 2007). *Encarsia bimaculata* was found exclusively on *Bemisia* as part of an extensive survey of whiteflies in Florida by Fred Bennett where it was introduced (Heraty and Polaszek 1999); however, Schmidt et al. (2001) reared this species from *Bemisia* and the invasive greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). *Encarsia bimaculata* may be host specific under natural conditions or may attack different genera within its native range (Southeast Asia). There does not seem to be a correlation between the phylogeny of the *Encarsia* groups and the number and/or the type of host utilized (Fig. 4.3).

Of the species of *Encarsia* with known host associations, 119 have been reared from a single host and 73 from multiple hosts, and of these, 22 species have been reared from more than five host genera (Table 4.1). Because of problems of correct parasitoid or host identification, a general focus on rearing records from agricultural systems, and the chance of encountering both host and parasitoid in the field, the numbers of host genera attacked in Table 4.1 may not be overly representative of most species. Although the number of species that attack 1–3 host genera may be debatable, there is little doubt that 11 of the species groups include species that are extreme generalists.

4.6 Biological Control of *Bemisia*

From 1991 to 1998, the Mission Biological Control Laboratory processed 18 foreign shipments of seven species of *Encarsia*, which included *Enc. bimaculata* (as *Enc.* nr *strenua*) (India, Thailand), *Enc. formosa* (Greece, Egypt, Thailand), *Enc.* near *hispida* (Brazil), *Enc. lutea* (Cyprus, Israel, Spain), *Enc.* near *pergandiella* (Brazil), *Enc. sophia* (as *Enc. transvena*) (Malaysia, Philippines, Spain, Taiwan, Thailand) and *Encarsia* sp. (*parvella* group) (Dominican Republic) (Goolsby et al. 1998). Only three of these species were released into the field in the Lower Rio Grande Valley of Texas (*Enc.* nr *hispida* [ex Brazil, 2,400 specimens], *Enc. lutea* [ex Cyprus, 5,600 specimens] and *Enc. sophia* [ex Spain, 60,000]). All species were initially recovered in Texas, but in very low numbers. *Encarsia bimaculata*, which had the second highest laboratory evaluation but a poor field cage evaluation, was not released in Texas. *Encarsia bimaculata* is widespread in Southeast Asia (Huang and Polaszek 1998; Schmidt et al. 2001). This species was released in Florida (climatically similar to Southeast Asia) and was recovered from field collections of *Bemisia* on *Euphorbia, Sesamum, Chamaesyce*, and *Magnolia* in 1992 and 1993 (Heraty and Polaszek 1999). However, recent recoveries have not been made in Florida (Evans, personal communication). Geographic populations of six of the aforementioned *Encarsia* species (excepting *Enc.* sp. nr. *parvella*) were released in desert valleys of Arizona and California, but only *Enc. sophia* (*ex* Pakistan) eventually became established (see Chapter 13). This is noteworthy because large numbers ("hundreds of thousands") of *Enc. sophia* from Pakistan (obtained earlier through another project) had been released into California's Imperial Valley from 1991 to

1992 against earlier outbreaks of *B. tabaci* biotype "A", but without any recoveries (Hoelmer 1995, see Chapter 13). Most of the common species attacking *Bemisia* (*Enc. formosa*, *Enc. lutea*, *Enc. pergandiella*, *Enc. protransvena* and *Enc. sophia*) are essentially cosmopolitan (Polaszek et al. 1992; Huang and Polaszek 1998; Schmidt et al. 2001). However, different populations often exhibit very different behavioral and ecological responses (Goolsby et al. 1998). As an example, the Nile and Netherlands strains of *Enc. formosa* are successful in attacking *Bemisia* on *Poinsettia*, whereas other strains of *Enc. formosa* are not (Heinz 1995). The number of host species attacked and the success of the parasitoid is likely to be determined by ecological factors such as plant characteristics and habitat, as well as historical associations with particular host groups (Hoelmer 1995).

We would contend that insufficient effort has been focused on the evaluation of species and populations in the *inaron* and *strenua* groups, both of which have the highest proportion of *Bemisia* parasitoids. Notably, in the control of the citrus blackfly, *Aleurocanthus woglumi* Ashby, more than 25,000 individuals of five species of *Encarsia* were imported for the control program in Mexico, and more than 4 million parasitoids captured and re-released in Mexico (Clausen 1978). This was one of the first programs to demonstrate the importance of different species or populations in different habitats and the differential success of various species at different stages of the control program. Control by species of *Encarsia* has ranged from single species introductions followed by immediate success (Bellows et al. 1992), augmentative releases for economic control (van Lenteren and Woets 1988; Hoddle et al. 1998), to multiple releases of locally important species (Clausen 1978). Along with the large numbers of species that remain to be discovered, *Encarsia* will continue to have significant impact on the control of whitefly and scale pests.

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References

Babcock, C.S. and J.M. Heraty. 2000. Molecular markers distinguishing *Encarsia formosa* Gahan and *Encarsia luteola* Howard (Hymenoptera: Aphelinidae). Annals of the Entomological Society of America 93: 738–744.

Babcock, C.S., J.M. Heraty, P.J. De Barro, F. Driver, and S. Schmidt. 2001. Preliminary phylogeny of *Encarsia* Förster (Hymenoptera: Aphelinidae) based on morphology and 28S rDNA. Molecular Phylogenetics and Evolution 18: 306–323.

Bellows, T.S., T.D. Paine, J.R. Gould, L. Bezark, J.C. Ball, W. Bentley, R. Coviello, J. Downer, P. Elam, D. Flaherty, P. Gouveia, K. Koehler, R. Molinar, N. O'Connell, E. Perry, and G. Vogel. 1992. Biological control of ash whitefly: A success in progress. California Agriculture 46: 24–28.

Blackeljau, T., L. De Bruyn, H. De Wolf, K. Jordaens, S. Van Dongen, R. Verhagen, and B. Winnepenninckx. 1995. Random amplified polymorphic DNA (RAPD) and parsimony methods. Cladistics 11: 119–130.

Chou, K.-C., Y.-S. Su, L.-Y.Chou, and C.-C. Ko. 1996. New records of Aphelinidae (Hymenoptera) from Taiwan. Journal of Agricultural Research 45: 195–202.

Clausen, C.P. 1978. Introduced parasites and predators of arthropod pests and weeds: A world review. US Department of Agriculture, Agricultural Research Service Agricultural Handbook 480.

DeBach, P. and M. Rose. 1981. A new genus and species of Aphelinidae with some synonymies, a rediagnosis of *Aspidiotiphagus* and a key to pentamerous and heteromerous Prospaltellinae (Hymenoptera: Chalcidoidea: Aphelinidae). Proceedings of the Entomological Society of Washington 83: 658–679.

Evans, G.E. 1997. A new *Encarsia* (Hymenoptera: Aphelinidae) species reared from the *Bemisia tabaci* complex (Homoptera: Aleyrodidae). Florida Entomologist 80: 24–27.

Evans, G.E. and C.L. Angulo. 1996. A new species of *Encarsia* (Hymenoptera: Aphelinidae) from Costa Rica. Florida Entomologist 79: 582–586.

Evans, G.E. and J.A. Castillo. 1998. Parasites of *Aleurotrachelus socialis* (Homoptera: Aleyrodidae) from Colombia including descriptions of two new species (Hymenoptera: Aphelinidae Platygasteridae). Florida Entomologist 81: 171–178.

Evans, G.E., A. Polaszek, and F.D. Bennett. 1995. The taxonomy of the *Encarsia flavoscutellum* species-group (Hymenoptera: Aphelinidae), parasitoids of Hormaphididae (Homoptera: Aphidoidea). Oriental Insects 29: 33–45.

Evans, G.E. and A. Polaszek. 1997. Additions to the *Encarsia* parasitoids (Hym.: Aphelinidae) from Costa Rica. Florida Entomologist 79: 582–586.

Evans, G.E. and A. Polaszek. 1998. The *Encarsia cubensis* species-group (Hymenoptera: Aphelinidae). Proceedings of the Entomological Society of Washington 100: 222–233.

Giorgini, M. and M.M. Monti. 2003. Molecular differentiation of closely related species (Hymenoptera: Aphelinidae) based on mitochondrial COI gene. Abstracts from the XIII International Entomophagous Insects Workshop. Journal of Insect Science 3 (33): 9.

Gomez, J. and O. Garcia. 2000. A new species of *Encarsia* (Hymenoptera: Aphelinidae), a parasitoid of whitefly *Aleurodicus* sp. (Homoptera: Aleyrodidae) in Mexico. Pan-Pacific Entomologist 76: 49–51.

Goolsby, J.A., M.A. Ciomperlik, B.C. Legaspi Jr., J.C. Legaspi, and L.E. Wendel. 1998. Laboratory and field evaluation of exotic parasitoids of *Bemisia tabaci* (Gennadius) (Biotype "B") (Homoptera: Aleyrodidae) in the lower Rio grande Valley of Texas. Biological Control 12: 127–135.

Hayat, M. 1983. The genera of Aphelinidae (Hymenoptera) of the world. Systematic Entomology 8: 63–102.

Hayat, M. 1989. A revision of the species of *Encarsia* Foerster (Hymenoptera: Aphelinidae) from India and the adjacent countries. Oriental Insects 23: 1–131.

Hayat, M. 1998. Aphelinidae of India (Hymenoptera: Chalcidoidea): A taxonomic revision. Memoirs of Entomology, International, Vol. 13.

Heinz, K. 1995. Predators and parasitoids as biological control agents of *Bemisia* in Greenhouses. In D. Gerling and R.T. Mayer, eds., Bemisia: 1995: Taxonomy, Biology, Damage, Control and Management, pp. 435–449. Intercept Press, Andover.

Heraty, J.M. 2003. Molecular Systematics, Chalcidoidea and Biological Control. In L. Ehler, R. Sforza, and T. Mateille, eds., Genetics, Evolution and Biological Control, pp. 39–71. CAB International, Wallingford, Oxfordshire.

Heraty, J.M. and A. Polaszek. 2000. Morphometric analysis and descriptions of selected species in the *Encarsia strenua* group (Hymenoptera: Aphelinidae). Journal of Hymenoptera Research 9: 142–169.

Heraty, J.M., J.B. Woolley, and A.P. Polaszek. 2007. Catalog of the *Encarsia* of the World. http://cache.ucr.edu/~heraty/Encarsia.cat.pdf.

Hernández-Suárez, E., A. Carnero, A. Aguiar, G. Prinsloo, J. LaSalle, and A. Polaszek. 2003. Whitefly parasitoids (Hemiptera: Aleyrodidae; Hymenoptera: Aphelinidae, Euophidae, Platygastridae) from the Macaronesian archipelagos of the Canary Islands, Madiera and the Azores. Systematics and Biodiversity 1: 55–108.

Hoelmer, K.A. 1995. Whitefly parasitoids: Can they control field populations of *Bemisia*? In D. Gerling and R.T. Mayer, eds., *Bemisia*: 1995: Taxonomy, Biology, Damage, Control and Management, pp. 451–476. Intercept Press, Andover.

Hoddle, M.S., R.G. Van Dreische, and J.P. Sanderson. 1998. Biology and use of the whitefly parasitoid *Encarsia formosa*. Annual Review of Entomology 43: 645–669.

Huang, J. 1994. Systematic Studies on Aphelinidae of China, Chongqing Publishing House, Chongqing, Sichuan.

Huang, J. and A. Polaszek. 1998. A revision of the Chinese species of *Encarsia* Förster (Hymenoptera: Aphelinidae): Parasitoids of whiteflies, scale insects and aphids (Hemiptera: Aleyrodidae, Diaspididae, Aphidoidea). Journal of Natural History 32: 1825–1966.

Hunter, M.S. and J.B. Woolley. 2001. Evolution and behavioral ecology of heteronomous aphelinid parasitoids. Annual Review of Entomology 46: 251–290.

Jasnosh, V.A. 1989. Species of the genus *Encarsia* Foerster (Hymenoptera: Aphelinidae) – parasites of aleyrodids in the USSR. Proceedings of the Zoological Institute, Leningrad 191: 109–121.

Jasnosh, V.A. 1995. 48. Family Aphelinidae. In P.A. Ler, ed., Keys to Insects of the Far East of Russia, 4:506–551. Vladivostok: Dal'nauka.

Kirk, A.A., L.A. Lacey, J.K. Brown, M.A. Ciomperlik, J.A. Goolsby, D.C. Vacek, L.E. Wendel, and B. Napompeth. 2000. Variation in the *Bemisia tabaci s. l.* species complex (Hemiptera: Aleyrodidae) and its natural enemies leading to successful biological control of *Bemisia* biotype B in the USA. Bulletin of Entomological Research 90: 317–327.

Krishnan, B. and B.V. Vasantharaj David. 1996. Records and descriptions of some aphelinid parasitoids of Aleyrodidae (Homoptera: Insecta) from India. Jai Research Foundation, Valvada, Gujarat.

Kuwana, I. 1934. Notes on a newly imported parasite of the spiny whitefly attacking citrus in Japan. 5th Pacific Science Congress Proceedings (1933) 5: 3521–3523.

Manzari, S., A. Polaszek, R. Belshaw, and D.L.J. Quicke. 2002. Morphometric and molecular analysis of the *Encarsia inaron* species-group (Hymenoptera: Aphelinidae), parasitoids of whiteflies (Hemiptera: Aleyrodidae). Bulletin of Entomological Research 92: 165–175.

Mazzone, P. 1983. Contributo alla conocenza morfo-biologica degli Afenlinidi. 1. Osservazioni sugli stadi preimmaginali e sulla biologia de *Encarsia partenopea* Masi. ca delle specie del complesso *Encarsia* Foerster - *Prospaltella* Ashmead (Hym. Aphelinidae). Bollettino del Laboratario di Entomologia Agraria 'Filippo Silvestri' di Portici 40: 125–136.

McAuslane, H.J., F.A. Johnson, D.A. Knauft, and D.L. Colvin. 1993. Seasonal abundance and within-plant distribution of parasitoids of *Bemisia tabaci* (Homoptera: Aleyrodidae) in peanuts. Environmental Entomology 22: 1043–1050.

Myartseva, S.N. 2001. A new species of parasitoid wasp of the genus *Encarsia* (Hymenoptera: Aphelinidae) from Tamaulipas, Mexico. Acta Zoologica Mexicana (Nueva Serie) 82: 13–18.

Nemec, V. and P. Stary. 1984. Population diversity of *Encarsia formosa*, a biological control agent in glasshouses (Hymenoptera: Aphelinidae). Entomologica Generalis 9: 231–236.

Noyes, J.S. 1989. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. Ecological Entomology 14: 197–207.

Noyes, J.S. 2001. Encyrtidae of Costa Rica (Hymenoptera: Chalcidoidea), 1. Memoirs of the American Entomological Institute 62: 1–355.

Noyes, J.S. and M. Hayat. 1994. Oriental Mealybug Parasitoids of the Anagyrini (Hymenoptera: Encyrtidae). CAB International, London.

Pedata, P. and A. Polaszek. 2003. A revision of the *Encarsia longifasciata* species group (Hymenoptera: Aphelinidae). Systematic Entomology 28: 361–374.

Polaszek, A. 1991. Egg parasitism in Aphelinidae (Hymenoptera: Chalcidoidea) with special reference to *Centrodora* and *Encarsia* species. Bulletin of Entomological Research 81: 97–106.

Polaszek, A., S. Abd-Rabou, and J. Huang. 1999. The Egyptian species of *Encarsia* (Hymenoptera: Aphelinidae): a preliminary review. Zoologische Medelingen Leiden 73: 131–163.

Polaszek, A.P., G.A. Evans, and F.D. Bennett. 1992. *Encarsia* parasitoids of *Bemisia tabaci* (Hymenoptera: Aphelinidae, Homoptera: Aleyrodidae): A preliminary guide to identification. Bulletin of Entomological Research 82: 375–392.

Polaszek, A. and M. Hayat. 1992. A revision of the genera *Dirphys* Howard and *Encarsiella* Hayat (Hymenoptera: Aphelinidae). Systematic Entomology 17: 181–197.

Polaszek, A., S. Manzari, and D.L.J. Quicke. 2004. Morphological and molecular taxonomic analysis of the *Encarsia meritoria* species-complex (Hymenoptera, Aphelinidae), parasitoids of whiteflies (Hemiptera, Aleyrodidae) of economic importance. Zoologica Scripta 33: 403–421.

Schauff, M.E., G.A. Evans, and J.M. Heraty. 1996. A pictorial guide to the species of *Encarsia* (Hym: Aphelinidae) parasitic on whiteflies (Homoptera: Aleyrodidae) in North America. Proceedings of the Entomological Society of Washington 98: 1–35.

Schmidt, S., I.D. Naumann, and P.J. De Barro. 2001. *Encarsia* species (Hymenoptera: Aphelinidae) of Australia and the Pacific Islands attacking *Bemisia tabaci* and *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae): A pictorial key and descriptions of four new species. Bulletin of Entomological Research 91: 369–387.

Schmidt, S. and A. Polaszek 2007a. The Australian species of *Encarsia* Foerster (Hymenoptera, Chalcidoidea: Aphelinidae), parasitoids of whiteflies (Hemiptera, Sternorrhyncha, Aleyrodidae) and armoured scale insects (Hemiptera, Coccoidea: Diaspididae). Journal of Natural History 41: 2099–2265.

Schmidt, S. and A. Polaszek 2007b. *Encarsia* or *Encarsiella*? - redefining generic limits based on morphological and molecular evidences (Hymenoptera, Aphelinidae). Systematic Entomology 32: 81–94.

Stouthamer, R., H. Jianguo, F. van Kan, G.R. Platner, and J.D. Pinto. 1999. The utility of internally transcribed spacer 2 DNA sequences of the nuclear ribosomal gene for distinguishing sibling species of *Trichogramma* (Hymenoptera: Trichogrammatidae). Biocontrol 43: 421–440.

Swofford, D.L. 2002. *PAUP**. Version 4.0*b9. Sinauer, Sunderland, MA.

Toscano, N.C., S.J. Castle, T.J. Henneberry, and N.P. Castle. 1998. Persistent silverleaf whitefly exploits desert crop systems. California Agriculture 52: 29–33.

van Lenteren, J.C. and J. Woets. 1988. Biological and integrated control in greenhouses. Annual Review of Entomology 33: 239–269.

Viggiani, G. 1984. Bionomics of Aphelinidae. Annual Review of Entomology 29: 257–276.

Viggiani, G. 1988 [1987]. Le specie italiane del genere *Encarsia* Foerster (Hymenoptera: Aphelinidae). Bollettino del Laboratario di Entomologia Agraria 'Filippo Silvestri' di Portici 44: 121–179.

Viggiani, G. and P. Mazzone. 1979. Contributi alla conoscenza morfo-biologica delle specie del complesso *Encarsia* Foerster - *Prospaltella* Ashmead (Hym. Aphelinidae). Bollettino del Laboratario di Entomologia Agraria 'Filippo Silvestri' di Portici 36: 42–50.

Walter, G.H. 1983a. Differences in host relationships between male and female heteronomous parasitoids (Aphelinidae: Chalcidoidea): A review of host location, oviposition and pre-imaginal physiology and morphology. Journal of the Entomological Society of South Africa 46: 261–282.

Walter, G.H. 1983b. Divergent male ontogenies in Aphelinidae (Hymenoptera: Chalcidoidea): A simplified classification and a suggested evolutionary sequence. Biological Journal of the Linnean Society 19: 63–82.

Williams, T. and A. Polaszek. 1996. A re-examination of host relations in the Aphelinidae (Hymenoptera: Chalcidoidea). Biological Journal of the Linnean Society 57: 35–45.

Zchori-Fein, E. Y. Gottlieb, J.K. Brown, J.M. Wilson, T.L. Karr, and M.S. Hunter. 2001. A newly discovered bacterium associated with parthenogenesis and a change in host selection behavior in parasitoid wasps. Proceedings of the National Academy of Sciences 98: 12555–12560.