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Encarsia or *Encarsiella*? – redefining generic limits based on morphological and molecular evidence (Hymenoptera, Aphelinidae)

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Abstract. The genus *Encarsiella* (**syn.n.**) (Hymenoptera, Chalcidoidea, Aphelinidae) is synonymized with *Encarsia* on the basis of molecular and morphological characters. A phylogenetic analysis was conducted of the D2 expansion region of the 28S ribosomal DNA including thirty-eight *Encarsia* species. Our phylogenetic analysis revealed a polyphyletic origin of *Encarsiella* and confirmed the results of earlier analyses indicating the paraphyly of *Encarsia*. Four species are described as new (*Encarsia bifasciata* **sp.n.**, *E. caelata* **sp.n.**, *E. obliqua* **sp.n.** and *E. pilosa* **sp.n.**). The following species are transferred from *Encarsiella* to *Encarsia*: *Encarsia aleurodici* (Girault, 1916) **comb.n.**, *E. amabilis* (Huang & Polaszek, 1998) **comb.n.**, *E. boswelli* (Girault, 1915) **comb.n.**, *E. magniclava* (Girault, 1915) **comb.n.**, *E. narroi* Gómez & García **comb.n.**, *E. nepalensis* (Polaszek & Hayat, 1992) **comb.n.**, *E. noyesi* (Hayat, 1983) **comb.n.**, *E. pithecura* (Polaszek, 1999) **comb.n.**, *E. tachii* (Polaszek & Hayat, 1992) **comb.n.**, *E. taiwanensis* (Chou & Chou, 1994) **comb.n.** and *E. tamaulipeca* (Myartseva & Coronado-Blanco, 2002) **comb.n.** The generic limits of *Encarsia* are re-defined based on a re-assessment of morphological characters, and the results are discussed with respect to the current classification of the aphelinid subfamily Coccophaginae.

Introduction

The Coccophaginae is a moderately sized subfamily of the family Aphelinidae (Hymenoptera, Chalcidoidea) with currently about 690 species (Noyes, 2001). The genus *Encarsia* Förster is, with about 280 species (Polaszek *et al*., 1999), by far the most diverse group within the subfamily, followed by *Coccophagus* Westwood with about 230 described species (Noyes, 2001). Most remaining genera of the subfamily, including *Encarsiella* Hayat and *Dirphys* Ashmead, contain only a few or even a single species. All known *Encarsiella* and *Dirphys* species are primary endoparasitoids of Aleyrodidae, a biology which is also widespread within *Encarsia*. However, several apparently derived lineages of *Encarsia* parasitize Diaspididae, eggs of Plataspidae and, very occasionally, eggs of Lepidoptera (Williams & Polaszek, 1996).

Phylogenetic relationships within the subfamily were investigated by Polaszek & Hayat (1992) based on twenty-four morphological characters. In their analysis, the three genera *Dirphys*, *Encarsia* and *Encarsiella* together formed a monophyletic clade which was supported by five synapomorphies. The monophyly of each of the three genera was supported by a single synapomorphy, but relationships between them remained unresolved (Polaszek & Hayat, 1992). As a general tendency, for several characters, the resulting phylogeny suggested a character state evolution towards reduction: for instance, fewer antennal (in particular claval) segments, fewer setae on the dorsal mesosoma, fewer tarsal segments and a reduced wing venation (in particular, the postmarginal and stigmal veins are reduced).

A more recent phylogenetic analysis of twenty-four *Encarsia* and one *Encarsiella* species, based on morphological and molecular data, recovered all species groups that had been defined previously on the basis of morphology (Babcock *et al*., 2001). The analysis of fourteen morphological

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characters supported, although weakly, a sister group relationship between *Encarsia* and *Encarsiella*. However, the molecular analysis of the second expansion region of the 28S ribosomal RNA placed *Encarsiella* consistently within *Encarsia*, rendering *Encarsia* as paraphyletic with respect to *Encarsiella* (Babcock *et al*., 2001).

As part of an ongoing revision of the Australian *Encarsia* species (S. Schmidt & A. Polaszek, in prep.), additional sequence data of several *Encarsia* and apparent *Encarsiella* species were obtained. The phylogenetic analysis of the data confirmed the paraphyly of *Encarsia* found previously (Babcock *et al*., 2001). Furthermore, some *Encarsiella* species were separated from the previously analysed representatives of the genus as a monophyletic clade in a different part of the tree. In addition to supporting the paraphyly of *Encarsia*, the analysis suggests *Encarsiella*, as currently defined, to be polyphyletic. Apart from necessitating a comprehensive re-investigation of phylogenetic relationships within the Coccophaginae and related subfamilies, the current definition of the generic limits of the genus *Encarsia* hampers taxonomic revisions, because the generic placement of several species is currently highly problematic. This paper investigates and re-defines the generic limits of the genus *Encarsia* on the basis of morphological and molecular characters.

Materials and methods

The specimens used in this study were slide mounted as described by Noyes (1982) with the following modifications: specimens were placed in 10% KOH for approximately 5–7 min (depending on whether the specimen was dry or preserved in ethanol) and incubated at *c*. 97 °C using a block heater. The terminology of morphological characters follows Heraty & Polaszek (2000). All measurements of antennae and legs refer to the maximal length of the morphological structure in lateral view. Lengths of antennal segments were taken excluding the intersegmental membranes because they can vary depending on how much the antenna was stretched during slide preparation. The fore wing length is the distance between its most apical point and the proximal end of the submarginal vein, excluding the tegula. The length of the ovipositor was measured as the distance between the proximal margin of the basal ring to the extreme apex (fig. 1B in Heraty & Polaszek, 2000: 145). Care should be taken if specimens are distorted because this can affect measurements, in particular of the ovipositor; all reference points of the structure to be measured should be equidistant from the microscope objective.

DNA was extracted from single, whole specimens as described in De Barro & Driver (1997). The second expansion region of the 28S ribosomal DNA gene was amplified according to the protocol given in De Barro *et al*. (2000). Sequences were aligned using ClustalW (Thompson *et al*., 1994; Higgins *et al*., 1996). The selection of cost parameters can influence phylogenetic reconstruction (Wheeler, 1995; Giribet, 2003), and a sensitivity analysis was conducted to assess node stability across sets of parameters. The following ClustalW parameters were used: /align /type=dna /gapopen=x /gapextension=x /gapdist=2 /nopgap /nohgap /transweight=1. Gap costs were set at 1 : 1, 2 : 1, 2 : 2, 5 : 1, 5 : 5, 10 : 1, 10 : 5 and 10 : 10 (Table 1). Aligned sequences were analysed with PAUP* version 4.0b10 (Swofford, 2002) using maximum parsimony, heuristic search option with 1000 random addition sequences, maxtrees set to 1000, ten trees held at each step, and branch swapping by tree bisection and reconnection (TBR). All characters were assigned equal weight and gaps were treated as missing characters. The way in which gaps are treated can have a considerable effect on the phylogenetic reconstruction (Giribet & Wheeler, 1999), and hence all analyses were repeated with gaps coded as a fifth character state. Bootstrap analyses were performed using PAUP* with 10 000 replicates and ten random addition sequences, each with a single tree held at each addition step by assigning a value of unity to the parameters nchuck and chuckscore.

The specimens examined for this study are deposited in the following institutions: Australian National Insect Collection, Canberra, Australia (ANIC), Queensland Museum, Brisbane, Australia (QMBA), The Natural History Museum, London, U.K. (BMNH) and Zoologische Staatssammlung, Munich, Germany (ZSMG).

The molecular dataset includes fifty-seven *Encarsia* sequences representing thirty-eight species and sixteen species groups. Three species are not placed in any species group (*E. bifasciata* **sp.n.**, *E. pilosa* **sp.n.** and *E. quercicola* (Howard)). The species, their species group placement and the origin of the sample used for the molecular analysis are given in the Appendix. *Coccophagoides fuscipennis* (Girault) was used as outgroup species. Sequences have been deposited in the GenBank database under accession numbers DQ830991–DQ830999.

Phylogenetic analysis

Depending on the multiple alignment parameters employed in ClustalW, alignments of the D2 region comprised between 499 and 534 characters of which 255–261 positions were variable. The D2 sequences contained between 201 and

Table 1. Gap costs used for alignments in ClustalW and tree statistics resulting from the phylogenetic analysis of each alignment.

GO : GE	*N*	PI (%)	MPT	TL	H (%)
1 : 1	534	39.0	34	774	96.4
2 : 1	528	38.4	8	778	34.6
2 : 2	525	38.9	61	780	80.8
5 : 1	522	38.9	15	780	96.5
5 : 5	504	39.9	508	806	98.0
10 : 1	506	39.7	165	812	95.1
10 : 5	501	40.7	52	817	90.3
10 : 10	499	41.5	82	824	99.7

GE, gap extension penalty; GO, gap opening penalty; H, percentage of the number of times MPT was found; MPT, number of most parsimonious trees; *N*, number of characters; PI, percentage of parsimony-informative characters; TL, tree length of MPT.

208 parsimony-informative sites (38.4–41.5%, Table 1), and the number of most parsimonious trees resulting from heuristic searches across parameter sets resulted in trees with lengths of between eight (gap cost 2 : 1) and 508 (gap cost 5 : 5), with a consistency index of 0.44–0.45 and a retention index of 0.78–0.79. Figure 1 shows four strict consensus trees resulting from analyses with alignment gap costs set at 1 : 1 (a), 2 : 1 (b), 5 : 1 (c) and 10 : 5 (d). The analyses with gaps treated as an additional character state resulted in identical topologies with similar or identical bootstrap values, which did not differ by more than 10% from the values obtained in the analyses with gaps treated as missing characters. The χ^2 test of homogeneity of base frequencies across taxa did not result in significant differences ($P = 1.0$).

In all analyses, *Encarsiella* (= *Encarsia noyesi* species group) was placed within *Encarsia*. Furthermore, in six of the eight models, the ingroup consisted of two major clades (Fig. 1A–C): species which would have been included in *Encarsiella* under the traditional definition of the genus were placed in one clade, and species of the *E. noyesi* group were placed in the other major clade (Fig. 1A–C). The composition of these two major clades did not vary across reconstructions, and consisted of a clade containing *citrina*, *inaron*, *lahorensis*, *parvella* (partim), *smithi*, *tristis* species groups, and two unplaced species (*E. bifasciata* and *E. pilosa*), and a second clade containing all remaining species groups (but also a member of the *parvella* species group).

Nearly all species groups defined previously on the basis of morphological characters were recovered and received high bootstrap support (bootstrap values > 80), e.g. *E. strenua*, *E. lutea*, *E. luteola*, and *E. inaron* groups (Fig. 1 A–D). The species group placement of a few species needs to be re-investigated as they did not form monophyletic groups, e.g. *E. mineoi* (Viggiani) and *E. pergandiella* Howard, both of which belong to the *E. parvella* group. In addition, the two members of the *E. aurantii* group were placed in different parts of the tree, i.e. *E. aurantii* (Howard) and *E. perniciosi* as sister group of *E. flavoscutellum* Zehntner. The *E. aurantii* species group is currently very poorly delimited and needs to be re-defined.

Morphological characters

Clava

In *Encarsia*, the number of antennal claval segments varies from zero, i.e. clava not defined, to four segments, with a higher number of segments more common than an undefined or two-segmented clava. In members of the *E. noyesi* species group, the clava is three-segmented and the apical segment possesses an enlarged sensorial complex (cf. Fig. 4B). This sensorial area extends on F5, resulting in an oblique suture between F5 and F6. In all other *Encarsia* species, the apical claval segment is simple without a sensory area. In very rare cases, the clava is obliquely truncate and has a sensorial complex (as in *E. obliqua* **sp.n.**), but then the clava is only two-segmented (Fig. 4B).

Maxillary palp segments

The number of maxillary palp segments has long been regarded as separating *Encarsia* from *Encarsiella*, with the former having one and the latter two segments. However, *E. pulliclava* (Girault) and a few other *Encarsia* species have a two-segmented maxillary palp. In *Encarsiella*, the maxillary palp is always two-segmented. As a result of redefining the generic limits of *Encarsia*, this genus now includes several species with a two-segmented maxillary palp. Two-segmented maxillary palps probably have evolved several times independently within *Encarsia*, and/or reduction may have occurred in several lineages. Those species having two-segmented maxillary palps do not represent a monophyletic group.

Mandibles

All *Encarsia* species have either a three-toothed mandible or two teeth and a truncation. The only known exception so far is *E. boswelli* (Girault) which has a four-segmented mandible. This species is otherwise unusual for *Encarsia* because it is an egg-parasitoid of black stink bugs (Heteroptera: Plataspidae).

Setation of mesoscutum

The genus *Encarsia* traditionally included species with a low to moderate number of setae on the mesoscutal midlobe, ranging from zero to almost thirty, with the majority of species having four to twelve setae that are usually arranged in bilateral symmetry. Species with a large number of mesoscutal midlobe setae (thirty or more, up to about 100 setae) were usually placed in *Encarsiella* (Hayat, 1983). *Encarsia boswelli* was placed exceptionally in *Encarsiella*, despite having only six to fourteen setae on the mesoscutal midlobe.

Axilla

The relative length of the axillae has been used traditionally to separate *Encarsiella* from *Coccophagoides* and *Encarsia*, with *Encarsiella* having larger axillae separated from each other by not more than their own lengths (Hayat, 1983; Hayat, 1998). In *Coccophagoides* and *Encarsia*, the axillae are smaller and separated by more than the length of an axilla. Traditionally, in *Encarsia*, the distance between the axillae ranged from 1.2 to 2.0× the length of an axilla measured longitudinally as its greatest length, whereas, in *Encarsiella*, the distance was less than the length of an axilla due to its larger size. However, several examined *Encarsiella* species show marginal values, and, in some undescribed species, the distance ranges from 1.3 to 1.6, values typical for *Encarsia*. In a few species which are now included in *Encarsia* (*E. bifasciata* **sp.n.**, *E. tachii* (Polaszek & Hayat), *E. nepalensis* (Polaszek & Hayat), and *E. obliqua* **sp.n.**), the axillae are separated by a distance equal to or less than their greatest length.

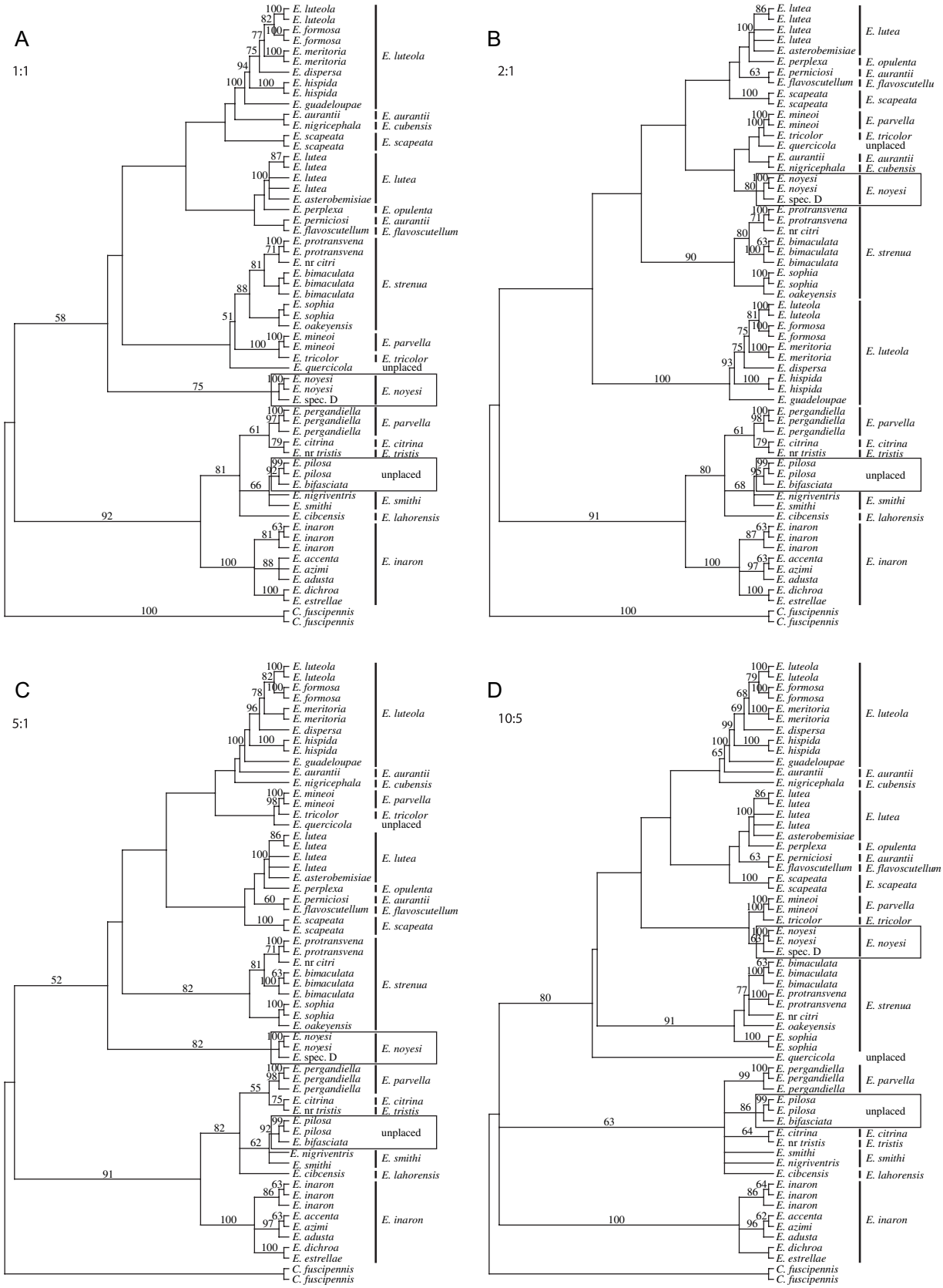

Table 2. Species formerly placed in *Encarsiella* and transferred to *Encarsia*, with geographical distribution and, if established, species group placement.

Species	Distribution	*Encarsia* species group
Encarsia aleurodici (Girault, 1916) **comb.n.**	Central & South America	*E. noyesi*
Encarsia amabilis (Huang & Polaszek, 1998) **comb.n.**	China	
Encarsia boswelli (Girault, 1915) **comb.n.**	Palaeotropical	
Encarsia magniclava (Girault, 1915) **comb.n.**	Central America	*E. noyesi*
Encarisa narroi (Gómez & García, 2000) **comb.n.**	Mexico	*E. noyesi*
Encarsia nepalensis (Polaszek & Hayat, 1992) **comb.n.**	Nepal	
Encarsia noyesi (Hayat, 1983) **comb.rev.**	Central America	*E. noyesi*
Encarsia pithecura (Polaszek, 1999 in Martin & Polaszek, 1999) **comb.n.**	Central America	*E. noyesi*
Encarsia tachii (Polaszek & Hayat, 1992) **comb.n.**	China	
Encarsia taiwanensis (Chou & Chou, 1994) **comb.n.**	Taiwan	
Encarsia tamaulipeca (Myartseva & Coronado-Blanco, 2002) **comb.n.**	Mexico	*E. noyesi*

Scutellum

The sculpture of the scutellum was used as a diagnostic character to separate *Encarsiella* from *Encarsia* (Hayat, 1983; Hayat, 1998). Most *Encarsia* species have a rather narrow, lens-shaped scutellum which is distinctly broader than its medial length, ranging from 1.5 to 2.2× broader than long. The sculpture of the scutellum is reticulate with a longitudinally sculptured area of elongate cells in the mid-line, or the sculpture is obscure and hardly discernible. In some species, including members of the *E. noyesi* species group (= *Encarsiella*), the scutellum is typically more rounded, usually not more than 1.5× as long as wide, and lacks the area of elongate cells in the mid-line.

Submarginal vein

The majority of *Encarsia* species have two setae on the submarginal vein. Exceptions are species of the *E. pulliclava* species complex with four to six setae, and several species described as new in the present study with three to four setae (*E. bifasciata* **sp.n.**), three to five setae (*E. pilosa* **sp.n.**), or four to five setae (*E. obliqua* **sp.n.**).

Stigmal vein

All species included previously in *Encarsiella* have a reduced stigmal vein, lacking a distinct constriction and not or only slightly angled away from the distal end of the marginal vein (cf. fig. 134a in Hayat, 1983: 93). This character shows some variation in *Encarsia* and, in most species, the stigmal vein is not as clearly defined as in members of the *E. strenua* group. Several species which we now recognize as *Encarsia* have a reduced stigmal vein, and some species which, on the basis of other characters would previously have been regarded as *Encarsiella*, have a pronounced stigmal vein with a pronounced constriction, for instance *E. pilosa* **sp.n.** (Fig. 5D).

Basal cell

The basal cell in *Encarsia* normally contains fewer than ten setae. The highest numbers have been recorded in *E. pulliclava* with nineteen to twenty-eight setae, a species which is similarly recognized by a very large number of setae on the mesoscutal midlobe (see character *Setation of mesoscutum*). The species described here as new are unusual in this respect because they all possess relatively large numbers of basal cell setae.

Taxonomy

Genus *Encarsia* Förster

Encarsia Förster, 1878: 65–66. Type species: *Encarsia tricolor* Förster, by original designation and monotypy.

Aspidiotiphagus Howard, 1894a: 229. Type species: *Coccophagus citrinus* Craw, by original designation. Synonymy by Viggiani & Mazzone 1979: 44.

Prospalta Howard, 1894b: 6. Type species: *Coccophagus aurantii* Howard, by designation of the ICZN under its Plenary Powers, Opinion 845, 1968: 12–13. Preoccupied by *Prospalta* Walker, 1857 in Lepidoptera.

Fig. 1. Strict consensus trees of phylogenetic analyses based on ClustalW alignments with gap costs set at 1 : 1 (A), 2 : 1 (B), 5 : 1 (C), and 10 : 5 (D). Numbers above branches indicate bootstrap support. The two frames on each tree contain species which agree to the definition of the genus *Encarsiella* as it was originally defined (*E. noyesi* species group) or species which would have been placed into *Encarsiella* on the basis of the traditional generic definition (*E. bifasciata* **sp.n.** and *E. pilosa* **sp.n.**).

Prospaltella Ashmead, 1904: 126. Replacement name for *Prospalta* Howard. Synonymy by Viggiani & Mazzone 1979: 44.

Mimatomus Cockerell, 1911: 464. Type species: *Mimatomus peltatus* Cockerell, by monotypy. Synonymy with *Prospaltella* by Girault 1917: 114.

Doloresia Mercet, 1912: 294–296. Type species *Prospaltella filicornis* Mercet, by original designation. Synonymy by Mercet 1930: 191.

Prospaltoides Brèthes, 1914: 12. Type species *Prospaltoides howardi* Brèthes, by original designation. Synonymy with *Aspidiotiphagus* by Brèthes 1916: 429.

Aspidiotiphagus (Paraspidiotiphagus) Alam, 1956: 359. Type species *Aspidiotiphagus flavus* Compere, by original designation. Synonymy by Viggiani & Mazzone 1979: 44 (subgenus not mentioned, but synonymy implied by synonymy of *Aspidiotiphagus* with *Encarsia*).

Aleurodiphilus De Bach & Rose, 1981: 659. Type species: *Aleurodiphilus americanus* DeBach and Rose, by original designation. Synonymy by Hayat 1983: 85.

Encarsiella Hayat, 1983: 85. Type species: *Encarsiella noyesi* Hayat, by original designation. Synonymy by Shafee & Rizvi, 1984: 379. **Syn.rev.**

Diagnosis

Colour. Variable from completely pale to partly brown and (particularly males) completely brown to dark brown or black; pale colours in life often yellow, but range from very pale yellow to dark yellow and orange. Wings hyaline or with dark infuscation behind marginal vein, very rarely with two cross bands.

Morphology. Head in frontal view usually wider than long. Eyes bare or setose. Mandibles normally with three teeth or two teeth and a truncation which may be separated by a distinct gap. Maxillary palp one-, rarely two-segmented. Labial palp one-segmented. Female antenna (excluding radicle and anellus) with eight segments, apical two or three segments often forming a distinct clava which is usually apically rounded and not distinctly spindle-shaped. In some species (*E. noyesi* species group, *E. obliqua*), suture between F5 and F6 at least slightly oblique, and F6 with sensory area, either conically shaped or obliquely truncate. Anellus usually small and often indistinct. Male antenna eight- or often seven-segmented. Pronotum medially with membranous incision. Mesoscutal midlobe with 0–28, usually 2–12, setae, very rarely with more (up to about 100) setae, these often arranged in bilateral symmetry, in particular if midlobe with small or moderate number of setae. Each mesoscutal side lobe with 1–5, usually 2–3 setae. Axillae small to large, longer than wide. Scutellum wider than long and usually with more or less distinct median furrow indicated by absent, weak, or longitudinal sculpture, rarely whole scutellum with distinctly reticulate sculpture; anterior and posterior margins convex, with two pairs of setae and one pair of placoid sensilla. Fore wing with distinct marginal fringe of very variable length from about one-tenth up to distinctly longer than maximal width of the disc. Submarginal vein shorter than marginal vein, normally with two setae, rarely with only one or more (5–6) setae. Anterior margin of marginal vein with a variable number of setae (often 6–8). Stigmal vein very short, always less than one-quarter of the length of the marginal vein. Stigmal vein often with a distinct constriction, distinctly angled with marginal vein, sometimes without constriction and hardly angled with marginal vein, often inconspicuous anteriorly and apically, with four sensilla. Postmarginal vein absent. Fore wing disc sparsely to densely setose, in some species with bare or sparsely setose area near anterior margin proximal of stigmal vein. Linea calva absent. Basal cell usually with less than ten setae, rarely without setae or with a larger number of setae (up to about twenty-eight). Legs with tarsi of fore and hind legs five-segmented; tarsi of mid leg five- (most species) or four-segmented. Basitarsus of mid and hind legs sometimes ventrally with stout, peg-like setae. Gaster (= metasoma without petiole) with seven tergites (T1–T7); length of tergite 7 (T7) very variable, ranging from distinctly wider than long to longer than wide; apex of T7 always membranous and pale/translucent; T1 usually without setae, T2–T4 usually with 1–5 setae on each side, T5–T6 usually each with two setae on each side (occasionally more) and T7 with four setae (occasionally six). Male genitalia usually with the phallobase several times as long as wide, with a truncate or rounded apex and without digiti; aedeagus generally longer than phallobase.

The presence of the following character states is required for a positive diagnosis of *Encarsia* (females): fore and hind tarsi five-segmented; antenna eight-segmented (excluding radicle); scutellum with two pairs of setae; marginal vein longer than submarginal vein; postmarginal vein absent; stigmal vein very short, always less than one-quarter of the length of the marginal vein.

The closest relatives to *Encarsia* appear to be *Coccophagus* and *Dirphys*. However, the phylogeny of the Coccophaginae is by no means resolved, and we are working on this project currently using a combination of morphological and molecular analyses. Preliminary results suggest that *Coccophagus* is almost certainly both polyphyletic and paraphyletic with respect to several other coccophagine genera. *Encarsia*, as defined here, can be separated from *Coccophagus* best by the latter having a minimum of six (and often more) setae on the scutellum (four in *Encarsia*). *Dirphys* can be separated from *Encarsia* by the apparent division of the mesoscutal side lobe (entire in *Encarsia*) (Polaszek & Hayat, 1992), but this character requires re-examination and re-evaluation.

Encarsia bifasciata **sp.n.**

(Fig. 2A–D)

Female. *Colour*. Head (Fig. 2C) brown, vertex and lower face paler, or head pale/mostly pale with brown markings. Mesosoma (Fig. 2A) brown except mesoscutum pale and brown only anteriorly. Metasoma brown. Antenna (Fig. 2B)

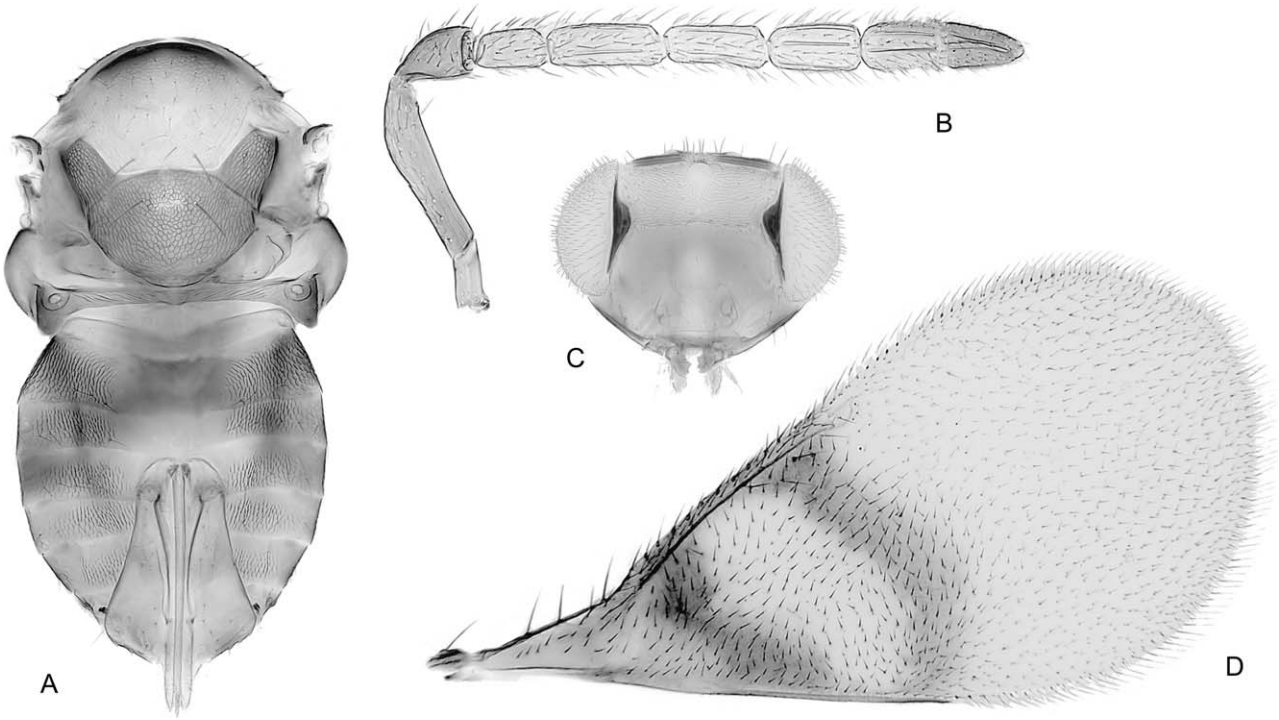

Fig. 2. *Encarsia bifasciata* **sp.n.**: A, mesosoma and gaster; B, female antenna; C, head; D, fore wing.

yellow, radicle, pedicel, scape and clava brown. Fore wing (Fig. 2D) with two narrow dark bands behind marginal vein and base of wing brown. Legs yellow except coxae and bases of femora brown.

Morphology. Vertex with rugosely strigose surface sculpture. Maxillary palp two-segmented. Antennal formula 1,1,4,2 (Fig. 2B). F1–F5 cylindrical, F6 conical and slightly shorter than or subequal in length to preapical segment. Pedicel subequal in length to or slightly longer than F1 (1.00–1.28). F1 1.47–1.81× as long as broad, distinctly shorter than F2 (0.54–0.59) and F3 (0.58–0.65). F2 slightly longer than F3 (1.08–1.10). Flagellomeres with the following number of longitudinal sensilla: F1, 0; F2, 3; F4, 3; F4, 3–4; F5, 4–5; F6, 3. F1–F5 apically with papillate sensilla. Mandible with two teeth and a truncation. Midlobe of mesoscutum (Fig. 2A) with about 50–70 setae, evenly reticulate, side lobes with three setae each. Axillar seta placed in anterior half, closer to inner than to outer margin. Posterior pair and lateral setae of mesoscutal midlobe larger than remaining setae of mesoscutum. Scutellum about 1.5× as broad as long with distinctly reticulate surface sculpture, lateral cells slightly elongate and larger than cells in the medial part of scutellum. Scutellar sensilla separated by approximately 2–4× the width of a sensillum. Distance between anterior pair of scutellar setae subequal to distance between posterior pair, anterior pair located anterior to scutellar sensilla. Fore wing (Fig. 2D) 2.1× as long as width of disc, densely setose, setation of disc slightly denser than those of area behind marginal vein. Basal cell with 17–23 setae. Longest setae of marginal fringe slightly less than one-tenth of width of disc. Submarginal vein with 3–4 setae, marginal vein anteriorly with 10–15 setae. Stigmal vein distinct with slight constriction, slightly angled with marginal vein. Apical spur of mid tibia longer than half the length of the corresponding basitarsus (0.72–0.73). Mid tarsus about 0.7× as long as mid tibia. Basitarsus of mid leg ventrally with stout setae with distinct bases, almost as long as combined length of four following tarsal segments. Metasoma with distinct longitudinally strigose surface sculpture. Tergites on each side with the following number of setae: T1, 3–4; T2, 4–7; T3, 5–6; T4, 5–6; T5, 2–7; T6, 3; T7 with 4 setae. Ovipositor subequal in length to mid tibia (1.03–1.07). Third valvula very narrow and 0.50× as long as second valvifer.

Male. Unknown.

Species group placement. Not established.

Distribution. Australia: Queensland.

Host. Aleyrodidae: *Aleurodicus* sp.

Material examined. Holotype ♀, Australia, Queensland, Forty Mile Scrub, 6.vii.2000 (*P. De Barro*) ex *Aleurodicus* sp. on *Diospyus* sp. (Ebenaceae) (ANIC); paratypes 3 ♀, same location and collector as holotype, but ex *Aleurodicus* sp. on *Diospyus* sp. and ex dark-bodied whitefly pupae on rainforest plant (ANIC, BMNH, ZSMG).

***Encarsia caelata* sp.n.**
(Fig. 3A–D)

Female (holotype). *Colour*. Head yellow, frontovertex anteriorly, gena, postgena, and malar space brown (Fig. 3C). Mesosoma and metasoma brown (Fig. 3A), metasomal tergite 8 apically yellow. Third valvula darker brown than second valvifer (Fig. 3A). Antenna (Fig. 3B) yellow except basal third and apex of scape, pedicel, F1, F5, and F6 brown. Fore wing (Fig. 3D) with dark band behind proximal half of marginal vein and a second, narrow band proximal of stigmal vein, fading towards posterior margin of wing; basal cell with brown infuscation distally. Legs yellow except mid and hind coxae, and hind femur brown.

Morphology. Maxillary palp one-segmented. Frontovertex with rugosely strigose surface sculpture. Antennal formula (Fig. 3B) 1,1,3,3. F1 broader than F2, F2 and F3 cylindrical, F4 and F5 slightly widening towards apex, F6 conical and subequal in length to preapical segment. Scape rather stout, 2.9× as long as broad, apically truncate. Pedicel almost globular, shorter than F1 (0.70). F1 subequal in length to F2 and F3. Flagellomeres with the following number of longitudinal sensilla: F1, 3; F2, 3; F4, 3; F4, 4; F5, 4; F6, 3. F1–F5 apically with papillate sensilla. Eyes with scattered setation (Fig. 3C), setae dark and distinct. Mandible with two teeth and a truncation. Midlobe of mesoscutum with eight setae, arranged symmetrically, all setae close to margins, central part asetose, densely reticulate, cells strongly longitudinally elongate, side lobes with two setae each. Axillar seta placed close to anterior margin of axilla, slightly closer to inner than to outer margin. Posterior pair and lateral setae of mesoscutal midlobe slightly larger than remaining setae of mesoscutum. Scutellum about 1.9× as broad as long with distinct reticulate surface sculpture, and a broad very weakly sculptured medial furrow. Scutellar sensilla separated by approximately 8× the width of a sensillum. Distance between anterior pair of scutellar setae distinctly greater than between posterior pair, anterior pair located anterior to scutellar sensilla. Fore wing (Fig. 3D) 2.4× as long as width of disc, moderately dense setose, setation behind distal part of marginal and stigmal veins slightly more scattered. Basal cell with thirteen setae. Longest setae of marginal fringe about 0.23× as long as width of disc. Submarginal vein with two setae, marginal vein anteriorly with eight setae. Stigmal vein distinct with very weak constriction, slightly angled with marginal vein. Apical spur of mid tibia longer than half the length of the corresponding basitarsus (0.8). Mid tarsus about 0.7× as long as mid tibia. Basitarsus of mid leg ventrally with stout setae with distinct bases, slightly shorter than combined length of four following tarsal segments. Propodeum with distinct strigose-reticulate surface sculpture. Metasoma including petiole with very distinct surface sculpture, medially reticulate, laterally

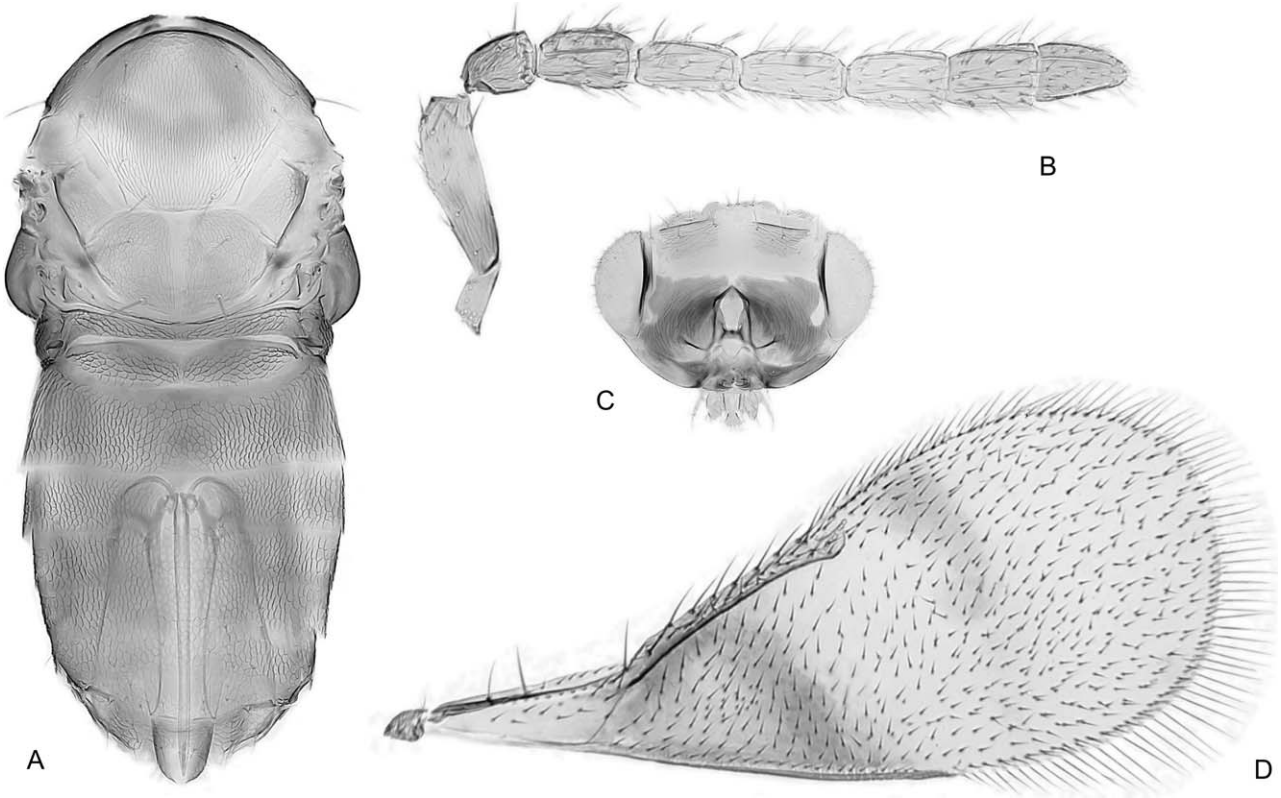

Fig. 3. *Encarsia caelata* **sp.n.**: A, mesosoma and gaster; B, female antenna; C, head; D, fore wing.

imbricate. Cells of scutellum, axilla and metasoma internally with weak striations. Tergites on each side with the following number of setae: T1, 0; T2, 2; T3, 2; T4, 2–3; T5, 3; T6, 2; T7 with 4 setae. Ovipositor longer than mid tibia (1.15). Third valvula (Fig. 3A) 0.28× as long as second valvifer.

Male and host. Unknown.

Species group placement. Not established.

Distribution. Indonesia: Bogor.

Material examined. Holotype ♀, Indonesia, Bogor, Bodi Agung, 13.vii.1997 (*D. Sartiani*) (BMNH).

***Encarsia obliqua* sp.n.**
(Fig. 4A–C)

Female. *Colour*. Head yellow, vertex partly brown and occiput with brown spot. Mesosoma (Fig. 4A) yellow except mesoscutal midlobe anteriorly and axilla brown. Posterior margin of mesoscutal midlobe and anterior margin of scutellum medially dark brown. Metasoma brown except petiole yellow. Antenna (Fig. 4B) yellow, clava brownish. Fore wing (Fig. 4C) hyaline. Legs yellow.

Morphology. Maxillary palp two-segmented. Mandible with two teeth and a truncation. Antennal formula (Fig. 4B) 1,1,4,2. F1–F3 cylindrical, F4 slightly and F5–F6 strongly widening towards apex, F6 obliquely truncate, sulcus between F5 and F6 oblique, F6 with sensory area. Pedicel subequal in length to F1. F1 1.44–1.60× as long as broad, distinctly shorter than F2 (0.52–0.60) and F3 (0.59–0.70). F2 longer than F3 (1.09–1.13). Flagellomeres with the following number of longitudinal sensilla: F1, 0; F2, 4; F3, 4; F4, 5; F4, 6–7; F5, 8; F6, 6. F1–F5 apically with papillar sensilla. Midlobe of mesoscutum (Fig. 4A) with about sixty setae, evenly reticulate, side lobes with three setae each. Posterior pair and lateral setae of mesoscutal midlobe larger than remaining setae of mesoscutum. Axillar seta placed in anterior half of axilla. Scutellar sensilla separated by approximately 3× the width of a sensillum. Scutellum about 1.7× as broad as long with distinct surface structure, lateral cells larger than cells in medial part of scutellum. Distance between anterior pair of scutellar setae smaller than distance between posterior pair, anterior pair located on the same level as scutellar sensilla. Fore wing (Fig. 4C) 2.1–2.2× as long as width of disc, with moderately dense setation, distal third of wing more dense than proximal wing. Basal cell with 7–8 setae. Longest setae of marginal fringe slightly longer than one-tenth of the width of the disc. Submarginal vein with 4–5 setae, marginal vein anteriorly with 10–11 setae. Stigmal vein distinct with weak constriction, slightly angled with marginal vein. Apical spur of mid tibia longer than half the length of the corresponding basitarsus (0.72–0.85). Mid tarsus about 0.55× as long as mid tibia. Basitarsus of mid leg ventrally with stout setae with distinct bases, about as long as combined length of three following tarsal segments. Metasoma without distinct surface sculpture. Tergites on each side with the following number of setae: T1, 1; T2, 3;

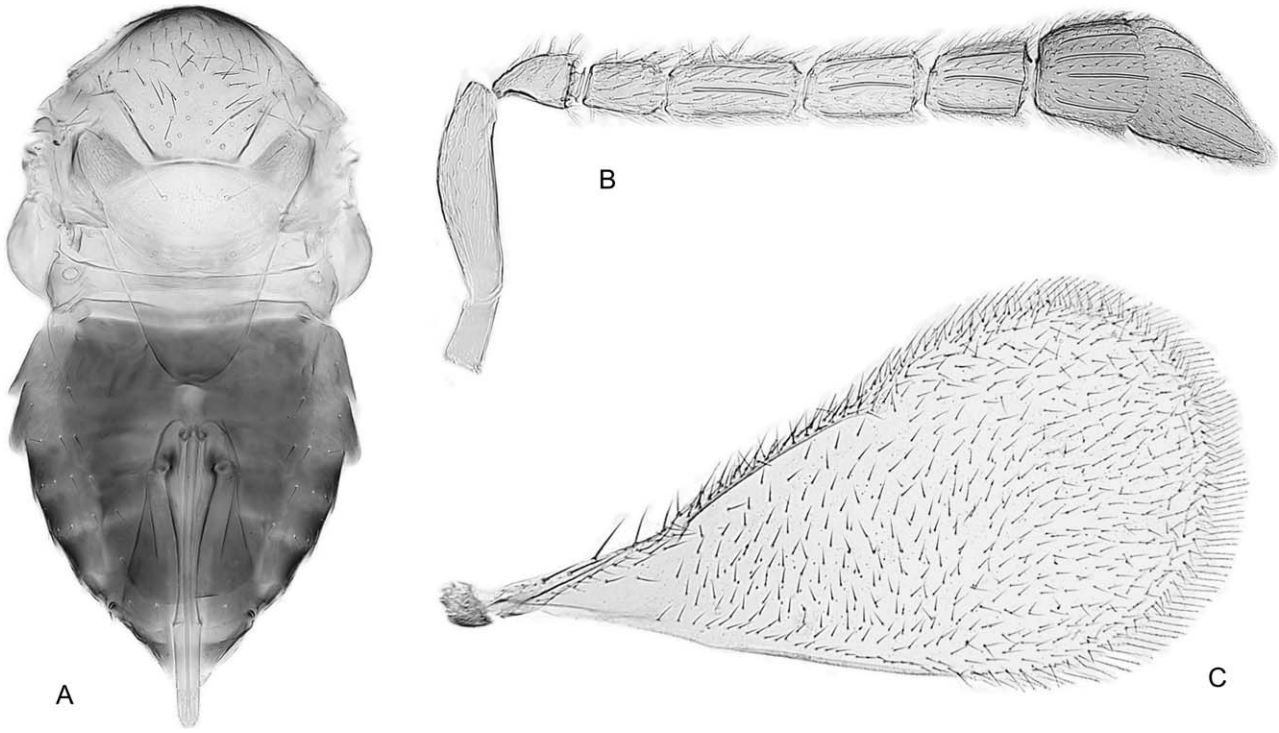

Fig. 4. *Encarsia obliqua* **sp.n.**: A, mesosoma and gaster; B, female antenna; C, fore wing.

T3, 4; T4, 5; T5, 3; T6, 3; T7 with 4 setae. Ovipositor (Fig. 4A) longer than mid tibia (1.19–1.30). Third valvula very narrow and 0.50–0.59× as long as second valvifer.

Male. Unknown.

Species group placement. *E. noyesi* group.

Distribution. Australia: Queensland; Papua New Guinea: Central District.

Host. Aleyrodidae: *Aleurodicus destructor* Mackie.

Material examined. Holotype ♀, Papua New Guinea, Central District, Aroa ptn [plantation], 11.viii.1959 (*F.J. Simmonds & J.J.H. Szent-Ivany*), C.I.E. Coll. No. 16778, suspected parasitoid of aleyrodid damaging fronds of coconut (BMNH). Paratypes 1♀, Australia, Queensland, Thursday Island, 1933 (*Hockings*) ex *Aleurodicus destructor* (BMNH); 1♀, Australia, Queensland, Heathlands dump (11.45°S 142.35°E), 18.viii.–17.ix.1992 (*Zborowski*, *Miller*) Malaise #2, open forest (ANIC).

***Encarsia pilosa* sp.n.**
(Fig. 5A–E)

Female. *Colour*. Head (Fig. 5C) brown. Mesosoma (Fig. 5A) brown except mesoscutal midlobe posteriorly and laterally lighter, and mesoscutal side lobes posteriorly, scutellum and metanotum yellow. Metasoma brown, apical tergite occasionally yellow. Antenna yellow, radicle brown. Fore wing (Fig. 5E) hyaline, venation brown, occasionally with dark infuscation behind proximal half of marginal vein. Legs yellow except mid and hind coxae and hind femur brown.

Morphology. Vertex with rugosely strigose surface sculpture. Maxillary palp one-segmented. Antennal formula (Fig. 5B) 1,1,4,2. Pedicel half as long as F1. F1 2.22–2.46× as long as broad, subequal in length to F2 and F3. Flagellomeres each with 8–10 longitudinal sensilla. F1–F5 cylindrical and similar in shape and size, F6 conical and slightly shorter than preapical segment. F1–F5 apically with papillar sensilla. Mandible with three teeth or two teeth and a truncation. Midlobe of mesoscutum (Fig. 5A) with about 60–70 setae, evenly reticulate, side lobes with three setae each. Posterior pair and lateral setae of mesoscutal midlobe larger than remaining setae. Scutellum about 1.5× as broad as long with very weak and inconspicuous surface sculpture, anteriorly with smaller, posteriorly with very large and elongate cells. Scutellar sensilla separated by approximately 3–4× the width of a sensillum. Distance between anterior pair of scutellar setae smaller than distance between posterior pair, anterior pair located at least slightly anterior to scutellar sensilla. Fore wing (Fig. 5E) 2.1× as long as width of disc, densely setose, setation of disc slightly more dense than area behind marginal vein. Basal cell with 14–16 setae.

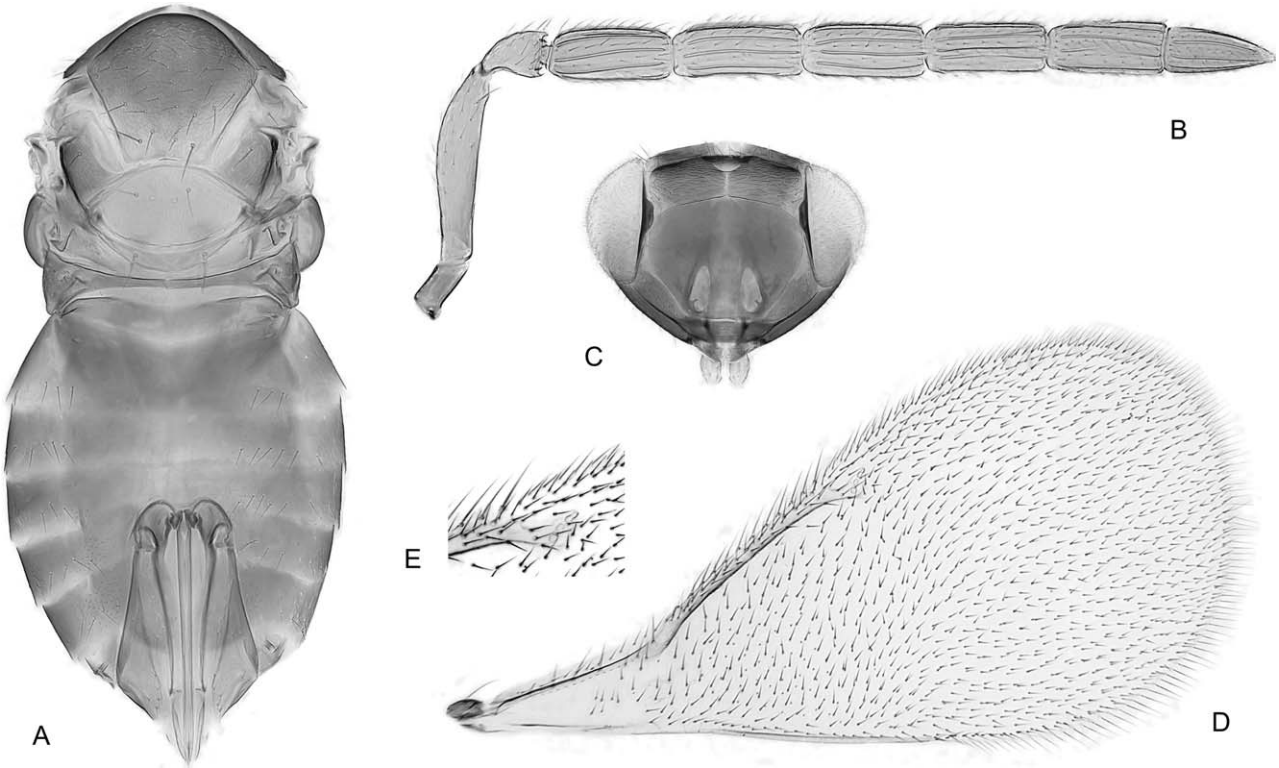

Fig. 5. *Encarsia pilosa* **sp.n.**: A, mesosoma and gaster; B, female antenna; C, head; D, detail of fore wing showing stigmal vein; E, fore wing.

Longest setae of marginal fringe about one-tenth of the width of the disc. Submarginal vein with 3–5 setae, marginal vein anteriorly with 10–12 setae. Submarginal vein 0.65–0.77× as long as marginal vein. Stigmal vein distinctly angled with marginal vein and with distinct constriction. Apical spur of mid tibia longer than half the length of the corresponding basitarsus (0.77–0.89). Mid tarsus 0.6× as long as mid tibia. Basitarsus of mid leg ventrally with stout setae with distinct bases, almost as long as combined length of three following tarsal segments. Tergites on each side with the following number of setae: T1, 2–4; T2, 4–6; T3, 5–7; T4, 7–8; T5, 12–16; T6, 3–4; T7 with 4–6 setae. Ovipositor (Fig. 5A) slightly longer than mid tibia (1.06–1.09). Third valvula in addition to several apical setae with one pair of subapical setae, 0.34–0.35× as long as second valvifer.

Male. Colour and structural details similar to female, but brown colour more extensive.

Species group placement. Not established.

Distribution. Australia: Queensland.

Host. Aleyrodidae: *Aleurodicus destructor* Mackie.

Material examined. Queensland: Holotype ♀, Cunningham's Gap via Aratula, 18.vi.1998 (*C.J. Burwell*) ex *Aleurodicus destructor* on *Lomandra* sp. (ANIC); paratypes 6♀, 2♂, same data as holotype (BMNH, ZSMG) and 1♀, 1♂, Maryborough, 11.v.1971 (*Young*) ex *Aleurodicus destructor*. C.I.E.A 5170/12550 (QDPI).

Discussion

The genus *Encarsiella* was erected by Hayat (1983) for one described and two undescribed species. Since then, six *Encarsiella* species have been described as new and four species have been transferred from other genera to *Encarsiella*, including three species described by A.A. Girault in *Coccophagus* (*C. aleurodici*, *C. boswelli*, and *C. magniclava*) and *E. narroi* (Gómez & García). The current total of eleven species of *Encarsiella* occur in South America and the Australasian and Oriental regions (Hayat, 1989; Huang & Polaszek, 1998), with one pantropical species (*E. boswelli*) also occurring in Africa (Polaszek & Hayat, 1990). Most of the species are associated with hosts of the whitefly subfamily Aleurodicinae (Sternorrhyncha, Aleyrodidae), which is primarily distributed in the Neotropical region. Exceptions include *E. boswelli*, which is an egg-parasitoid of Plataspidae (Heteroptera) (Polaszek & Hayat, 1990), and an undescribed species from India which was reared from nymphs of *Trioza jambolanae* (Crawford) (Sternorrhyncha: Psyllidae) (Huang & Polaszek, 1998).

Encarsiella was created for a species exhibiting characters of two closely related aphelinid genera, *Encarsia* and *Coccophagus* (Hayat, 1983). In addition, it differed from both genera by several characters, most importantly the oblique suture between the preapical and apical segment of the clava and the obliquely truncate apical segment. Subsequently the type species, *E. noyesi*, was placed into related genera by various authors, e.g. *Encarsia* (Shafee & Rizvi, 1984), *Dirphys* (Hayat, 1989) and *Encarsiella* (Viggiani, 1985a,b, 1986; Polaszek & Hayat, 1992), illustrating the taxonomically problematic position of *Encarsiella*. Polaszek & Hayat (1992) re-established the genus on the basis of a phylogenetic analysis of twenty-four morphological characters. The results of this analysis suggested the monophyly of the three closely related genera *Dirphys* + *Encarsia* + *Encarsiella*. These genera formed a trichotomy in most phylogenetic analyses conducted, which was supported by five synapomorphies: (1) pronotum divided centrally; (2) one axillar seta; (3) four scutellar setae; (4) lateral mesosternal setae absent, and (5) postmarginal vein absent (Polaszek & Hayat, 1992). The monophyly of each of the three genera *Encarsia*, *Dirphys* and *Encarsiella* was supported by a single synapomorphy in each case: scutellar sculpture imbricate/reticulate with longitudinally elongated cells medially, aciculate mesoscutal sculpture and reduced stigmal vein, respectively.

Since Polaszek & Hayat (1992), several new species of this complex have been discovered, some of which were placed in *Encarsiella* (e.g. Chou & Chou, 1994; Huang & Polaszek, 1998; Myartseva & Coronado-Blanco, 2002). Most of these species share characters that have been used traditionally to define generic limits of the genus *Encarsiella*, i.e. the oblique fifth antennal segment, the obliquely truncate F6, the large axillae, the reticulate/imbricate sculpture of the mesoscutal midlobe and scutellum, and the weakly developed stigmal vein. Despite their placement in *Encarsiella*, a few of these species are closer morphologically to *Encarsia* than to typical *Encarsiella* species in that the antennal clava lacks an oblique suture and the stigmal vein is constricted and angled with the marginal vein as in most *Encarsia* species. However, several taxonomically important characters suggested their placement in *Encarsiella*, including the absence of a weakly sculptured or longitudinally elongate medial line on the scutellum (synapomorphy for *Encarsia*) and the two-segmented maxillary palp (rarely two-segmented in *Encarsia*).

The status of the genus *Encarsiella* was put to the test again in a preliminary analysis of several *Encarsia* species, including *E. noyesi* (as *Encarsiella*), using the D2 region of 28S rDNA. In no molecular analysis conducted by Babcock *et al*. (2001) did *Encarsia* emerge as monophyletic because *E. noyesi* was placed within the ingroup. Only by forcing *Encarsiella* to be an outgroup was it possible to achieve congruence between the trees resulting from morphological and molecular data (Babcock *et al*., 2001). Here, we have introduced four new species, all of which would have been described as *Encarsiella* under the traditional generic definition. For three of these and an undescribed species close to *E. noyesi* (*E.* spec. D), we obtained molecular evidence confirming the paraphyletic situation found by Babcock *et al*. (2001) (Fig. 1). Furthermore, two of the species described

as new from Australia (*E. pilosa* and *E. bifasciata*) are placed separately from the two New World representatives of the *E. noyesi* species group (*E. noyesi* and *E.* sp. D) on the tree resulting from the molecular analysis (Fig. 1). Given this profound body of evidence, it is highly problematic to retain the status of *Encarsiella* as distinct from *Encarsia*, and therefore we regard the former genus in partim as a subgroup of *Encarsia*. However, rather than treating *Encarsiella* as a subgenus of *Encarsia*, we treat the species which formerly belonged to *Encarsiella* as a species group named after *E. noyesi*, the type species of that genus.

We regard the *E. noyesi* species group as containing only New World species occurring in Central and South America, and our results indicate that this group represents a monophyletic clade (Fig. 1). Hence, we adopt a narrower definition of this group compared with the previous generic definition of *Encarsiella* (e.g. Huang & Polaszek, 1998; Myartseva & Coronado-Blanco, 2002). We know of several dozen undescribed species from the Neotropical region that belong to this species group and that are all characterized by having a three-segmented clava with an oblique suture between F5 and F6, or both segments partly fused and F6 with a sensillar plate. No other non-Neotropical species previously included in *Encarsiella* shows this combination of morphological characters, and either the apical segment is not obliquely truncate, or, if it is truncate (as in *E. obliqua*), the clava consists of only two segments.

Apart from these antennal characters, which are diagnostic for the *E. noyesi* species group, they have in common several other characteristics, although none of these is unique to this species group. These include a large number of setae on the mesoscutal midlobe (usually 50–100), a narrow stigmal vein which is very slightly angled with the marginal vein and without constriction, a two-segmented maxillary palp, large axillae which are strongly projecting forwards, no medial furrow on the scutellum, and a variable number of robust, spinelike setae on the mid basitarsus. Apart from the species now placed in the *E. noyesi* species group, no other species placed previously in *Encarsiella* can be assigned currently to any existing species group within *Encarsia* (Table 2).

For the evolution of character states within *Encarsia sensu lato*, our results do not support the notion that there is a tendency towards reduction. For instance, the two closely related Australian species, *E. pilosa* and *E. bifasciata*, neither of which shares the phylogenetic position of the two members of the *E. noyesi* species group, and which emerged as the sister group of *E. smithi* (Fig. 1) on the molecular tree, have a very large number of setae on the mesoscutal midlobe (50–70). *Encarsia smithi* has ten setae on the mesoscutal midlobe. One of the species (*E. bifasciata*) has a two-segmented maxillary palp, whereas, in its sister species (*E. pilosa*), it is one-segmented, the same condition as found in *E. smithi*. Both Australian species have a two-segmented clava, whereas in *E. smithi* the antenna is not clavate.

The genus *Dirphys* is most closely related to *Encarsia* and would need to be reconsidered when re-defining the generic limits of *Encarsia*. However, the generic status of *Dirphys* and other genera of the aphelinid subfamily Coccophaginae is currently being dealt with in an ongoing study to resolve the phylogenetic relationships within the Coccophaginae.

The taxonomic difficulty described in this study illustrates a rather general problem often encountered in systematics. At the time of description of the genus *Encarsiella*, only three representatives were known, and the genus *Encarsia* contained about half the number of species now known. The discovery of new, morphologically sometimes distinct, species led to an increase in the morphological variation observed within both genera, and the necessity of placing new taxa into existing categories diffused the boundary between both genera. The frequent transfer of species of the subfamily Coccophaginae from one to another genus (and often reverse) exemplifies this difficulty and is symptomatic for the current situation of systematics within this group of microhymenoptera. Our example demonstrates that molecular tools provide fundamental new means of re-examining phylogenetic relationships and directions for the assessment of the phylogenetic value of morphological characters, which will eventually lead to an improved classification. The 28S D2 region has been shown to be very promising for the investigation of phylogenetic relationships at the generic level (Babcock *et al.*, 2001; Manzari *et al.*, 2002; Schmidt *et al.*, 2006). A major weakness of the D2 region is the inability to resolve lower nodes within the Coccophaginae or even within *Encarsia*, and this deficiency needs to be addressed by the search for and application of other more suitable gene regions.

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Appendix. *Encarsia* species, species group and origin of samples used for the molecular analysis.

Species group	Species	Origin
E. aurantii	*E. aurantii*	U.S.A.: Texas
	E. perniciosi	U.S.A.: California
E. citrina	*E. citrina*	U.S.A.: California
E. cubensis	*E. nigricephala*	French Polynesia: Tahiti
E. flavoscutellum	*E. flavoscutellum*	India
E. inaron	*E. accenta*	Australia: South Australia
	E. adusta	Australia: Western Australia
	E. dichroa	Spain
	E. estrellae	Portugal (Azores)
	E. inaron	India; U.K.
	E. azimi	Australia: Queensland
E. lahorensis	*E. cibcensis*	Cook Islands: Raratonga
E. lutea	*E. asterobemisiae*	Italy
	E. lutea	Australia: Western Australia; Cook Islands: Raratonga; Cyprus; Italy
E. luteola	*E. dispersa*	Nauru
	E. formosa	Australia: Canberra; Egypt
	E. guadeloupae	Tonga
	E. hispida	Italy; U.S.A.: California
	E. luteola	U.S.A.: California
	E. californica	U.S.A.: California
E. noyesi	*E. noyesi*	U.S.A.: California
	E. sp. D	Trinidad and Tobago
E. opulenta	*E. perplexa*	U.S.A.: Hawaii
E. parvella	*E. mineoi*	Egypt
	E. pergandiella	Australia: Queensland; U.S.A.
E. scapeata	*E. scapeata*	Israel
E. smithi	*E. nigriventris*	Australia: Queensland
	E. smithi	Hawaii: Makakilo, Oahu Is.
E. strenua	*E. bimaculata*	Australia: Queensland; India
	E. oakeyensis	Australia: Queensland
	E. protransvena	French Polynesia: Tahiti
	E. sophia	Australia: Queensland; French Polynesia: Tahiti
	E. sp. nr *citri*	Australia: Queensland
E. tricolor	*E. tricolor*	Portugal (Azores)
E. tristis	*E.* nr *tristis*	South-East Asia
Unplaced	*E. bifasciata*	Australia: Queensland
Unplaced	*E. pilosa*	Australia: Queensland
Unplaced	*E. quercicola*	U.S.A.: California